BioOne DIGITAL LIBRARY

CARNIVORE OCCURRENCE ALONG AN URBAN–RURAL GRADIENT: A LANDSCAPE-LEVEL ANALYSIS

Authors: Randa, Lynda A., and Yunger, John A.

Source: Journal of Mammalogy, 87(6) : 1154-1164

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/05-MAMM-A-224R2.1

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Mammalogy, 87(6):1154–1164, 2006

CARNIVORE OCCURRENCE ALONG AN URBAN–RURAL GRADIENT: A LANDSCAPE-LEVEL ANALYSIS

LYNDA A. RANDA AND JOHN A. YUNGER*

Natural and Applied Sciences Division, College of DuPage, Glen Ellyn, IL 60137, USA (LAR)
Environmental Biology Program, Governors State University, University Park, IL 60466, USA (JAY)

Human development impacts the landscape by altering the size and shape of natural habitat patches, replacing natural vegetation with other types such as lawns and row crops, or introducing environmental stressors such as increased human activity and pollutants. We investigated the effects of human alterations to the landscape on the distribution of 3 mammalian carnivores (coyote [*Canis latrans*], raccoon [*Procyon lotor*], and red fox [*Vulpes vulpes*]) along an urban–rural gradient in northern Illinois. Distribution of each species was assessed from occurrence at scent stations placed within or along the edges of 47 sites $\geq$ 4 ha, representing 7 different natural or anthropogenically altered habitats. We averaged presence or absence scores across several seasonal samples over a year, and used an outlying mean index analysis to compare them to environmental variables gathered for each site, including habitat and landscape metrics presumed to reflect varying degrees of anthropogenic influence across the urban–rural gradient. Coyotes used a variety of habitats within the rural part of the gradient. Red foxes were found in forest interiors or shrubland and old fields near forests where coyotes were least detected. Both canids were detected more often in areas of lower human densities but prey abundance was not a strong determinant of their occurrence. Overall occurrence along the gradient was highest for raccoons, which were positively associated with urban areas with relatively high residential land use.

Key words: *Canis latrans*, coyote, Illinois, landscape, outlying mean index analysis, *Procyon lotor*, raccoon, red fox, urban–rural gradient, *Vulpes vulpes*

Urbanization, the anthropogenic conversion of land into residential, commercial, and industrial uses, leads to pronounced landscape-level changes that significantly alter the structure and function of affected ecosystems (Niemelä 1999). Cities and surrounding suburbs of urban areas in the United States occupy more than 5% of the country's surface area and contain about 80% of its population (United States Census Bureau 2001). These urban areas are defined by a high-density core of $\geq$386 people/km^2 (1,000 people/mile^2) and surrounding census blocks with at least 193 people/km^2 (500 people/mile^2); adjacent areas with lower human density are typically designated as rural (United States Census Bureau 2002). Native habitat has been largely eliminated in the core of many urban and industrial centers (McKinney 2002). The vegetated areas that remain are highly isolated and heavily managed or disturbed (Whitney 1985). Expansion of suburban residential areas into the rural zone, a leading cause of the phenomenon known as "urban sprawl" (Lindstrom and Bartling 2003), fragments remaining native habitat patches while affiliated recreational areas such as parks, gardens, and golf courses introduce new types of habitats. Although the latter may serve as attractors of some wildlife (Blair 1996), overall species diversity may be negatively impacted at the urban–rural interface by the creation of abrupt habitat boundaries, introduction of nonnative species, and degradation of areas that receive human-generated wastes (McKinney 2002; Pickett et al. 2001). Habitat loss and fragmentation occur in rural areas in which agricultural crops have replaced extensive areas of native vegetation (Neely and Heister 1987).

In general, the degree of land cover alteration and intensity of land use tends to decrease with the decrease in human population densities from the urban center to surrounding rural locations (McDonnell et al. 1997). This urban–rural gradient can be used to study the effects of urbanization on vertebrate species diversity as well as reciprocal influences between urban centers and less-populated surroundings (Nilon and Pais 1997; Pickett et al. 2001). The more developed parts of urban–rural gradients are associated with high local extinction rates and long-term habitat loss (McKinney 2002). There are a few examples of vertebrate species that can exploit the highly developed urban core, such as some birds and lizards that are adapted to living in or on structures

* *Correspondent: j-yunger@govst.edu*

© **2006 American Society of Mammalogists**
www.mammalogy.org

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

broadly replicated in the urban environment (e.g., former cliff dwellers—Blair 1996; Clergeau et al. 1998; Germaine and Wakeling 2001). More species tolerate areas of moderate development, characteristic of most suburbs, possibly because of their preference for occupying habitat edges or their ability to find food sources not normally available in their natural environments (Adams 1994; Blair 1996; Germaine and Wakeling 2001; McKinney 2002). Small habitat patches within urban and suburban areas may support viable populations of some native amphibians, reptiles, and small mammals, if they are arranged in an interconnected system that includes some relatively undisturbed patches (Dickman 1987; Mackin-Rogalska et al. 1988).

Animals with extensive space requirements, low reproductive rates, or susceptibility to human persecution, such as many large mammalian carnivores, have been negatively impacted by land alteration and human activity associated with urbanization (Matthiae and Stearns 1981). Nonetheless, some medium-sized generalist predators may be able to persist (McKinney 2002). Studies in Great Britain have shown use and colonization of urban areas by red foxes (*Vulpes vulpes*—Harris and Smith 1987). Red foxes initially immigrated into low-density residential areas on the edge of British cities, and subsequently have been shown to occur in habitat patches of various sizes within higher density residential areas, including woodland, grassland, and gardens (Dickman 1987). Red fox expansion into urban areas of other countries such as Switzerland, Poland, Australia, and Japan has become the subject of recent investigations on urban carnivore distributions, zoonoses, and human–carnivore interactions (Gloor et al. 2001; Jakubiec-Benroth and Jakubiec 2001; Marks and Bloomfield 1999; Tsukada et al. 2000).

In North America, red foxes and coyotes (*Canis latrans*) may occur not only in rural areas but also suburban and occasionally more densely populated urban areas (Atkinson and Shackleton 1991; Gibeau 1998; Grinder and Krausman 2001; Lewis et al. 1999). Both these canids can exhibit variable diets dependent upon local and seasonal food availability (Brillhart and Kaufman 1995; Scott and Klimstra 1955) and exploit small mammal prey in urban–rural environments (Cepek 2004; Lavin et al. 2003). Coyotes also shift from typical diurnal and nocturnal activity patterns to largely nocturnal movements in response to high human activity or depredation (Kitchen et al. 2000; McClennen et al. 2001; Patterson et al. 1999) but are generally more sensitive to habitat fragmentation (i.e., small and isolated habitat patches) than are smaller predators (Crooks 2002). Other North American carnivores associated with urban areas include the striped skunk (*Mephitis mephitis*), kit fox (*Vulpes macrotis*), gray fox (*Urocyon cinereoargenteus*), and raccoon (*Procyon lotor*—Crooks 2002; Cypher and Frost 1999; Rosatte et al. 1991). Raccoons, in particular, may achieve their highest densities in urban areas (Prange et al. 2003), due in part to maintaining consistently smaller home-range sizes than rural conspecifics (Prange et al. 2004) and their omnivorous feeding habits. These examples suggest that predators with smaller space requirements or relatively adaptable behaviors, mediated through flexible diets, habitat use, or activity patterns, are more likely to persist in areas of urban development. However, the tolerance threshold mammalian carnivores have for urbanization may be dependent on a variety of landscape-level factors and vary with the degree of anthropogenic disturbance.

We investigated how landscape patterns, habitat characteristics, and prey availability along an urban–rural gradient in the midwestern United States affect the distribution of mammalian carnivores. Environmental factors such as anthropogenic structures, individual habitat characteristics, and interrelatedness of habitat patches along an urban–rural gradient may interact to yield a complex, nonlinear gradient (McDonnell et al. 1993). Hence, we used a multivariate gradient analysis to address whether carnivore occurrence varies in general and by species along an urban–rural gradient and how landscape-level metrics and anthropogenic alterations to the environment may affect carnivore occurrence.

We predicted that raccoons would have the most widespread distribution among the possible carnivores occurring in the urban–rural gradient, because of their highly omnivorous diets and known association with urban areas. We also predicted that other medium-sized carnivores in our region, such as striped skunks and red foxes, would be tolerant of and therefore occur in moderately fragmented habitats characteristic of near-urban and suburban development. Last, we expected the largest carnivore in our study area, the coyote, to most commonly occur within the largest habitat patches, which are likely to persist further from urban development.

Materials and Methods

Study area.—Our study was located in the metropolitan area of Chicago, Illinois, which supports approximately 9 million human residents and is characterized by significant urban sprawl (United States Census Bureau 2002). We identified sites to sample carnivores along a 100 × 15-km transect (Fig. 1), originating at the center of the urban population of Chicago, the approximate center of the downtown area. The transect ended at a 12,000-ha complex that included several conservation areas, natural areas, and preserves, most notably Midewin National Tallgrass Prairie (sites 57–63; Fig. 1). Some major land-use features, particularly extensive industry and agriculture, were not adequately sampled by a direct straight-line transect from the urban area to the conservation areas. We therefore used geographical information system (GIS; ArcView 3.2a—Environmental Systems Research Institute, Inc. 2000) databases, in particular the Illinois Department of Natural Resources Land Cover Atlas (Illinois Department of Natural Resources 1996), to guide selection of the urban–rural gradient with a goal of maximizing the range of land-use features. The selection procedure broadly identified an area proceeding south of downtown Chicago, then west, as maximizing the diversity of land coverages along the gradient. To avoid bias when delineating the gradient within these areas, the transect was established due south of Chicago for 50 km and then due west for 50 km (Fig. 1). The north–south portion passed through commercial, industrial, high-density residential, and suburban areas, whereas the east–west portion passed through suburban, agricultural, and large natural areas.

Environmental features of the gradient.—For the purposes of several concurrent studies, we identified a total of 70 sites $\geq$ 4 ha and with the potential for long-term persistence along the urban–rural gradient (Fig 1). These sites were discreet areas representing 8 different habitat categories: mowed lawn, nonnative grassland, old

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

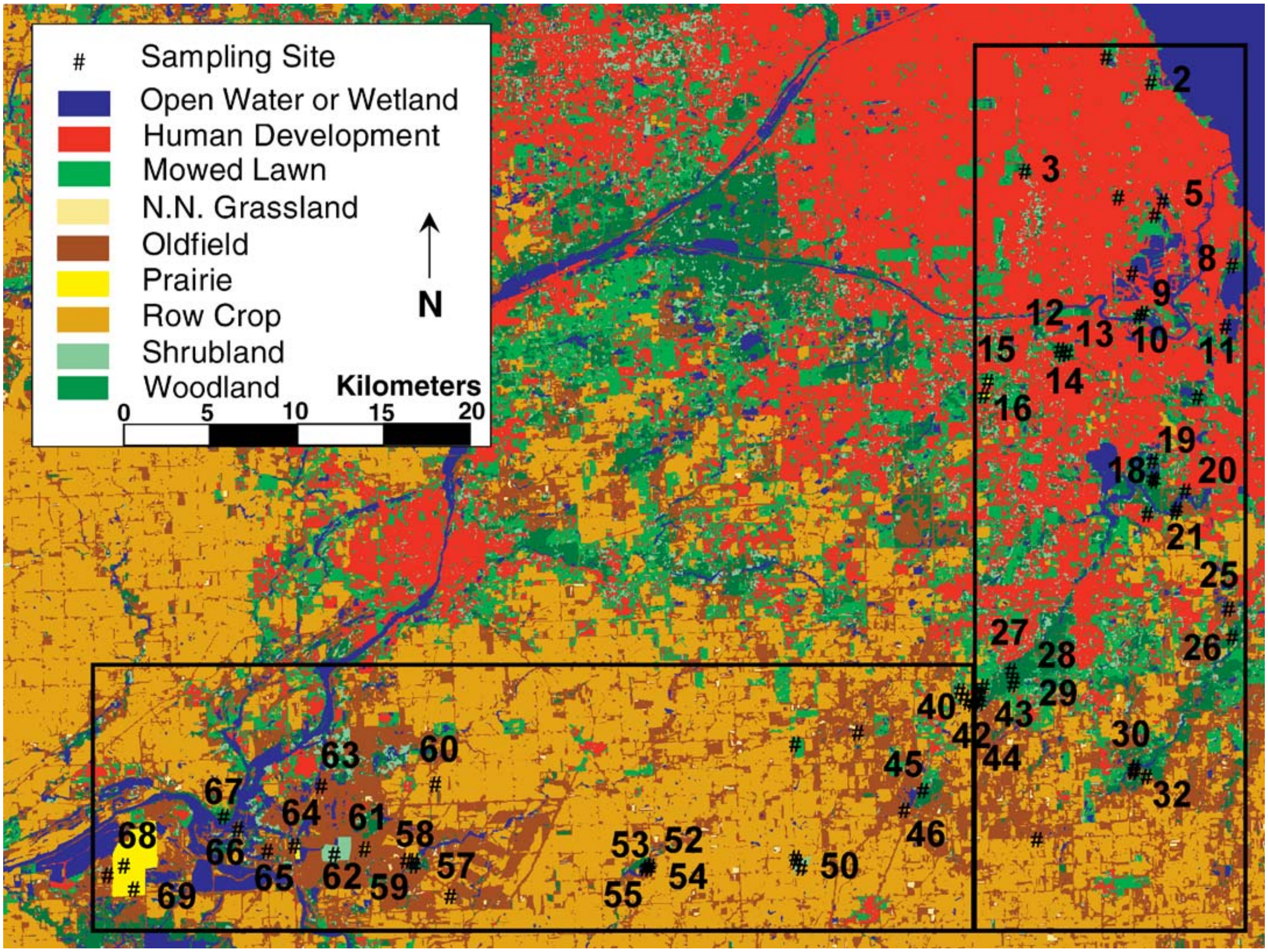

Fig. 1.—Land coverages, based upon Landsat thematic mapping data (United States Geological Survey 1995) for the urban–rural gradient in the Chicago metropolitan area, and the 70 sampling sites originally identified along the urban–rural gradient. For this study, 47 of these sites (numbered) were used. The southwestern shore of Lake Michigan appears in the northeastern corner of the map; the large brown area near the southwestern portion of the gradient is Midewin National Tallgrass Prairie and the large yellow area is Goose Lake Prairie State Natural Area (41°21′54″N, 88°19′30″W). N. N. = nonnative.

field, prairie, row crops, shrubland, woodland, and woodland edge. We selected 11 landscape variables that were presumed to be representative of anthropogenic influences (Table 1). Small mammal prey abundance (Prey) was ascertained from trapping data at each site. Prey sampling was conducted in the autumn during 1998 and 1999 at each site using three 100-m-long transects with mouse traps placed every 10 m and rat traps every 20 m (51 traps per site; Victor snap traps, Woodstream Corporation, Lititz, Pennsylvania). Small mammal densities tend to peak in autumn in northern Illinois (Getz et al. 1979; Yunger 1996); thus we chose autumn to help maximize the sampling effort. Each trapping transect was at least 50 m from the nearest transect and change in vegetation or edge, except when sampling woodland edge habitat. Traps were baited with a mixture of rolled oats and peanut butter and sites were sampled for 3 consecutive days per year. Abundance of prey at each site was calculated by averaging the total number of small mammals captured over the 2 years. All field procedures met the guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee 1998).

We used a GIS (ArcView 3.2a—Environmental Systems Research Institute, Inc. 2000) to calculate the spatial variables related to individual habitat patches and landscape characteristics. Habitat patch size (Patch Size) equaled the area of the patch in which the sampling site was located (zero for woodland edge habitat) and was determined from digitized 3.75-min digital orthophoto quadrangles with 1-m resolution (United States Geological Survey 1999). Boundaries were defined as either distinct changes in vegetation or anthropogenic alterations. Area-weighted mean patch fractal dimension (AWMPFD) was used as a measure of landscape fragmentation (Milne 1991). It incorporates perimeter-to-area ratios for patches across the landscape with higher weighting to larger patches. Values for this metric range from 1 to 2; lower values (near 1) indicate a more homogeneous or less-fragmented environment (McGarigal and Marks 1995). Values of AWMPFD for a 10-km radius from each site's center were determined using the Patch Analyst extension (Rempel et al. 1999) for ArcView 3.2 GIS. A road density index (Road Density) was calculated for an area within a 1-km radius of the center of each sampling site,

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 1.—Explanations and descriptive statistics of the environmental variables examined along the urban–rural gradient in the Chicago metropolitan area.

Variable	Units	Description	$\bar{X} \pm SE$	Median	Range
Prey	Mean no. per site	Average number of small mammal prey captured between 1998 and 1999.	8.24 ± 1.00	6.50	0–31.00
Patch size	ha	The area of the habitat patch in which the sampling site was located.	82.47 ± 27.18	12.81	0–1,261.87
Ratio	(none)	The ratio of area to perimeter of the habitat patch within which each site occurred.	106.36 ± 14.32	68.64	0–599.66
AWMPFD[a]	(none)	Index of fragmentation (range 1–2) within a 10-km radius from the center of each site.	1.299 ± 0.003	1.297	1.250–1.516
Urban distance	km	Distance from the center of the sampling site to the center of urban Chicago.	48.29 ± 2.22	49.15	9.10–80.80
Road density	km per 3.14 km^2	The sum of the linear distance of roads within a 1-km radius from the center of each site multiplied by a weighting factor for each road type.	22.04 ± 2.11	14.00	0.15–72.96
Human density	no. per 5.76 km^2	Number of people in 9 quarter sections associated with each site.	3,082.53 ± 741.95	242.50	0–31,829
Industry	ha per 5.76 km^2	The total area of industrial land use located within 9 quarter sections associated with each site.	13.02 ± 2.78	0.04	0–108.25
Commercial	ha per 5.76 km^2	The total area of commercial land use located within 9 quarter sections associated with each site.	10.68 ± 2.18	3.82	0–104.98
Residential	ha per 5.76 km^2	The total area of residential land use located within 9 quarter sections associated with each site.	72.51 ± 10.53	43.64	0–384.22
Agricultural	ha per 78.54 km^2	The total area of agricultural land use located within a 5-km radius from the center of each sampling site.	521.79 ± 53.48	471.66	0.28–1,533.13

[a] AWMPFD = area-weighted mean patch fractal dimension.

represented by the formula: Road Density = Σ(linear distance $\times$ weighting factor). Both paved surfaces and greater road width are positively correlated with traffic volume, whereas road crossing and adjacent habitat use by mammals is negatively correlated with traffic volume (Clevenger et al. 2001; Oxley et al. 1974; Waller and Servheen 2005). Hence, we ranked the assigned weighting factors from high to low according to the amount of traffic and potential disturbance to wildlife: interstate highway = 5, United States highway = 4, primary county road = 3, residential street = 2, and secondary county road = 1. Density of the human population (Human Density) associated with each sampling site was calculated within the quarter section in which a site occurred and the 8 surrounding quarter sections (totaling 5.83 km^2), using United States Census Bureau (1990) data. Each quarter section is 0.805 $\times$ 0.805 km and represents a subdivision of a section (640 acres or 2.6 km^2), a standard area in which land has been surveyed by the United States government. Likewise, industrial, residential, and commercial densities within blocks of 9 quarter sections surrounding sampling sites were obtained from the Northeastern Illinois Planning Commission's Digital Map of the Greater Chicago Area (Version 1.0, 1999, in litt.). Proportion of agricultural land use (Agricultural) included the total area of either corn (*Zea mays*) or soybean (*Glycine max*) row crops within a 5-km radius surrounding the center of each sampling site.

Carnivore sampling.—We evaluated carnivore occurrences at 47 of the 70 established sites within the urban–rural gradient. These 47 sites were chosen to include the diversity of habitats and land use along the urban–rural gradient while maintaining at least 1.0 km between site boundaries, except for sites representing woodland edge habitat. We documented carnivore occurrence using scent stations constructed by smoothing hydrated lime ($CaCO_3 \cdot H_2O$) over a 0.75-m-diameter cardboard disk. A cotton swab was dipped in a commercial predator lure (Cronk's Predator 500; Cronk's Outdoor Supplies, Wiscasset, Maine) and placed upright in the middle of the disk. To maximize the likelihood of detection, the stations were arranged at 20-m intervals along three 100-m transects spaced >50 m apart within each site (18 stations per site). Each scent-station transect was at least 50 m from the nearest change in vegetation or edge (except when sampling woodland edge habitat). Carnivore tracks at the scent stations were identified to species and recorded for 2–3 consecutive days, weather permitting, per site, over 3 seasons: autumn 1998, winter–spring 1999, and summer 1999. Because of a lack of independence among scent stations (Sargeant and Johnson 1997; Smith et al. 1994), we scored a carnivore species as present (1) at a site if its tracks were detected at any of the scent stations over the days sampled per season or absent (0) if not detected (Sargeant et al. 1998). To account for potential differences in number of sampling days across seasons, we divided each site's seasonal score by number of days sampled then averaged across seasons.

Statistical analyses.—We used a cluster analysis (STATISTICA 5.5—StatSoft, Inc. 2000), based upon a tree clustering algorithm of the environmental variables, to organize all 70 sites in the urban–rural gradient into discreet regions. Although only 47 sites were used for this study, all 70 sites initially identified along the urban–rural gradient were retained in the cluster analysis to facilitate better grouping into regions. To maximize within-group similarity, the distance coefficient was city-block (Manhattan), which is a derivation of the Euclidean distance between 2 values. It computes average differences of input variables and helps dampen the effect of outliers (StatSoft, Inc. 2000). We chose a complete linkage strategy, which aggregates clusters based upon distances of furthest neighbors, to minimize between-group similarities (McGarigal and Marks 1995).

We tested for significant differences of environmental variables among the regions identified by the cluster analysis with a 1-way multivariate analysis of variance (MANOVA; SAS PROCEDURE GLM—SAS Institute Inc. 1999). We used a 2-way MANOVA to determine whether occurrence of different carnivore species varied significantly among different regions and habitats of the urban–rural gradient. Interpretation of the MANOVAs was based on type III sum

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

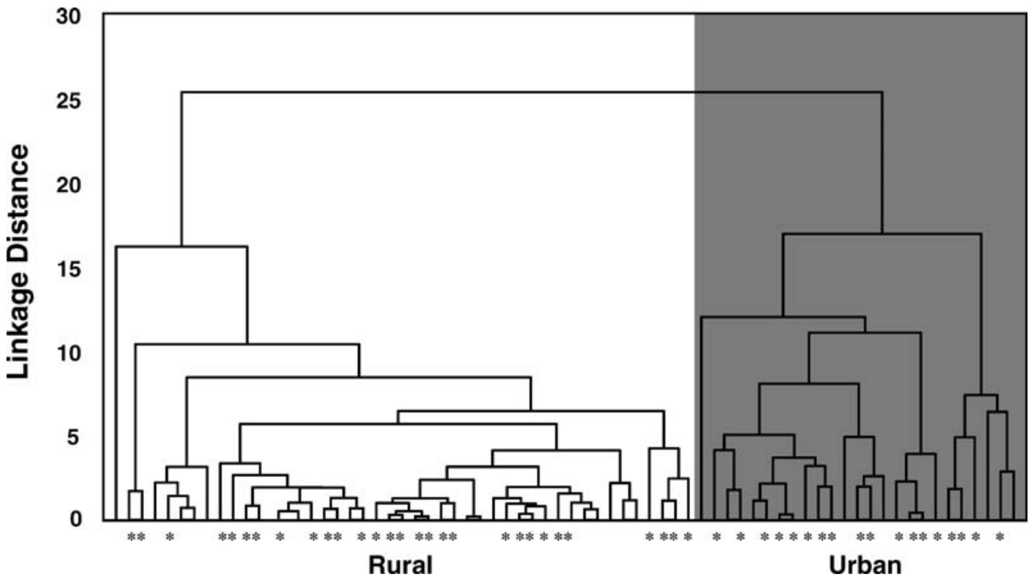

FIG. 2.—Dendrogram resulting from a cluster analysis of the 70 sampling sites within the urban–rural gradient in the Chicago metropolitan area. Asterisks along the horizontal axis correspond to sites used to assess relationship of occurrence of Carnivora species to environmental variables in this study. Site numbers corresponding to asterisks from left to right: rural sites ($n = 29$) are numbers 69, 68, 50, 61, 62, 66, 64, 32, 30, 65, 46, 26, 60, 55, 54, 53, 52, 43, 42, 57, 59, 58, 44, 67, 40, 63, 29, 28, and 8; urban sites ($n = 18$) are numbers 21, 18, 25, 20, 19, 27, 45, 11, 10, 9, 14, 13, 12, 5, 16, 15, 3, and 2.

of squares. If a MANOVA was significant at $P \leq 0.05$, we conducted a series of post hoc 1-way analyses of variance (ANOVAs) on the individual environmental variables and 2-way ANOVAs using the average presence scores for each carnivore species in different regions and habitats. Although alpha levels may be inflated when using multiple ANOVAs, no alternative post hoc tests for MANOVA are available (Scheiner 1993). Consequently, we determined significance through a more conservative value of $P \leq 0.01$. If the carnivore response variables were significant in a 2-way ANOVA, Ryan's Q multiple range analysis was used to identify differences among regions or habitats (Day and Quinn 1989).

We ascertained the influence of environmental variables on carnivore occurrences along the urban–rural gradient through an outlying mean index or marginality analysis using the software program ADE-4 (Thioulouse et al. 2001). The outlying mean index analysis is a multivariate ordination technique designed for gradient studies and is broadly similar to canonical correspondence analysis in that variance in species occurrence is maximized along ordination axes derived from the input of environmental data (Dolédec et al. 2000; Dray et al. 2003; Ter Braak 1986). The outlying mean index, or marginality, is interpreted to represent the deviation of average environmental conditions used by a species and the average environmental conditions for the entire study area. Hence, species with high marginality values are assumed to be influenced by a subset of the measured environmental variables. Low marginality indicates no specific response of a species to the environmental variables; such species tend to be more common throughout the study area. An additional variable, tolerance, is a function of the number of sites with which a species is associated and the location of those sites along the synthetic environmental gradient. Tolerance is similar to the niche breadth concept of Hurlbert (1978); higher tolerance values would be analogous to a broader niche. Residual tolerance is the variation in species occurrence not accounted for by the main gradient. Outlying mean index is robust to unimodal, linear, or a mixture of species response curves and is not biased against species-poor or low-abundance sites on the synthetic gradient. Its interpretations also are robust to multicollinearity among the explanatory variables (Dolédec et al. 2000). We determined significance of the outlying mean index analysis at $\alpha = 0.05$ based upon a Monte Carlo simulation (Metropolis and Ulam 1949), in which observed marginalities were statistically compared to 10,000 random permutation values of species marginalities or the null hypothesis that species are distributed equivalently in relation to the environmental variables.

RESULTS

Environmental features of the gradient.—Habitat and landscape metrics varied considerably across the urban–rural gradient, especially human density, patch size, and patch area to perimeter ratio (Table 1). Using results of the cluster analysis, we segregated sites within the urban–rural gradient into 2 broad groups, urban and rural (Fig. 2). Of the 47 sites in which carnivores were sampled, 18 sites were grouped within the urban region and 29 sites within the rural region. All habitat types were included in each region except row crop in the urban region and lawn in the rural region. Some sites (sites 8, 27, and 45) of our study area were categorized into regions that differed from adjacent sites because of a variety of site-specific attributes and surrounding land-use characteristics (Figs. 1 and 2).

Environmental features were significantly different between urban and rural regions (Wilks' lambda $= 0.2123$, $F = 10.12$, *d.f.* $= 11, 30$, $P < 0.0001$). Variables associated with human development, namely human, industrial, commercial, and road densities, were greater in the urban region, whereas the amount of agricultural land surrounding sites was significantly greater in the rural region (Table 2). The average abundance of small mammal prey, patch sizes, area to perimeter ratios, and

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 2.—A comparison of means (± 1 *SE*) of environmental variables among sampling sites for Carnivora in different regions of the urban–rural gradient of the Chicago metropolitan area. Variables are described in Table 1.

Variable	Urban	Rural	*F*	*P*
Prey (no. per site)	8.58 ± 2.12	10.31 ± 1.54	0.078	0.7820
Patch size (ha)	39.86 ± 7.90	128.14 ± 59.83	1.415	0.2411
Ratio	70.85 ± 12.33	124.93 ± 27.45	2.896	0.0965
AWMPFD[a]	1.296 ± 0.001	1.294 ± 0.002	0.200	0.6491
Urban distance (km)	58.42 ± 3.09	44.46 ± 3.90	58.901	<0.0001
Road density (km per 3.14 km^2)	10.70 ± 0.79	29.34 ± 3.59	64.454	<0.0001
Human density (no. per 5.76 km^2)	364.94 ± 179.28	4,609.31 ± 1,223.81	22.011	<0.0001
Industry (ha per 5.76 km^2)	4.79 ± 2.95	18.08 ± 4.92	12.456	0.0010
Commercial (ha per 5.76 km^2)	3.99 ± 1.48	15.09 ± 3.44	18.647	0.0001
Residential (ha per 5.76 km^2)	22.04 ± 4.95	108.56 ± 19.81	43.546	<0.0001
Agricultural (ha per 78.54 km^2)	5.67 ± 0.001	15.63 ± 3.10	19.994	<0.0001

[a] AWMPFD = area-weighted mean patch fractal dimension.

AWMPFD did not significantly differ between the urban and rural regions. Of these, AWMPFD differed the least among sites across the urban–rural gradient (Table 2), indicating a similar and smaller than expected degree of habitat fragmentation or average patch complexity between these 2 regions. Thus, size, shape, and configuration of sampling sites did not differ between regions but the surrounding land use did differ.

Carnivore occurrence along the urban–rural gradient.—Coyote, red fox, and raccoon were the 3 carnivore species most commonly recorded within the urban–rural gradient, with red fox the least common (scent-station occurrences: $\bar{X} = 0.030 \pm 0.012$, range 0–0.333) and raccoon the most common (scent-station occurrences: $\bar{X} = 0.176 \pm 0.021$, range 0–0.333). We documented coyotes (scent-station occurrences: $\bar{X} = 0.118 \pm 0.020$, range 0–0.333) in 6 of 18 urban sites, 18 of 29 rural sites, and in all habitat types except lawn. In the urban region, red foxes only occurred in an old field and only 1 shrubland and 3 woodland sites in the rural region. We detected raccoon tracks in every urban site, 12 of 29 rural sites, and in all habitats across the urban–rural gradient.

The 2-way MANOVA indicated that occurrence of carnivores differed significantly between the 2 regions (Wilks' lambda = 0.4660, $F = 11.84$, *d.f.* = 3, 31, $P < 0.0001$). Overall, habitat and region × habitat effects also differed significantly among carnivores (habitat: Wilks' lambda = 0.3328, $F = 1.99$, *d.f.* = 21, 89.6, $P = 0.0137$; region × habitat: Wilks' lambda = 0.4572, $F = 1.88$, *d.f.* = 15, 86.0, $P = 0.0365$). Individual ANOVAs indicated that red fox occurrences varied significantly by the interaction between region and habitat ($MS = 0.0306$, $F = 1.13$, *d.f.* = 7, $P = 0.0006$) and raccoon occurrences at scent stations varied significantly between regions ($MS = 0.2882$, $F = 21.41$, *d.f.* = 1, $P < 0.0001$). Subsequent post hoc comparisons revealed that raccoons occurred more frequently in the urban region (Fig. 3), whereas red foxes exhibited the highest occurrence in woodland of the rural region (Figs. 3 and 4), principally at sites 40, 57, and 67 ($\bar{X} = 0.315 \pm 0.018$; Fig. 1). Although not statistically significant, coyotes did tend to avoid sites within the urban region more than those of the rural region ($MS = 0.0869$, $F = 5.23$, *d.f.* = 1, $P = 0.0278$; Fig. 3).

The overall outlying mean index analysis, or sensitivity of carnivores to environmental variables along the gradient, was significant ($P = 0.0023$) based upon 10,000 permutations of a Monte Carlo simulation. Raccoons exhibited a significant and relatively high tolerance to average habitat conditions of the synthetic gradient. Red foxes had relatively low tolerance, or were less likely to be associated with a diversity of sites along the gradient, but their overall response was not significant. Coyotes did respond significantly to the urban–rural gradient and their tolerance level was between that of red foxes and raccoons (Table 3). The first 2 axes of the outlying mean index analysis accounted for 88.5% and 0.09% of the variation in environmental variables. Axis 2 explained a negligible amount of the variation in carnivore occurrences (Table 4) but was retained to generate a biplot of carnivore occurrences in relation to the environmental variables. Biplot scores of the environmental variable loadings, or canonical coefficients, indicate that axis 1 described a gradient extending from the urban center. It was most influenced by road density and residential and commercial land uses in proximity to the urban center and proportion of agricultural land at the opposing end

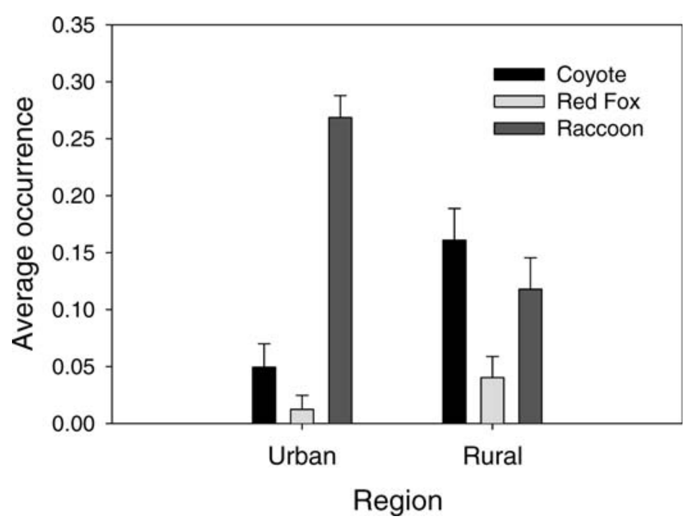

FIG. 3.—Average site occurrence of species of Carnivora from scent-station data across all sampling seasons in different regions of the urban–rural gradient in the Chicago metropolitan area (mean ± 1 *SE*).

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

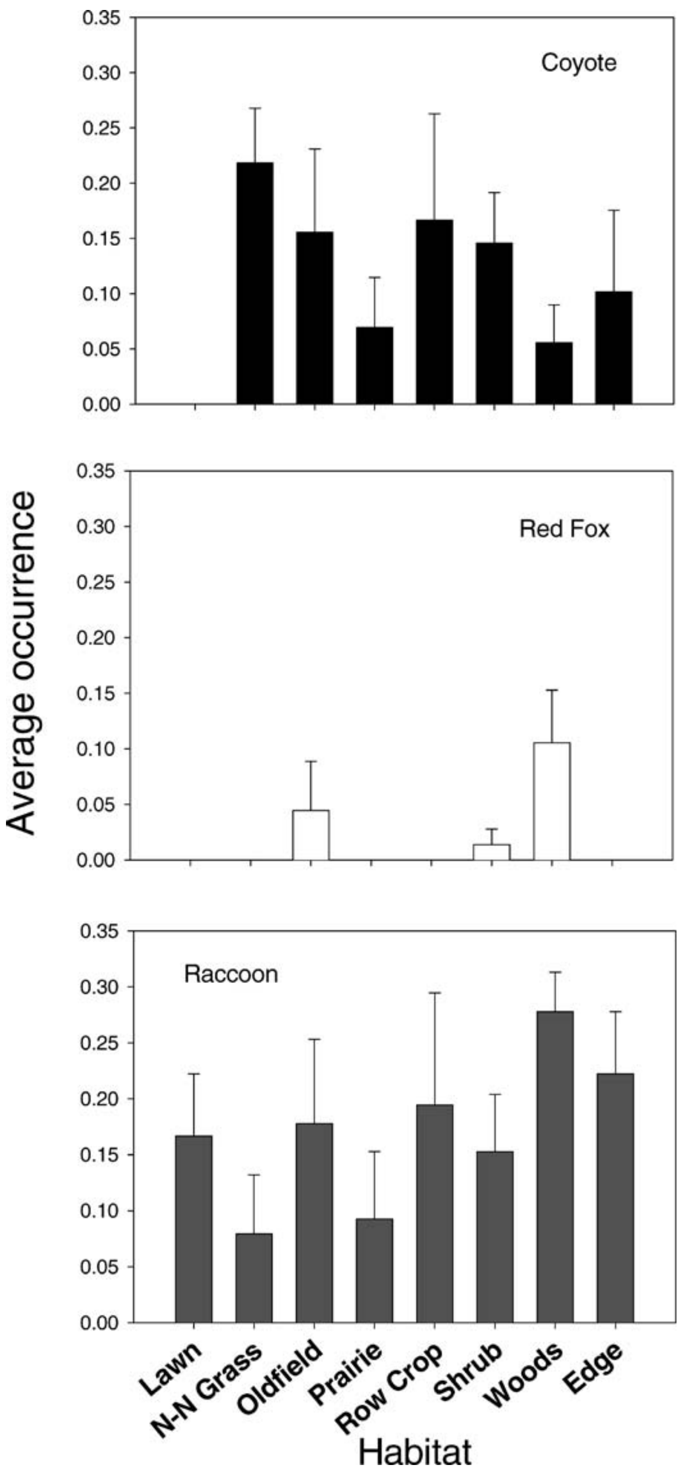

FIG. 4.—Results of post hoc multiple comparisons, using Ryan's Q multiple range analysis, of average site occupancy of Carnivora from scent-station data across all sampling seasons in different habitats along the urban–rural gradient (mean ± 1 *SE*). Habitat abbreviations: Lawn = mowed lawn, N-N Grass = nonnative grassland, Shrub = shrubland, Woods = woodland, Edge = woodland edge.

of the gradient. Small mammal prey abundance (Prey) and AWMPFD contributed the least toward explaining distributions of all 3 carnivores along the urban–rural gradient (Table 4; Fig. 5). Raccoon occurrence was strongly negatively associated with axis 1 (Fig. 5), and thus was negatively related to patches distant from the urban center and positively correlated with residential areas. Conversely, red foxes and coyotes were more likely to be found in areas further from the urban center.

DISCUSSION

Some environmental features along our transect followed characteristics of a traditionally defined urban–rural gradient: as distance from the urban center increased, densities of roads, people, and commercial development decreased, whereas area of habitat patches increased. Yet a cluster analysis, used to group sites based upon all environmental variables measured, indicated a slightly more complex, nonlinear gradient. For example, 1 site categorized within the rural region was located only 23.3 km from the urban center and was surrounded by sites categorized in the urban region. This particular site was relatively large compared to adjacent urban sites and had little commercial or residential development surrounding it. In addition, 2 sites in the southeastern part of our gradient were categorized in the urban region but were surrounded by rural sites. Unlike the adjacent sites, housing developments abutted both of these.

Distributions of the 3 most commonly occurring carnivores differed significantly between regions and among habitats of the urban–rural gradient. In particular, raccoons were significantly more common in the urban sites, whereas coyotes showed a tendency to occupy more rural sites. Red foxes showed a strong and significant preference for woodland habitat within the rural region. The gradient, as reflected by the outlying mean index, was strongly influenced by distance of sampling sites from the urban center. Two statistics characteristic of the outlying mean index analysis, marginality and tolerance, differed among the 3 carnivore species and were greatest for raccoons. Higher marginality was likely due to raccoon occurrence in all habitat types and relatively high tolerance attributed to this species' fairly widespread distribution across the urban–rural gradient. Distribution of raccoons was most strongly influenced by residential areas with moderate density of roads in relative proximity to the urban center, characteristic of near-urban to suburban developments in our study. Raccoons used a variety of habitats across the gradient as a whole, but were absent in nonnative grassland, old field, and prairie of the rural region.

Mark–recapture and radiotelemetry studies in northeastern Illinois (Prange et al. 2003, 2004) also have shown that raccoon densities are greater in urban and suburban sites than in rural sites. Higher raccoon densities in urban areas appear to be related to a relatively stable supply of anthropogenic food sources, especially food refuse. Raccoons in agricultural landscapes of Illinois are active within relatively large home ranges (Rosenblatt et al. 1999), whereas their urban counterparts usually maintain smaller home ranges (Prange et al. 2004). Concentration of anthropogenic food sources, high-density urban development, and greater vehicle traffic along roadways contribute to decreased movements and dispersal rates of raccoons in urban areas (Hatten 2000; Rosatte et al. 1991).

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

TABLE 3.—Results of the outlying mean index analysis depicting relationships of occurrences of Carnivora species to the suite of environmental variables measured across sampling sites of the urban–rural gradient in the Chicago metropolitan area. Inertia = variance or weighted sum of squared distances to the origin of the environmental axes; OMI = outlying mean index (marginality) or the deviation of a particular species' distribution from the overall mean habitat conditions (origin of outlying mean index axes), described by the environmental variables; Tol = tolerance index, which is analogous to ''niche breadth'' or spatial variance of an organism's ''niche'' across the measured environmental variables—a function of all sampling sites with which the species is associated; RTol = residual tolerance. Italicized terms represent the percentages of variability corresponding to a specific statistic. P = frequency based on number of random permutations (out of 1,000) that yielded a higher value than the observed outlying mean index ($P \leq 0.05$ indicates a significant influence of the environmental variables for a species).

Species	Inertia	OMI	Tol	RTol	*OMI*	*Tol*	*RTol*	*P*
Coyote	7.99	0.85	2.01	5.13	10.7	25.1	64.2	0.035
Red fox	6.12	0.96	1.36	3.80	15.7	22.3	62.0	0.736
Raccoon	9.97	0.85	4.02	5.11	8.5	40.3	51.2	0.001

In contrast to raccoons, coyotes were more commonly observed in rural sites and were absent in lawn, prairie, and woodland edge of the urban region. Voles (*Microtus ochrogaster* and *M. pennsylvanicus*), a common prey of coyotes, were relatively abundant in nonnative grassland, old field, and shrubland sites in the urban region (Atkinson and Shakleton 1991; Cepek 2004; Randa 1996). The greatest number of coyote tracks were recorded at opposite ends of the east–west aspect of our transect, along woodland edge of the rural region and in open (nonforested) habitats, namely nonnative grassland and row crop. These locations were in or near relatively large clusters of natural areas away from dense residential, commercial, or industrial developments, and the combination of open and forested habitats could provide suitable foraging and den sites, respectively. Although coyotes are behaviorally quite adaptable and will alter their activity patterns to avoid humans (Kitchen et al. 2000; McClennen et al. 2001), our results support our initial prediction as well as previous findings that coyotes will preferentially use less-developed sections of large, metropolitan areas (Riley et al. 2003).

Red foxes were the least frequently detected of the 3 main carnivore species at our tracking stations. Their occurrence was significantly related to woodland habitat in the rural region, with their greatest occurrence in a relatively large (>50-ha) preserve. Red foxes are known to use a variety of habitats and eat a diversity of food resources (Knable 1970; Major and Sherburne 1987). Their more restricted habitat use in the rural region could have resulted from their avoidance of coyotes, a phenomenon well documented between these 2 potential competitors (Harrison et al. 1989; Sargeant et al. 1987; Voight and Earle 1983); coyotes were not detected within woodlands of the rural region where red foxes occurred. Urban areas were apparently used less by red foxes than by coyotes, because their tracks were observed in only 1 urban site, a 24-ha old field. This contrasts with our initial predictions and with studies in other urban areas that have shown red foxes associated with human dwellings in residential areas (Gloor et al. 2001; Gosselink et al. 2003). Red foxes may have been displaced from potentially suitable urban sites by coyotes or the urban regions of our study area may have exceeded the tolerance threshold of red foxes to human activity. With >8 million people and extensive urban sprawl, the Chicago metropolitan area is one of the most heavily urbanized areas in which red foxes occur. The impacts of intensive land use and land alteration and the overall low occurrence of red foxes across our 100-km transect support the idea that red foxes were intolerant of extensive human activity, especially in the urban region.

Although we could not determine mechanisms for carnivore distributions, such as changes in movement patterns of individuals in our study area, our multivariate gradient model helped reveal particular responses of these species to different attributes of human-altered ecosystems. In general, distance from the urban center, residential and commercial land use, and road density were the most important predictors of carnivore occurrence in our study area. Distribution of raccoons was positively correlated with these variables but they negatively affected coyote and red fox distributions. The degree of habitat fragmentation and the overall availability of small mammal prey, especially in regards to coyotes and red foxes, did not significantly differ among urban and rural regions nor significantly influence carnivore distributions across the urban–rural gradient. The lack of response to habitat fragmentation may be partly because the more commonly occurring raccoons and coyotes used woodland edge, which can increase due to fragmentation. More importantly, large-scale habitat loss after

TABLE 4.—Loadings of environmental variables for the first 2 axes of the outlying mean index analysis. Values represent the best linear combinations that explain occurrences of Carnivora along an urban–rural gradient in the Chicago metropolitan area. Variables are described in Table 1.

Variable	Axis 1	Axis 2
Prey	0.1030	−0.5181
Patch size	0.1023	0.4614
Ratio	0.1869	0.3281
AWMPFD[a]	−0.0094	0.0770
Urban distance	0.4644	0.0845
Road density	−0.4049	0.1814
Human density	−0.2939	0.2322
Industry	−0.2208	0.1722
Residential	−0.4459	0.1017
Commercial	−0.3900	0.0355
Agricultural	0.2798	0.5194
Eigenvalue	0.763	0.076
Percentage variance explained	88.5	0.09

[a] AWMPFD = area-weighted mean patch fractal dimension.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

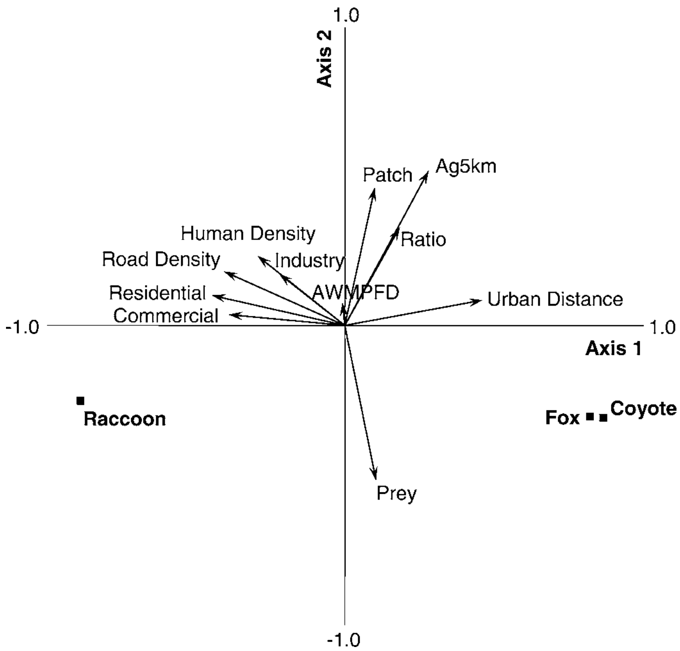

Fig. 5.—Location of Carnivora species scores or weighted distributions (black squares) in relation to the ordination of environmental variables along the urban–rural gradient in the Chicago metropolitan area, defined by the outlying mean index analysis. The origin of the biplot represents the most general conditions based upon all environmental variables used in the model. Environmental variables are depicted as vectors; relatively longer lines reflect greater influence in the model and their direction indicates how well correlated the particular environmental variable is with each axis. The rank of each species to an environmental variable is approximated by projecting a perpendicular line from each species' point to the environmental variable's vector. A vector may be extended in either direction to serve as an axis for such comparison. Abbreviations of environmental variables: Ag5km = proportion of agriculture within 5-km radius of sampling site; AWMPFD = area-weighted mean fractal dimension; Commercial = density of commercial development; Human Density = human population density; Industry = density of industrial development; Patch = area of habitat patch comprising a sampling site; Prey = prey abundance; Residential = density of residential development; Ratio = area to perimeter ratio for each sampling site; Road Density = indexed road density; Urban Distance = distance from urban center. (See text and Table 1 for explanations of environmental variables and their calculations.)

extensive elimination of native prairie, woodland, and savanna in both the urban and rural regions and the tendency for large-scale movements by raccoons, coyotes, and red foxes (Atwood et al. 2004; Rosenblatt et al. 1999) has likely usurped the effects of habitat fragmentation and had a significant impact on the distributions of these species over time. Indeed, the carnivores sampled in this study are only a subset of those that occurred before human development. Carnivore species extirpated in recent history (within the last 160 years) from our study area include wolves (*Canis lupus*), pumas (*Puma concolor*), and possibly fishers (*Martes pennanti*—Cory 1912; Hoffmeister 1989). Only 1 record of a bobcat (*Felis rufus*) exists within the last 10 years near the far southwestern portion of our gradient (D. Mauger, pers. comm.), and American badgers (*Taxidea taxus*) probably no longer occur in our study area. With continued expansion of urban development into the rural region of our study site, we expect to see reduced occurrence of extant carnivores such as the coyote and red fox.

Acknowledgments

We especially thank R. Slusinski for valuable assistance with carnivore scent-station work. D. Gohde, J. Kuipers, R. Grass, and a number of undergraduate students from the College of DuPage and Governors State University also assisted in the field. C. Petersen provided editorial comments and R. Kays and an anonymous reviewer offered many suggestions that helped improve earlier drafts of this manuscript. Funding for this work was provided by the National Science Foundation's Chicago Area Alliance for Minority Participation and the Environmental Biology Program, Governors State University.

Literature Cited

Adams, L. W. 1994. Urban wildlife habitats. University of Minnesota Press, Minneapolis.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Atkinson, K. T., and D. M. Shackleton. 1991. Coyote, *Canis latrans*, ecology in a rural–urban environment. Canadian Field-Naturalist 105:49–54.

Atwood, T. C., H. P. Weeks, and T. M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 68:1000–1009.

Blair, R. B. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Brillhart, D. E., and D. W. Kaufman. 1995. Spatial and seasonal variation in prey use by coyotes in north-central Kansas. Southwestern Naturalist 40:160–166.

Cepek, J. D. 2004. Diet composition of coyotes in the Cuyahoga Valley National Park, Ohio. Ohio Journal of Science 104:60–64.

Clergeau, P., J.-P. L. Savard, G. Mennechez, and G. Falardeau. 1998. Bird abundance and diversity along an urban–rural gradient: a comparative study between two cities on different continents. Condor 100:413–425.

Clevenger, A. P., B. Chruszcz, and K. Gunson. 2001. Drainage culverts as habitat linkages and factors affecting passage by mammals. Journal of Applied Ecology 38:1340–1349.

Cory, C. B. 1912. The mammals of Illinois and Wisconsin. Field Museum of Natural History, Zoological Series XI:1–505.

Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Cypher, B. L., and N. Frost. 1999. Condition of San Joaquin kit foxes in urban and exurban habitats. Journal of Wildlife Management 63:930–938.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs 59: 433–453.

Dickman, C. R. 1987. Habitat fragmentation and vertebrate species richness in an urban environment. Journal of Applied Ecology 24:337–351.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

DOLÉDEC, S., D. CHESSEL, AND C. GIMARET-CARPENTIER. 2000. Niche separation in community analysis: a new method. Ecology 81:2914–2927.

DRAY, S., D. CHESSEL, AND J. THIOULOUSE. 2003. Co-inertia analysis and the linking of ecological data tables. Ecology 84:3078–3089.

ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE, INC. 2000. ArcView GIS 3.2a. Environmental Systems Research Institute, Inc., Redlands, California.

GERMAINE, S. S., AND B. F. WAKELING. 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biological Conservation 97:229–237.

GETZ, L. L., L. VERNER, F. R. COLE, J. E. HOFFMAN, AND D. E. AVALOS. 1979. Comparisons of population demography of *Microtus ochrogaster* and *Microtus pennsylvanicus*. Acta Theriologica 24:319–349.

GIBEAU, M. L. 1998. Use of urban habitats by coyotes in the vicinity of Banff Alberta. Urban Ecosystems 2:129–139.

GLOOR, S., F. BONTADINA, D. HEGGLIN, P. DEPLAZES, AND U. BREITENMOSER. 2001. The rise of urban fox populations in Switzerland. Mammalian Biology 66:155–164.

GOSSELINK, T. E., T. R. VAN DEELEN, R. E. WARNER, AND M. G. JOSELYN. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. Journal of Wildlife Management 67:90–103.

GRINDER, M. I., AND P. R. KRAUSMAN. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. Journal of Wildlife Management 65:887–898.

HARRIS, S., AND G. C. SMITH. 1987. Demography of two fox (*Vulpes vulpes*) populations. Journal of Applied Ecology 24:75–86.

HARRISSON, D. J., J. A. BISSONETTE, AND J. A. SHERBURNE. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. Journal of Wildlife Management 53:181–185.

HATTEN, S. 2000. The effects of urbanization on raccoon population demographics, home range, and spatial distribution patterns. Ph.D. dissertation, University of Missouri, Columbia.

HOFFMEISTER, D. F. 1989. Mammals of Illinois. University of Illinois Press, Urbana.

HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59:67–77.

ILLINOIS DEPARTMENT OF NATURAL RESOURCES. 1996. Illinois land cover, an atlas. IDNR/EEA-95/05. Illinois Department of Natural Resources, Springfield.

JAKUBIEC-BENROTH, D., AND Z. JAKUBIEC. 2001. Synanthropisation of the red fox *Vulpes vulpes* in Wroclaw. Przegląd Zoologiczny 45:121–126.

KITCHEN, A. M., E. M. GESE, AND E. R. SCHAUSTER. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. Canadian Journal of Zoology 78:853–857.

KNABLE, A. E. 1970. Food habits of the red fox (*Vulpes fulva*) in Union County, Illinois. Transactions of the Illinois Academy of Sciences 63:359–365.

LAVIN, S. R., T. R. VAN DEELEN, P. W. BROWN, R. E. WARNER, AND S. H. AMBROSE. 2003. Prey use by red foxes (*Vulpes vulpes*) in urban and rural areas of Illinois. Canadian Journal of Zoology 81:1070–1082.

LEWIS, J. C., K. L. SALLEE, AND R. T. GOLIGHTLY, JR. 1999. Introduction and range expansion of nonnative red foxes (*Vulpes vulpes*) in California. American Midland Naturalist 142:372–381.

LINDSTROM, M. J., AND H. BARTLING. 2003. Introduction. Pp. xi–xxvii in Suburban sprawl: culture, theory, and politics (M. J. Lindstrom and H. Bartling, eds.). Rowman and Littlefield Publishers, Inc., Lanham, Maryland.

MACKIN-ROGALSKA, R., J. PINOWSKI, J. SOLON, AND Z. WOJCIK. 1988. Changes in vegetation, avifauna, and small mammals in a suburban habitat. Polish Ecological Studies 14:293–330.

MAJOR, J. T., AND J. A. SHERBURNE. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 10:8–12.

MARKS, C. A., AND T. E. BLOOMFIELD. 1999. Distribution and density estimates for urban foxes (*Vulpes vulpes*) in Melbourne: implications for rabies control. Wildlife Research 26:763–775.

MATTHIAE, P. E., AND F. STEARNS. 1981. Mammals in forest islands in southeastern Wisconsin. Pp. 55–66 in Forest island dynamics in man-dominated landscapes (R. L. Burgess and D. M. Sharpe, eds.). Springer-Verlag, New York.

MCCLENNEN, N., R. R. WIGGLESWORTH, AND S. H. ANDERSON. 2001. The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). American Midland Naturalist 146:27–36.

MCDONNELL, M. J., ET AL. 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems 1:21–36.

MCDONNELL, M. J., S. T. A. PICKETT, AND R. V. POUYAT. 1993. The application of the ecological gradient paradigm to the study of urban effects. Pp. 175–189 in Humans as components of ecosystems: subtle human effects and the ecology of populated areas (M. J. McDonnell and S. T. A. Pickett, eds.). Springer-Verlag, New York.

MCGARIGAL, K., AND B. J. MARKS. 1995. Fragstats: spatial pattern analysis program for quantifying landscape structure. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, General Technical Report PN2-GTR-351:1–122.

MCKINNEY, M. L. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

METROPOLIS, N., AND S. ULAM. 1949. The Monte Carlo method. Journal of the American Statistical Association 44:335–341.

MILNE, B. T. 1991. Lessons from applying fractal models to landscape patterns. Pp. 153–162 in Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity (M. G. Turner and R. H. Gardner, eds.). Springer-Verlag, New York.

NEELY, R. D., AND C. G. HEISTER (COMPS.). 1987. The natural resources of Illinois: introduction and guide. Illinois Natural History Survey Special Publication, 6:1–224.

NIEMELÄ, J. 1999. Is there a need for a theory of urban ecology? Urban Ecosystems 3:57–65.

NILON, C. H., AND R. C. PAIS. 1997. Terrestrial vertebrates in urban ecosystems: developing hypotheses for the Gwynns Falls Watershed in Baltimore, Maryland. Urban Ecosystems 1:247–257.

OXLEY, D. J., M. B. FENTON, AND G. R. CARMODY. 1974. The effects of roads on populations of small mammals. Journal of Applied Ecology 11:51–59.

PATTERSON, B. R., S. BONDRUP-NIELSEN, AND F. MESSIER. 1999. Activity patterns and daily movements of the eastern coyote, *Canis latrans*, in Nova Scotia. Canadian Field-Naturalist 113:251–257.

PICKETT, S. T. A., ET AL. 2001. Urban ecological systems: linking terrestrial, ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127–157.

PRANGE, S., S. D. GEHRT, AND E. P. WIGGERS. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324–333.

PRANGE, S., S. D. GEHRT, AND E. P. WIGGERS. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. Journal of Mammalogy 85:483–490.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Randa, L. A. 1996. Prey selectivity and foraging activity of *Canis latrans* and *Vulpes vulpes* in response to prey fluctuations and habitat in a heterogeneous landscape. M.S. thesis, Northern Illinois University, DeKalb.

Rempel, R. S., A. Carr, and P. Elkie. 1999. Patch analyst and patch analyst (grid) function reference. Centre for Northern Forest Ecosystem Research, Ontario, Ministry of Natural Resources, Lakehead University, Thunder Bay, Ontario, Canada.

Riley, S. P. D., et al. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566–576.

Rosatte, R., M. J. Power, and C. D. MacInnes. 1991. Ecology of urban skunks, raccoons, and foxes in metropolitan Toronto. Pp. 31–38 in Wildlife conservation in metropolitan environments (L. W. Adams and D. L. Leedy, eds.). Symposium Series 2. National Institute for Urban Wildlife, Columbia, Maryland.

Rosenblatt, D. L., E. J. Heske, S. L. Nelson, D. M. Barber, M. A. Miller, and B. MacAllister. 1999. Forest fragments in east-central Illinois: islands or habitat patches for mammals? American Midland Naturalist 141:115–123.

Sargeant, A. B., S. H. Allen, and J. O. Hastings. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. Journal of Wildlife Management 51:285–293.

Sargeant, G. A., and D. H. Johnson. 1997. Carnivore scent-station surveys: statistical considerations. Proceedings of the North Dakota Academy of Science 51:102–104.

Sargeant, G. A., D. H. Johnson, and W. Berg. 1998. Interpreting carnivore scent-station surveys. Journal of Wildlife Management 62:1235–1245.

SAS Institute Inc. 1999. SAS/STAT user's guide, version 8. SAS Institute Inc., Cary, North Carolina.

Scheiner, S. M. 1993. MANOVA: multiple response variables and multispecies interactions. Pp. 94–112 in Design and analysis of ecological experiments (S. M. Scheiner and J. Gurevitch, eds.). Chapman & Hall, New York.

Scott, T. G., and W. D. Klimstra. 1955. Red foxes and a declining prey population. Southern Illinois University, Monograph Series 1:1–123.

Smith, W. P., D. L. Borden, and K. M. Endres. 1994. Scent-station visits as an index of abundance of raccoons: an experimental manipulation. Journal of Mammalogy 75:637–647.

StatSoft, Inc. 2000. STATISTICA version 5.5 for Windows. Computer program manual. StatSoft, Inc., Tulsa, Oklahoma.

Ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179.

Thioulouse, J., D. Chessel, S. Dolédec, J.-M. Olivier, F. Goreaud, and R. Pelissier. 2001. ADE-4 ecological data analysis: exploratory and euclidean methods in environmental sciences. French National Center for Scientific Research (CNRS), Lyon, France.

Tsukada, H., Y. Morishima, N. Nonaka, Y. Oku, and M. Kamiya. 2000. Preliminary study of the role of red foxes in *Echinococcus multilocularis* transmission in the urban area of Sapporo, Japan. Parisitology 120:423–428.

United States Census Bureau. 1990. Census of population and housing, 1990: summary tape file 1 on CD-ROM. Data User Services Division, Customer Services Branch, Bureau of the Census, Washington, D.C.

United States Census Bureau. 2001. Statistical abstract of the United States. United States Government Printing Office, Washington, D.C.

United States Census Bureau. 2002. Census 2000 urbanized area and urban cluster information. May 1, 2002. Federal Register Notice, Washington, D.C.

United States Geological Survey. 1995. Landsat thematic mapper imagery, Landsat 4. Earth Resources Observation and Science Data Center, Sioux Falls, South Dakota.

United States Geological Survey. 1999. 3.75-minute (quarter-quad) digital orthophoto quadrangles. Earth Resources Observation and Science Data Center, Sioux Falls, South Dakota.

Voight, D. R., and B. D. Earle. 1983. Avoidance of coyotes by red fox families. Journal of Wildlife Management 47:852–857.

Waller, J. S., and C. Servheen. 2005. Effects of transportation infrastructure on grizzly bears in northwestern Montana. Journal of Wildlife Management 69:985–1000.

Whitney, G. G. 1985. A quantitative analysis of the flora and plant communities of a representative midwestern U.S. town. Urban Ecology 9:143–160.

Yunger, J. A. 1996. Predation, competition, and abiotic disturbance: population dynamics of small mammals. Ph.D. dissertation, Northern Illinois University, DeKalb.

Submitted 28 June 2005. Accepted 12 May 2006.

Associate Editor was Edward J. Heske.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 20 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use