

# SPATIAL ECOLOGY OF COYOTES ALONG A SUBURBAN-TO-RURAL GRADIENT

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**Abstract:** Coyotes (*Canis latrans*) are now ubiquitous throughout most of the eastern United States; however, little information exists on how they are able to exploit and thrive in fragmented landscapes. We investigated home ranges, movements, and scale-dependent resource selection of coyotes along a gradient (suburban/exurban/rural) of anthropogenic disturbance. Home-range sizes varied along a suburban-to-rural gradient and were inversely correlated to urbanization ( $R^2 = 0.79$ ,  $P < 0.001$ ). Habitat composition and coyote use of 95% (home range) and 50% (core area) contours were nonrandom. Coyotes used corridor habitat extensively and avoided urban and crop-field habitats. Forested habitat was used extensively for diurnal cover. Rural coyotes traveled greater distances at faster rates than did suburban/exurban coyotes. Diel activity patterns were similar along the gradient, suggesting that coyotes responded similarly to differing levels and types of human activity. Coyotes appeared to assess habitat quality at the landscape scale and exploited small, disjunct resource patches present in developed landscapes. We believe that the availability of foraging habitat and travel corridors is critical to movement of coyotes in areas of high human activity.

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Habitat fragmentation resulting from agriculture and human development is ubiquitous (Saunders et al. 1991) and has been linked to the decline of many vertebrate species (Kareiva 1987). Typically, habitat fragmentation leads to decreased patch size, increased patch isolation, higher edge:interior ratios, and varying degrees of patch connectivity (Saunders et al. 1991, Wilcove et al. 1986). Environmental alteration, including fragmentation, has the potential to transform the spatiotemporal structure of vertebrate populations that are sensitive to disturbance (Noss et al. 1996, Palomares et al. 2000). However, predators with a wide niche breadth generally prosper in dissected landscapes because of their ability to exploit a variety of landscape elements (i.e., forest and grassland patches, corridors, agricultural fields) and traverse potentially hostile matrices (Gehring and Swihart 2003), potentially to the detriment of their prey (Swihart et al. 2001).

Much research has been conducted on the ecology and behavior of coyote populations in the western United States (Camenzind 1978; Andelt 1982, 1985; Gese 1988*a, b*, 1989, 1996; Mills and Knowlton 1991; McClennen et al. 2001), yet comparatively little information exists for populations occurring in the eastern United States.

Within the last decade, coyotes have become established in suburban areas with moderate-to-dense human settlement (Crooks and Soulé 1999, Grinder and Krausman 2001, McClennen et al. 2001). Presumably, coyotes are able to thrive in these areas because of their ability to adapt to new, altered habitats. In Indiana, USA—as in much of the eastern United States—the coyote is now considered the dominant large predator, and a precise understanding of its ecology is critical in determining the ability of coyotes to influence community structure in fragmented landscapes. Thus, we investigated whether variability in the dispersion of landscape elements and anthropogenic activity alter the dynamics of coyote habitat use, home-range size, and movement by examining space use, resource selection, travel rates, and movement distances along a gradient of anthropogenic disturbance.

Gehring (2000) found that the relative abundance of small mammals in row-crop (e.g., corn and soybean fields) agricultural habitat was substantially less than that of forest, grassland, and woody and grassy corridor patches. As a result, home ranges containing proportionately more row-crop monoculture habitat often must be larger to meet the energetic requirements of coyotes. High levels of human disturbance can result in the wide dispersion or spatial aggregation of critical resource patches (e.g., occurrence of diurnal cover, denning cover, foraging patches in close proximity). Further, the physical structure of row-crop habitat differs substantially between the fal-

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low and growing seasons and may influence a species' ability to perceive and orientate toward suitable habitat (Gehring 2000). In our study, the predominant form of land use varied from agricultural to urban/residential. Agricultural areas were characterized by a more uniform dispersion of resource patches and low human development and road densities; in suburban areas, resource patches tended to be aggregated and human development and road densities were high. We hypothesized that home-range size and distance and rate of travel may be related to human development and road densities contained within home ranges. Specifically, we predicted that resource aggregation in suburban areas would result in smaller coyote home ranges and reduced travel rates and distances compared to agricultural areas.

We believed that by investigating coyote movement and resource selection along a gradient of human disturbance (suburban/exurban/rural), we could identify variation in the ecology of eastern coyotes relative to fragmentation and assess impacts of anthropogenic disturbance. Our objectives were to (1) explain variation in coyote home-range size along a suburban/rural gradient; (2) determine whether varying levels of human disturbance alter diel activity patterns of coyotes; and (3) determine the degree to which coyotes exploit different spatial elements of the landscape. To date, no data are available on the use and resource selection of coyotes in an agriculturally fragmented landscape. Moreover, few data exist to assess the degree to which increasing urbanization may influence coyote social behavior (Grinder and Krausman 2001, McClennen et al. 2001).

## STUDY AREA

From February 2000 through December 2001, we conducted a radiotelemetry study of coyotes within the 812-km<sup>2</sup> Indian Pine Study Area (IPSA) in west-central Indiana, USA. The Coyote Study Area (CSA) was a 250-km<sup>2</sup> area within the IPSA delineated by extending a 1-km buffer around the outermost home ranges of focal coyotes. A Geographic Information System with 1-m spatial resolution in ArcView (Environmental Systems Research Institute 1997) was used to examine coyote use of spatial elements. We identified 6 habitat types in the CSA: forest, grassland (primarily *Bromus* spp. and *Festuca* spp.), fencerows (including railroad rights-of-way), grassy drainage ditches, agricultural matrix (corn and soybean fields), and human development (commercial

and residential). Human land use dominated the CSA, with approximately 12% of the area in human developments and 70% in agricultural production; forests, grasslands, and wetlands comprised approximately 10, 4, and 1% of the CSA, respectively (Gehring 2000). Fencerows and drainage ditches bisected some of the agricultural fields offering varying levels of patch connectivity.

## METHODS

We captured coyotes with padded foot-hold traps and immobilized them with an intramuscular injection of ketamine and xylazine (6.6 mg/kg ketamine + 2.2 mg/kg xylazine; Beheler-Amass et al. 1998). Immobilized animals were weighed and sexed, and we determined reproductive condition. We classified coyotes as juvenile (<1 yr old), yearling, or adult based on tooth development and wear (Parks 1979). We attached a 250-g radiocollar (Telonics, Inc., Mesa, Arizona, USA) to adults and administered yohimbine (0.30 mg/kg IM; Beheler-Amass et al. 1998) as an immobilant antagonist. We further classified coyotes as breeding residents, resident associates, juveniles, or transients based on group affiliations and movements derived from radiotelemetry monitoring (Messier and Barrette 1982, Patterson et al. 1999).

## Radiotelemetry and Resource Selection

We monitored coyotes using standard methods of ground-based triangulation (White and Garrett 1990). Telemetry bearing error was estimated with reference transmitters to be <4°. We converted triangulation data to point locations using the Maximum Likelihood Estimator computed by the software Locate II (Nams 1990). For the purpose of data analyses, we grouped radio locations into 2 seasons based on approximate vegetation phenology: growing season (15 Apr–15 Oct) and fallow season (16 Oct–14 Apr). Radiomarked coyotes were monitored daily, with 1 24-hr sequential (1 location/hr) monitoring session for each animal occurring monthly.

We estimated home-range sizes (95% contour) and core areas (50% contours) using the adaptive kernel method (ADK; Worton 1989) in program CALHOME (Kie et al. 1996). The ADK method (Worton 1989) is a nonparametric technique for estimating home-range size that allows identification of disjunct areas of activity, which may be an especially important consideration in fragmented landscapes. We constructed area-observation curves for each home range to assure that the number of locations obtained reached an asymp-

tote and were therefore sufficient to describe the size of that home range (Odum and Kuenzler 1955). Point and sequential locations were used in analyses; sequential locations were separated by >4 hr to ensure independence (Laundre and Keller 1984, Swihart and Slade 1985). We rejected triangulation fixes with error ellipses exceeding 0.5 km<sup>2</sup>. The remaining locations had an average 95% confidence ellipse of 0.098 ± 0.13 km<sup>2</sup> ( $\bar{x}$  ± SD). We used *t*-tests (Zar 1996) to test for differences in home-range size between sexes and seasons.

We used theme overlay routines in ArcView to estimate the proportion of used habitat for home ranges and core areas compared to available habitat in the CSA. Note that habitat classified as human development contained components (i.e., buildings, roads, parking lots) that may have reduced the actual amount of habitat available to coyotes. We were unable to accurately quantify how much habitat was rendered unavailable by human structures, but we present below our method for incorporating the effects of human development and road densities on coyote spatial ecology. We used the Animal Movement Extension for ArcView (Hooge and Eichenlaub 1997) to classify radio locations into used habitat-type classes for comparison to available habitat in the home range. Further, we used compositional analysis (Aebischer et al. 1993) to examine landscape-level, home-range, and core-area habitat selection by coyotes. We used SAS (SAS Institute 1998) code provided by Ott and Hovey (1997) to perform compositional analysis.

We hypothesized that composite home-range size might vary along a suburban/rural gradient. Accordingly, we developed an index of urbanization by regressing composite home-range size (95% ADK contour) on an urbanization variable generated by combining the mean squared difference (MSD) of nearest neighbor human-development patches and road densities and types within the home range. Home ranges with a value of >0.0 were then classified as rural, whereas values <0.0 were classified as suburban. For each composite home range, we measured the nearest-neighbor distance between human-development patches and calculated the MSD to generate a human-development metric. Further, we categorized roads (km/km<sup>2</sup>) within each home range into 4 classes as follows: class 1—primary roads (state routes and highways); class 2—secondary county roads (paved county roads); class 3—secondary town roads (suburban and residential subdivision roads); and class 4—unimproved

county roads (dirt and gravel roads). Roads were weighted by class based on traffic volume (Indiana Department of Transportation 2000) using values of 1–4, with higher traffic volume roads receiving higher weighting. For example, state routes and highways had the highest traffic volumes (Indiana Department of Transportation 2000), and thus received the highest weighting.

We used singularly the MSD of nearest-neighbor distances between human-development patches, weighted road values, and coyote social status as independent variables in a multiple regression to model cumulative effects on variation in home-range size. We selected the cumulative-effects regression model with the lowest Akaike's Information Criterion (AIC<sub>c</sub>; Burnham and Anderson 1998) as the best model. We rescaled AIC<sub>c</sub> values relative to the best model (i.e., model with the minimum AIC<sub>c</sub>), which received an AIC<sub>c</sub> value of zero. We calculated the difference between AIC values among models ( $\Delta_i$ ) and ranked models in ascending order relative to the  $\Delta_i$  values. We then calculated Akaike weights ( $w_i$ ) to aid in the determination of the best model;  $w_i$  values approximate the probability that a model is the best Kullback-Leibler model (Burnham and Anderson 1998). Subsequently, we determined the relative likelihood that 1 model was better than another as  $w_i/w_j$  (Burnham and Anderson 1998).

#### Rate and Distance of Travel Estimates and Activity Patterns

We used sequential radiotracking to determine travel rates and distances and diel activity patterns. Each individual was monitored for a 24-hr period once per month. During this period, we obtained locations hourly and calculated the distances between locations. We used the Animal Movement extension in ArcView (Hooge and Eichenlaub 1997) to determine the distance (m) between adjacent locations within an observation session. We then determined rate of movement (km/hr) between adjacent locations. We combined seasonal observation sessions for each individual to determine average rates of movement and distances traveled. We used the urbanization index value to categorize coyotes as suburban or rural. We compared mean distances traveled (km/interval) and mean travel rates during dawn (0500–0900 hr), day (0900–1700 hr), evening (1700–2100 hr), and night (2100–0500 hr) between individuals occupying suburban and rural home ranges using repeated measures

Table 1. Rank matrices for radiomarked coyotes comparing habitat composition within (A) 95% adaptive kernel (ADK) home-range contours and (B) 50% ADK core-area contours relative to habitat availability within the 250-km<sup>2</sup> Coyote Study Area (CSA) located in west-central Indiana, USA, Feb 2000–Dec 2001. The sign of *t*-values is indicated with positive or negative signs; a triple sign signifies nonrandom habitat use at  $\alpha = 0.05$ . Rank is equal to the sum of positive values in each row. A higher rank denotes a more preferred habitat type. Table format is adapted from Aebischer et al. (1993).

(A) Home-range habitat composition vs. habitat availability								
Habitat	Fencerow	Ditch	Wetland	Urban	Grass	Forest	Agriculture	Rank
Fencerow		–	+	–	---	+++	+	3
Ditch	+		+	–	---	+++	+	4
Wetland	–	–		–	---	+	–	1
Urban	+	+	+		---	+++	+	5
Grass	+++	+++	+++	+++		+++	+++	6
Forest	---	---	–	---	---		---	0
Agriculture	–	–	+	–	---	+++		2

(B) Core-area habitat composition vs. habitat availability								
Fencerow		+	+++	+++	+++	–	+++	5
Ditch	–		+	+	+	–	–	3
Wetland	---	–		+	–	---	–	1
Urban	---	–	–		–	---	–	0
Grass	---	–	+	+		–	–	2
Forest	+	+	+++	+++	+		+	6
Agriculture	---	+	+	+	+	–		4

ANOVA with time of day, type of home range (suburban or rural), and season (growing or fallow) as main effects. Statistical significance for all tests was accepted at  $\alpha = 0.05$ .

**RESULTS**

We caught 29 coyotes (14 F, 15 M) during 647 trap-nights for an average of 0.05 coyote/trap-night. Of the 29 individuals captured, 25 were radiomarked (14 F, 11 M). We classified, by age and social class, 11 breeding resident adults (7 F, 4 M), 3 pack associate adults (1 F, 2 M), 1 pack associate yearling (M), 5 pack juveniles (3 F, 2 M), and 2 transient yearlings (1 F, 1 M). A 12-week-old male pup, 2 male juveniles, and 1 female yearling were not radiomarked. The remaining 3 adults (2 F, 1 M) were located during <50% of all radiotracking attempts, so we considered these animals to be transients (Andelt 1982). We included only data collected from residents in subsequent analyses.

**Resource Selection**

We obtained 4,015 radiolocations on 20 resident coyotes from March 2000 to December 2001. Compositional analysis indicated that habitat composition was nonrandom in home ranges ( $\lambda = 0.134, F_{6,14} = 15.06, P < 0.001$ ) and core areas ( $\lambda = 0.254, F_{6,14} = 5.39, P = 0.008$ ) relative to availability within the CSA (Table 1). Coyote home ranges were composed of proportionately more grassland, urban, and corridor (fencerow and ditch) elements than forested habitat and agri-

cultural matrix (Table 1). Coyote core areas contained proportionately more forest and fencerow elements than agricultural or urban matrix (Table 1). Coyotes used available habitat within home ranges ( $\lambda = 0.306, F_{6,14} = 5.66, P = 0.003$ ) and core areas ( $\lambda = 0.432, F_{6,14} = 3.63, P = 0.023$ ) in a nonrandom fashion (Table 2). Within home ranges, coyotes made greatest use of fence, ditch, and grassland elements; forested habitat was used more than the agricultural or urban matrix (Table 2). Core areas of all coyotes contained proportionately more forested habitat than other available types (Table 2).

**Influence of Urbanization and Coyote Social Status on Home-range Size**

Composite home-range size varied greatly (range = 2.97–23.48 km<sup>2</sup>). Regression analysis indicated that composite home-range sizes varied along a suburban-to-rural gradient (Fig. 1) and that the human-development metric and weighted road value variables produced the most plausible model ( $AIC_c = 48.76, \Delta AIC_c = 0.0, w_i = 0.89$ ):

$$\{R^2 = 0.79, P < 0.001; \ln(\text{composite home range area}) = b_0 + 5.87(\text{development metric}) - 0.13(\text{weighted road value})\}.$$

Note that we combined these 2 variables to generate the urbanization index. The 6 remaining models ranged from 4 to 30  $\Delta AIC_c$  relative to the most plausible model (Table 3). Coyotes occupy-

Table 2. Rank matrix for radiomarked coyotes comparing habitat use and availability within (A) 95% adaptive kernel home-range contours and (B) 50% core-area contours in the 250-km<sup>2</sup> Coyote Study Area (CSA), located in west-central Indiana, USA, Feb 2000–Dec 2001. The sign of *t*-values is indicated with positive or negative signs; a triple sign represents nonrandom use at  $\alpha = 0.05$ . Rank is equal to the sum of positive values in each row. A higher rank denotes a more preferred habitat type. Table format is adapted from Aebischer et al. (1993).

(A) Radio locations vs. home-range habitat composition								
Habitat	Fencerow	Ditch	Wetland	Urban	Grass	Forest	Agriculture	Rank
Fencerow		+	+++	+++	+++	+++	+++	6
Ditch	–		+++	+++	+++	+	+++	5
Wetland	---	---		+	---	---	–	1
Urban	---	---	–		---	---	–	0
Grass	---	---	+++	+++		–	+++	3
Forest	---	–	+++	+++	+		+++	4
Agriculture	---	---	+	+	---	---		2

(B) Radio locations vs. core-area habitat composition								
Fencerow		+	+++	+	+++	–	+++	5
Ditch	–		+	+	+	–	+	4
Wetland	---	–		–	+	---	–	1
Urban	–	–	+		+	–	–	2
Grass	---	–	–	–		–	–	0
Forest	+	+	+++	+	+		+	6
Agriculture	---	–	+	+	+	–		3

ing areas with greater human-development densities (Fig. 2) and high traffic volume roads (Fig. 3) had substantially smaller home ranges than did those in rural areas where traffic volumes and development densities were substantially less. Home-range sizes did not vary by season ( $t_{39} = 0.40$ ,  $P = 0.924$ ) or sex ( $t_{19} = 1.13$ ,  $P = 0.266$ ).

### Diel Activity and Movement

We sequentially tracked coyotes for 1,536 hr from June 2000 through September 2001. Movement rates ( $F_{4,280} = 17.4$ ,  $P < 0.001$ ) and total distance traveled ( $F_{1,262} = 27.99$ ,  $P < 0.001$ ) differed by time and home-range type (Table 4). Annually, coyotes occupying areas with higher human-development densities and weighted road values traveled an average of  $9.19 \pm 1.51$  km/day, whereas rural coyotes traveled an average of  $13.46 \pm 2.09$  km/day. Mean hourly rate of travel varied by time of day ( $F_{3,281} = 14.70$ ,  $P < 0.001$ ) and between suburban and rural coyotes ( $F_{1,281} = 25.68$ ,  $P <$

0.001), with rural coyotes having higher mean hourly rates of travel. Rates of travel for all coyotes were greatest during evening and night intervals and least during daytime. Mean travel rates did not differ by season ( $F_{1,281} = 1.87$ ,  $P < 0.172$ ).

### DISCUSSION

To more fully understand mammalian spatial ecology in fragmented landscapes, we must consider habitat selection at multiple spatial scales

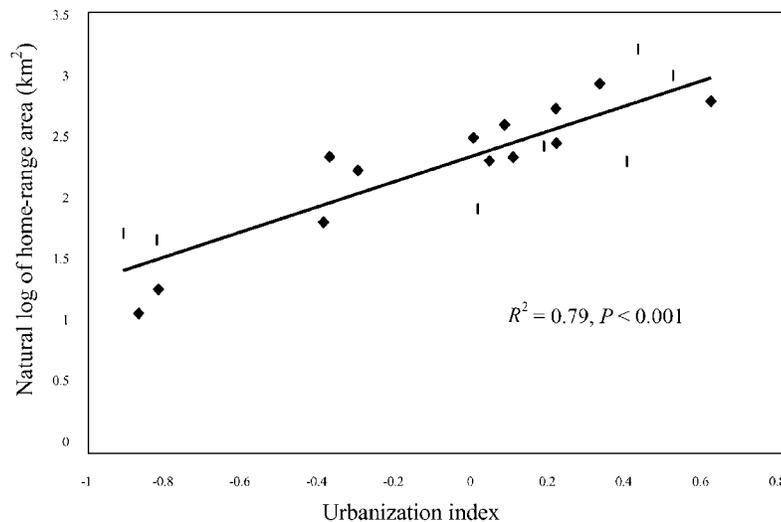


Fig. 1. Urbanization index generated from regressing composite coyote home-range size (95% adaptive kernel contour) on human development and road densities for coyotes occupying home ranges within the Coyote Study Area (CSA), west-central Indiana, USA, Feb 2000–Dec 2001. Home ranges with a value  $>0.0$  were classified as rural, values  $<0.0$  were classified as suburban.

Table 3. Model structure, corresponding Akaike's Information Criteria value corrected for sample size ( $AIC_c$ ),  $\Delta AIC_c$ , and Akaike weight ( $w_i$ ; Burnham and Anderson 1998) used to assess the effects of urbanization and social status on home-range size of coyotes in the Coyote Study Area, west-central Indiana, Feb 2000–Dec 2001.

Model structure	$AIC_c$	$\Delta AIC_c$	$w_i$
$\beta_0 + \beta_1(\text{development metric}) + \beta_2(\text{weighted road value})$	47.35	0.0	0.890
$\beta_0 + \beta_1(\text{development metric})$	51.78	4.43	0.097
$\beta_0 + \beta_1(\text{coyote social status}) + \beta_2(\text{development metric}) + \beta_2(\text{weighted road value})$	56.36	9.01	0.001
$\beta_0 + \beta_1(\text{coyote social status}) + \beta_2(\text{development metric})$	59.17	11.82	0.002
$\beta_0 + \beta_1(\text{weighted road value})$	65.91	18.56	0.000
$\beta_0 + \beta_1(\text{coyote social status}) + \beta_2(\text{weighted road value})$	69.68	22.33	0.000
$\beta_0 + \beta_1(\text{coyote social status})$	77.46	30.11	0.000

(Brown and Litvaitis 1995, Oehler and Litvaitis 1996, Gehring 2000, Gehring and Swihart 2003). Patterns of habitat selection relative to spatial scale (i.e., landscape vs. home range) reflect the interaction between a species' perceptual range and landscape structure (Lima and Zollner 1996, Wiens 1996). Random composition of 95% contour home ranges relative to availability within the landscape suggests that a limited perceptual range may constrain a species' ability to perceive habitat availability at larger spatial scales. For example, the presence of vegetative cover may inhibit inter-patch movement in smaller species due to their inability to visually perceive distant

habitat patches (Lima and Zollner 1996). Conversely, nonrandom home-range composition indicates that a species may have a greater ability to perceive qualitative differences in landscape elements. In such a case, matrix habitat may still represent a barrier that the animal is reluctant to cross; however, higher cognitive ability (i.e., assessment of risk) coupled with greater spatial recognition may facilitate the decision to either cross the matrix or seek an arrangement of landscape elements that reduces vulnerability (Atwood 2002).

Gehring (2000) found that long-tailed weasels (*Mustela frenata*) occupying an agriculturally fragmented landscape exhibited differential patterns

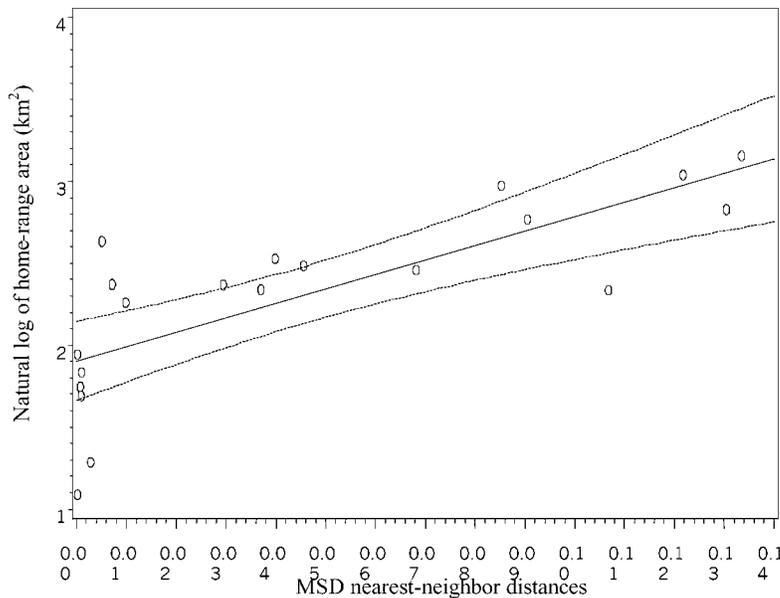


Fig. 2. Relationship of the mean squared difference (MSD) of nearest-neighbor distances between human-development patches to composite coyote home ranges (95% adaptive kernel contours) in the Coyotes Study Area (CSA), west-central Indiana, USA, Feb 2000–Dec 2001. The solid line is a linear regression to portray the general trend in observations. The dashed lines are 95% confidence intervals on the regression. Because the MSD of nearest-neighbor distances between human-development patches within a home range was used to assess housing density, smaller variances reflect higher housing densities. Thus, home-range size is positively correlated to the MSD of nearest-neighbor distances between human-development patches.

of scale-dependent habitat selection (i.e., landscape vs. home range), with random selection occurring at 95% contours, while nonrandom selection occurred at 50% contours. Nonrandom habitat selection suggests the ability to assess the distribution of resources at large spatial scales. In our study, coyotes occupying the same landscape as Gehring's (2000) long-tailed weasels exhibited nonrandom habitat selection at both 95% and 50% contours, but composition of those contours was quite different. Forested habitat was underrepresented in 95% contours but was the predominant element present in 50% contours. The dichotomy between proportion of forested

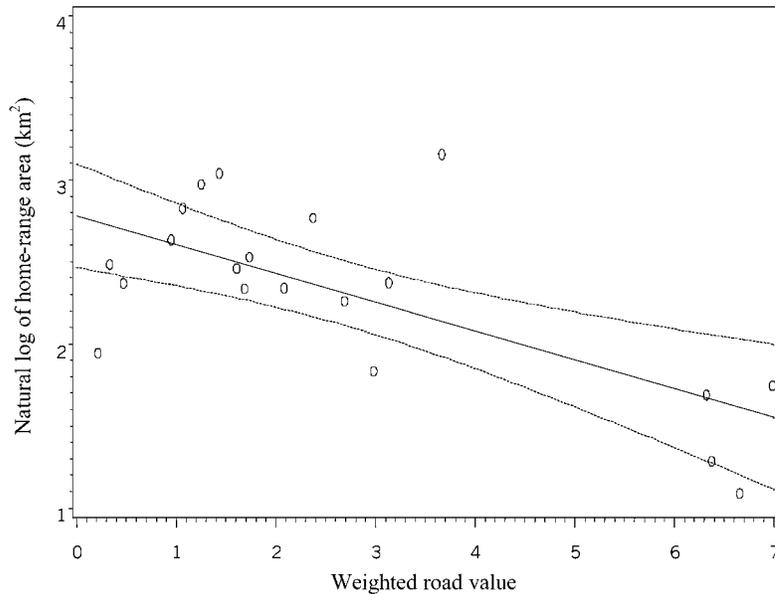


Fig. 3. Relationship of weighted road values to composite coyote home ranges (95% adaptive kernel contours) in the Coyote Study Area (CSA), west-central Indiana, USA, Feb 2000–Dec 2001. Roads were categorized by type and weighted by traffic volume. Composite home-range size was inversely related to weighted road values. The solid line is a linear regression to portray the general trend in observations. The dashed lines are 95% confidence intervals on the regression.

habitats within 95% and 50% contours highlights the importance of protective cover to coyotes present in developed landscapes. Although coyotes configure home ranges in a nonrandom fashion, the arrangement of critical resources within the landscape often constrains home-range content. Because the widely distributed forested patches in rural portions of the CSA are few in number and small in size, they are under-represented in 95% home-range contours.

Lidicker and Koenig (1996) suggested that an allometric relationship exists between landscape perception and body size, with small-bodied mammals viewing landscapes as more heterogeneous than larger species. Further, Gehring and

Swihart (2003) suggested that the combination of body size and niche breadth (food habits and habitat use) influences the use of spatial elements by predators. Thus, predators with large body size should demonstrate an increased ability to traverse matrix habitat because of a reduced risk of predation. Conversely, small predators appear to regard matrix habitat as a barrier, with juxtaposition of habitat patches or narrow habitat requirements constraining inter-patch movement (Gehring 2000; Gehring and Swihart 2003). The ability of coyotes in the CSA to perceive landscape heterogeneity facilitates exploitation of dispersed resource patches characteristic of fragmented landscapes.

Home-range size varied along a gradient of anthropogenic disturbance, with home-range size negatively correlated to human development and road densities. Our results indicate that both suburban/exurban and rural coyotes configure home ranges to minimize exposure to human development and matrix habitat, thereby reducing exposure to humans. Although spatial relationships and composition of habitat elements vary along a suburban/rural gradient, coyotes appear adept at exploiting different habitat elements for similar purposes. For example, while all coyotes made disproportionate use of corridor habitat, coyotes

Table 4. Mean distances (km) traveled during dawn, day, evening, and night hours, and 24-hr periods, for suburban and rural coyotes present in the Coyote Study Area, west-central Indiana, USA, Feb 2000–Dec 2001.

Season	Dawn	Day	Evening	Night	Mean distance traveled/24 hr		No. locations	No. monitoring sessions
					$\bar{x}$	SD		
Suburban								
Fallow	2.69	2.02	1.68	3.77	10.15	1.19	192	8
Growing	0.90	2.57	1.64	3.12	8.23	1.03	336	14
Rural								
Fallow	3.41	3.43	2.51	4.81	14.16	0.89	384	16
Growing	1.82	2.96	2.67	5.41	12.86	1.27	624	26

present in urbanized portions of the CSA used forested habitat as intensively as corridors. Historically, substantial amounts of the CSA consisted of forested habitat, which was lost in the conversion of native vegetation to an agro-ecosystem. As a result, forested habitats occurring in rural portions of the CSA rarely exceed 2 ha and are widely dispersed. However, relatively large forested tracts (>40 ha) are still present within suburban portions of the CSA, and consist mainly of wooded ravines that often are associated with single-family residential subdivisions. Within these areas, coyotes used forested ravines as travel conduits and as resource patches. Movement data indicated that suburban/exurban coyotes used forested habitat for protective cover, travel routes, and foraging, similar to the use of corridor habitat (fencerows and ditches) by rural coyotes.

All coyotes preferred corridor habitat when it was available. Disproportionate use of corridor habitat by coyotes is not surprising given that such habitat facilitates travel while allowing the avoidance of the matrix. In a separate study conducted concurrently with our investigation, Gehring (2000) found that the abundance and richness of small mammals and lagomorphs in the CSA were greatest in corridors relative to other habitat types. Coyotes occupying suburban/exurban home ranges typically had substantially less corridor habitat available, higher road densities, and more forested habitat; whereas rural coyotes had the opposite. Thus, suburban coyotes traveled shorter distances at slower rates than did rural coyotes.

Similar to reports of habitat associations of urban red foxes (*Vulpes vulpes*) in Canada (Adkins and Stott 1998), suburban/exurban coyotes typically avoided large mowed or paved areas, although they used some golf courses at night when humans were absent. Although we saw no direct evidence that coyotes were scavenging human refuse, in contrast with observations of urban foxes in Britain (Harris 1981, Doncaster et al. 1990), coyotes in our study area were difficult to observe, and we did not analyze diets. Thus, we cannot discount that human refuse may have comprised a portion of coyote diets. Most protracted bouts of suburban/exurban coyote foraging activity occurred along woodlot edges and grassy old fields, whereas rural coyotes foraged almost exclusively along corridors. All are habitats where we would expect staple food items, such as voles (*Microtus* spp.) and eastern cottontail rabbits (*Sylvilagus floridanus*), to be found.

In our study, coyotes in suburban, exurban, and rural areas exhibited primarily nocturnal activity patterns. These findings concur with those of other studies in which coyotes have been exposed to intensive agriculture or high levels of exploitation (Andelt and Gipson 1979, Laundre and Keller 1981, Smith et al. 1981, Holzman et al. 1992, Shivik and Crabtree 1995). Conversely, studies conducted in forested regions of northeastern North America suggest that coyotes often are active throughout both day and night (Major and Sherburne 1987, Morton 1988, Brundige 1993, Patterson et al. 1999), which probably is typical of unexploited coyote populations. Coyotes occupying rural portions of the CSA were subjected to higher levels of exploitation (primarily sport hunting) than those present in areas of greater urbanization. Similarity in activity patterns along the gradient suggests that coyotes responded to exploitation and high levels of human activity in a similar manner.

## MANAGEMENT IMPLICATIONS

The increasing presence of coyotes in urbanized areas of the eastern United States indicates that they are able to adapt to novel environments including disjunct urbanized landscapes. Thresholds of limiting factors (i.e., food, cover, water) exist below which coyotes can no longer persist (Grinder and Krausman 2001). Identifying linkages between urbanization and variation in coyote spatial ecology is important, particularly where human disturbance facilitates interaction between coyotes and other meso-predators such as red foxes and raccoons (*Procyon lotor*).

Spatial requirements impact group interactions (White and Garrott 1990) and ultimately population density. Higher densities increase the probability of vectoring disease between groups, heighten the likelihood of aggressive encounters between members of adjacent groups, and increase the potential for negative human-coyote interactions. Coyotes occupying home ranges within suburban/exurban areas of the CSA were able to tolerate relatively high levels of human activity because of the presence of substantial protective cover (Atwood 2002). Within the CSA, home ranges with greater housing densities and traffic volumes were associated with residential developments situated adjacent to relatively large forested tracts. Thus, in fragmented landscapes, the availability of substantial protective cover probably facilitates occupancy of areas with relatively high human activity. We believe that forest-

ed habitat served 3 functions within the CSA: (1) provided protective cover, (2) supplied foraging habitat, and (3) facilitated travel by serving as a surrogate to corridor habitat.

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