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HOME RANGE AND LANDSCAPE USE OF COYOTES IN A METROPOLITAN LANDSCAPE: CONFLICT OR COEXISTENCE?

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An understanding of how top mammalian carnivores respond to urbanization is important for conservation and management of human–wildlife conflicts. Coyotes (*Canis latrans*) have recently become more prevalent in many metropolitan areas; however, their apparent success is poorly understood. We estimated home-range size and selection of land-use types for coyotes in a heavily urbanized landscape, with a particular focus on responses of coyotes to those parts of the urban landscape with high levels of human development or activity. Mean ($\pm$ *SE*) annual home ranges of transient coyotes ($\bar{X} = 26.80 \pm 2.95$ km^2) were larger than those of resident coyotes ($\bar{X} = 4.95 \pm 0.34$ km^2), and home-range size for resident coyotes did not vary among seasons or between age and sex classes. Although most home ranges were associated with natural patches of habitat, there was considerable variation among coyotes, with some home ranges entirely lacking patches of natural habitat. Within home ranges, coyotes typically avoided land-use types associated with human activity (i.e., Residential, Urban Grass, and Urban Land) regardless of coyote characteristics, seasons, and activity periods. Few coyotes were nuisances, and conflicts occurred when coyotes were sick or exposed to wildlife feeding by humans. We found little evidence that coyotes were attracted to areas associated with human activity, despite at times having home ranges located in heavily developed areas.

Key words: *Canis latrans*, Chicago, coyote, Illinois, resource selection, urbanization

A fundamental question regarding the presence of wildlife in urban landscapes is whether they are attracted to human activities and somehow benefit from urban areas (i.e., synanthropic species—Johnston 2001), or alternatively occur in urban areas despite possible negative effects of human-dominated areas, and thereby require habitat fragments protected from development. Large carnivores tend to disappear from areas dominated by humans, either through direct persecution, competition for resources, or diminution of resources (Cardillo et al. 2004; Woodroffe 2000; but see Linnell et al. 2001). This trend would be expected to be particularly apparent in urban landscapes, where habitat fragmentation is extensive and human presence is the greatest, and conflicts between carnivores and humans would seem to be acute. Indeed, human intolerance or carnivore conflict may prohibit larger carnivore species from becoming synanthropic.

Coyotes (*Canis latrans*) have dramatically expanded their range across North America, in contrast to other, larger Carnivora (Gompper 2002; Laliberte and Ripple 2004), and are now found in an increasing number of cities in the United States and Canada (Gehrt 2004). The emergence of coyotes in urban systems can have important ecological implications (Gehrt and Riley, in press; Gompper 2002), such as through their role as an apex carnivore and subsequent effects on prey or the creation of trophic cascades (Crooks and Soulé 1999). However, the emergence of coyotes in urban landscapes also has increasingly resulted in conflicts with people (Gehrt 2004; Gehrt and Riley, in press). Coyotes have the potential to attack pets and, at times, people (Bounds and Shaw 1994; Carbyn 1989). Thus, the existence of coyotes in proximity to people can create concern among the public and present dilemmas for management agencies. An understanding of how coyotes respond to urban areas, especially landscapes dominated by high levels of human activities, is important for conservation and management efforts.

The appearance of coyotes in urban areas would suggest that they are relatively flexible in their use of the landscape, while maintaining a reliance on natural habitats. However, research to date has provided mixed results as to whether coyotes are a true synanthropic species. Monitoring of track stations has suggested that coyotes may have restrictions in

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their use of natural habitat patches or developed patches within the urban matrix (Crooks 2002; Randa and Yunger 2006). But monitoring track stations provides only limited information regarding use of developed areas, and provides no information on the types of individuals that are likely to occur in different parts of the landscape. Radiotelemetry studies of coyotes in urban areas have produced mixed results, with some studies reporting coyote avoidance of residential areas or other types of development (Quinn 1997; Riley et al. 2003) and others reporting use only at levels of availability (Gibeau 1998; Grinder and Krausman 2001; Way et al. 2004). However, these studies were limited in sample size and conducted near the perimeter of developed areas, in areas with large tracts of rural or undeveloped use. Coyote behavior may differ in areas with limited natural habitat and intense human presence. Additionally, coyote use of the landscape may vary in association with characteristics related to sex, age, social status, or season, any of which may be difficult to identify with small sample sizes.

Herein, we report on coyote use of the landscape within the Chicago metropolitan area, one of the largest urban centers in North America. Although common in the surrounding rural landscape, coyotes were rare in the metropolitan area until the 1990s (Gehrt 2004). An apparent consequence of their success was a dramatic increase in the number of coyotes captured for nuisance control. Before 1990, >20 individuals were typically removed from the area annually, and this increased to >300 annually within 10 years (Gehrt 2004). Given the level of development, size of the human population, and an apparently increasing coyote population, the Chicago area represents an excellent opportunity to investigate how carnivores exploit an urban landscape, and the implications for the humans sharing that space.

We used patterns of home-range size and landscape use within a heavily urbanized landscape to test predictions related to synanthropy in coyotes. Given the close relationship between home-range size and resource quality and distribution for carnivores (Gittleman and Harvey 1982), we predicted relatively smaller home ranges and no avoidance of developed areas if coyotes thrive in urban landscapes. Other species considered to be synanthropic, such as kit foxes (*Vulpes macrotis*), red foxes (*V. vulpes*), and raccoons (*Procyon lotor*), have smaller home ranges in urban landscapes (Cavallini 1996; Cypher, in press; Prange et al. 2004), and some fox species readily use developed parts of the landscape (Cypher, in press; Newman et al. 2003). Likewise, we predicted no relationship between home-range size and the proportion of the home range comprising developed land. However, if coyotes avoid developed areas and concentrate activities in natural habitat patches, we would predict a positive relationship between home-range size and the proportion of development in the home range. For both home-range analyses and patterns of landscape use, we construct a series of tests layered by potentially important covariates to the use of urban landscapes, including season; activity period; and age, sex, and social class of the coyote. We also provide the frequency and characteristics of nuisance coyotes, or those that come into apparent conflict with people. If urban coyotes develop an affinity for developed areas, we predict that a relatively high proportion of coyotes will be removed as nuisances because of human fear of coyotes (Gehrt and Riley, in press). Finally, we discuss the summary of these results with respect to the following question: Do coyotes reside in urban areas because of an attraction to human activities, or in spite of them?

Materials and Methods

Study area.—The Chicago metropolitan area spans all or parts of 6 counties in northeastern Illinois (Cook, DuPage, Kane, Lake, McHenry, and Will), and extends into parts of Wisconsin and Indiana. The 6 counties include >260 municipalities and a cumulative human population exceeding 9 million, making this one of the most heavily urbanized areas in North America. General land cover in 1997 for this area was estimated to be 33% agriculture, 30% urban, 16% natural areas, and 21% unassociated vegetation (Wang and Moskovits 2001). Natural areas (including savannas, woodlands, grasslands, and wetlands) were fragmented, 1st by agriculture in the early 1800s, and more recently through urbanization. The extensive process of urbanization has produced a dynamic landscape in these counties, especially recently. Between 1972 and 1997, urban land increased 49%, natural areas decreased 21%, and agricultural lands decreased 37% (Wang and Moskovits 2001). An important feature of this landscape is the patchwork of habitat fragments protected from development, most of which are county forest preserves (Gehrt and Chelsvig 2003). For example, forest preserves make up 11% of the land area of Cook County, Illinois, providing an important component of the landscape mosaic in addition to the >5 million human inhabitants in that county.

Our fieldwork was largely focused in the northwestern portion of the metropolitan area, including O'Hare International Airport (Fig. 1). The scope of the study area was determined by the cumulative area of locations of radiocollared, resident coyotes, which spanned approximately 1,173 km^2. It is important to note that this study area occurred within the urban matrix, in contrast to previous studies of coyotes conducted at the periphery of urban areas. Our study area had a paved road density of 6.11 km/km^2, with traffic volumes exceeding 100,000 vehicles daily for some roadways (Illinois Department of Transportation, Springfield, Illinois), and was composed of the following land-use types: agriculture (14%), natural habitat (13%), residential (20%), urban land (including commercial–industrial use, 43%), and other (10%).

Live captures.—Because of the constraints associated with working in public areas, our trapping was largely opportunistic. It was necessary to focus our trapping in areas that afforded some seclusion from the public. In most cases these were secure areas within large forest preserves, or private properties. Trapping was conducted opportunistically throughout the year excluding summer months when pups were emerging from dens. Coyotes were livetrapped with padded

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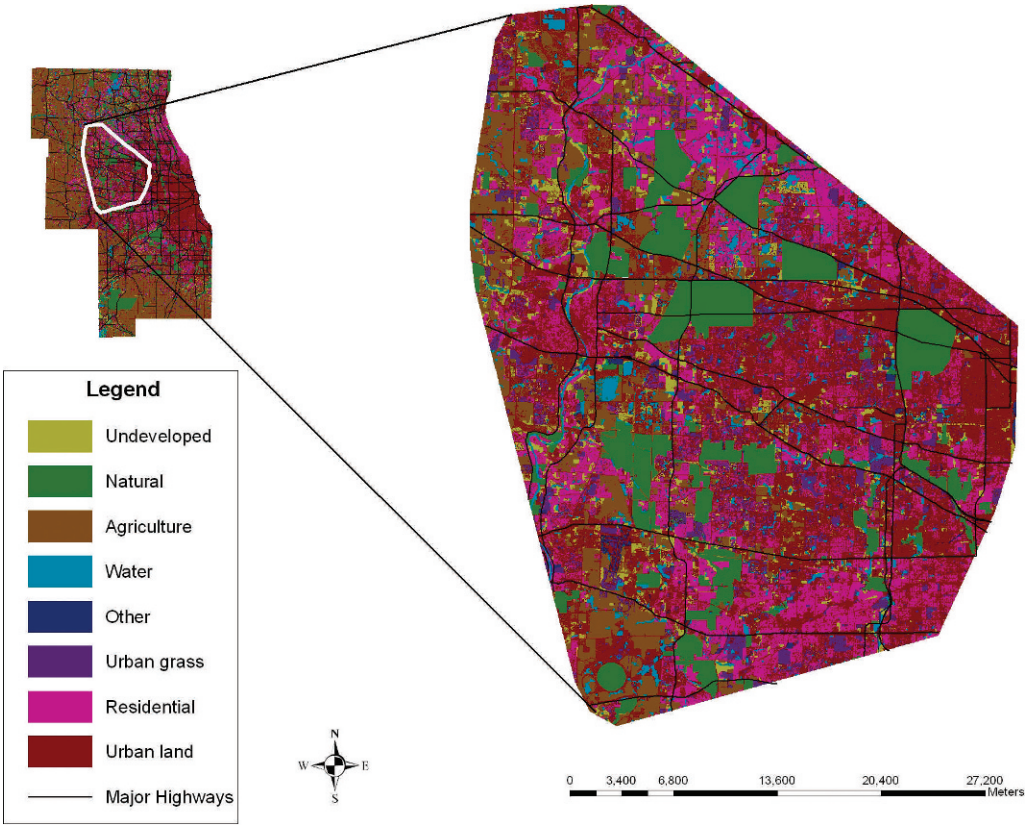


Fig. 1.—Study area and land use within the Chicago, Illinois, metropolitan area.

foothold traps and cable restraint devices. Upon capture of an unmarked individual, the coyote was usually transported to a laboratory area and immobilized with an injection of Telazol (Fort Dodge Animal Health, Fort Dodge, Iowa). Coyotes were removed from the field to avoid people and pets while we were processing animals. Coyotes were marked with uniquely numbered plastic ear tags (NASCO Farm & Ranch, Fort Atkinson, Wisconsin) and fitted with very-high-frequency radiocollars (Advanced Telemetry Systems, Isanti, Minnesota). We weighed each coyote, and determined sex, age (via tooth wear and reproductive condition), and physical condition. Once coyotes had recovered from immobilization, they were released at the capture site. Our trapping and handling protocols were approved by Ohio State University's Institutional Animal Care and Use Committee (IACUC 2003R0061), and followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Radiotelemetry.—We obtained radiolocations for coyotes using triangulation (with program LOCATE II; Pacer, Truro, Nova Scotia, Canada) with a truck-mounted antenna or by visual observations. We located coyotes once during the day, typically 2 or 3 times per week, and at night during tracking shifts in which we focused on a group of coyotes and obtained sequential locations at 60- to 120-min intervals for 5–6 h during the night. Early in the study, we determined that coyotes confined most of their activity to nocturnal hours (Morey 2004), which has been observed by virtually all studies of urban coyotes (Atkinson and Shackleton 1991; Gibeau 1998; Grinder and Krausman 2001; Quinn 1997; Riley et al. 2003; Tigas et al. 2002). Mean ($\pm$ *SD*) error for test transmitters was 108 $\pm$ 87 m via triangulation (Morey 2004). However, many of the coyotes were located within the urban matrix, and because of the extensive road system it was frequently possible to drive within a few meters of coyotes and record their location directly with a global positioning system unit. Coyote locations were recorded to the nearest meter using the Universal Transverse Mercator grid system.

Home-range estimates.—We used the Home Range Extension (Hooge and Eichenlaub 1997) for ArcView 3.2 geographical information system software (Environmental Systems Research Institute, Redlands, California) to plot 95% minimum convex polygon home-range estimates. We found that kernel models produced disjunct home-range boundaries for some coyotes that could not be smoothed without expanding home-range boundaries to an unrealistic size. This was especially true for coyotes with fragmented home ranges in the urban matrix, a situation also encountered by Riley et al. (2003). It was important to have continuous home ranges to correctly estimate areas available for use by coyotes within home ranges, and the minimum convex polygon yielded the most conservative areas without disjunct home-range boundaries.

We calculated annual home ranges for each coyote that had a minimum of 47 radiolocations recorded during an annual period (the minimum number of locations that spanned >1 season within an annual period). However, for transient

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coyotes we used a lower minimum number of ≥30 locations because of the difficulties associated with monitoring coyotes with large home ranges in the metropolitan area, such as locating telemetry signals, and because solitary individuals sometimes dispersed and truncated our time to acquire locations. Area-observation curves were not useful for identifying minimum location numbers because of the fluid nature of home ranges for transients. We classified a coyote as a resident if it used 1 unique area for ≥1 biological season and was observed with another coyote, and a transient if it maintained a home range that overlapped multiple territories of residents or was not observed associating with other coyotes for >1 season (adapted from Gese et al. 1988). Home ranges of residents were exclusive, whereas home ranges of transients overlapped each other and those of residents (Gese et al. 1988; Kamler and Gipson 2000). Coyotes that dispersed from the study area were censored from data analysis.

For seasonal analyses, we partitioned the data into 3 periods that corresponded to biological events: breeding (1 January–30 April), pup-rearing (1 May–31 August), and dispersal (1 September–31 December). We estimated seasonal home ranges using a criterion of ≥30 locations recorded in a season, providing that approximately equal numbers of locations were obtained during daytime and nighttime periods.

Because of high survival and site fidelity, multiple annual home ranges were calculated for some individuals. Thus, we reduced the resident data set to only 1 estimate per coyote by selecting the year with the greatest number of locations or complete monitoring throughout the year. We used 2-way fixed analysis of variance (ANOVA) with an interaction term to assess whether sex or age explained variation in annual home-range size. We subsequently pooled estimates across sex–age groups to compare resident and solitary home ranges with a *t*-test. Similarly, we determined if home-range sizes vary by season among sex–age groups with a 3-way ANOVA with sex, age, and season as main effects with interaction terms. For each of these tests, home-range estimates were log-transformed to conform to normal distributions.

We created a land-use–type coverage with 28.5-m resolution from 1997 Chicago Wilderness/NASA Landsat Thematic Mapper images for use in ArcView geographical information system software (Wang and Moskovits 2001). We reclassified the original 164 Landsat categories into 8 broad land-cover types: Agricultural (usually small fragments of row-crop land use, but may also include small produce such as pumpkin farms or vegetable gardens), Natural (fragments of natural habitat typically protected from development, but often exposed to extensive human use), Other (typically small areas with a mix of developed and undeveloped properties, such as golf courses or cemeteries), Residential (developed areas for human residents), Urban Grass (managed lawns or parks, including corporate campuses, mowed parks, or recreational areas), Urban Land (industrial or commercial development, often including a high degree of impervious surfaces), Undeveloped (usually small fragments not managed for wildlife, and either too small for development or in many cases a buffer between developments, such as easements along major thoroughfares), and Water (impoundments or streams, often retention ponds resulting from development).

We used simple linear regression to determine the relationship between the level of urbanization within a home range and home-range size by determining the composite proportion of Residential, Urban Grass, and Urban Land categories within an annual home range, and regressing this metric with home-range size. To satisfy assumptions of normality, we log-transformed home-range size and used the arcsine-transformed proportion of cumulative urban-associated land use. This analysis was restricted to the annual home ranges of resident coyotes.

Resource use and selection.—We defined coyote use of land-cover types as the observed proportion of locations observed in a land-cover type, whereas selection of land-cover types was defined as differences in observed use compared to expected based on the null model that use would equal availability if no selection occurred. Resource selection can occur at multiple spatial scales (Johnson 1980); however, we focused our analysis on 3rd-order selection (within the home range). We did not assess 2nd-order selection (home range within the study area) for 2 reasons. First, it was necessary to restrict our trapping to areas with sufficient cover to avoid conflicts with the public, which was either in private areas or, more typically, public nature areas. Trapping in the most heavily urbanized portions of the landscape was not possible. Thus, our distribution of radiocollars was necessarily nonrandom among coyotes across the landscape. Second, the territorial social system of coyotes likely prevented coyotes from using some portions of the landscape at the home-range scale, thereby altering our perception of the areas truly available to individuals in ways that we could not measure because we did not have all resident coyotes radiocollared across the study area. However, we provide the composition of home ranges to illustrate the range of use across the landscape exhibited by coyotes and the availability of land-use types within home ranges for 3rd-order selection. Use of landscape types by coyotes was calculated for each animal annually and by season by overlaying telemetry points on geographical information system layers.

We assessed coyote selection of land-cover types using Johnson's (1980) rank method with the program PREFER 5.1 (Northern Prairie Science Center, United States Geological Survey, Jamestown, North Dakota). This approach compares rankings of use versus availability for resource components (Johnson 1980), using the individual as the unit, and tests for a significant deviation from an equal distribution with a multiple comparison procedure (Waller and Duncan 1969). This method also provides a test to identify which habitat components differed in their rankings in the event of a significant *F*-test. However, we were more interested in general patterns of rankings among land-use types, and the direction of their selection scores, rather than specific statistical tests comparing 1 land-cover type to another. More specifically, our attention was focused on land-cover types

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associated with people (Residential, Urban Grass, and Urban Land) and whether their rankings varied with season or sex class. In this paper, we use the term ''selection score'' to refer to T-bar scores in Johnson (1980), which represent the mean use ranking minus the mean availability ranking. In this case, a large negative value would indicate selection for a land-use category, whereas a large positive value results from a type of patch with low use relative to availability and indicates possible avoidance. All analyses required a minimum of 9 individuals, so for some groups (i.e., transients) it was not possible to compare smaller subsets such as age or sex. As with the home-range analysis, we selected the year with the best data set for resident adults monitored in multiple years and excluded the other years for those individuals to reduce the possible effects of nonindependence. However, individuals that changed status (i.e., age or social status) or moved to new locations between years were retained in the analysis despite appearing more than once.

We assessed selection of land-cover types within annual home ranges separately for resident animals and transients. To determine if selection of land-cover types varied by season, we calculated mean selection scores for each year and used a 2-way ANOVA (season and land-use type as main effects) on these ratios with a focus on the interaction term between season and land-cover type. Because of small sample sizes, we did not assess seasonal variation in selection of land-cover types for transients. We used a similar analytical approach to compare land-cover selection by resident males and females, in which selection scores were determined for each year and compared with a 2-way ANOVA (sex and land-cover type as main effects) with a focus on the interaction term.

Because coyotes shift their activity toward nocturnal hours in more urban areas and rest in cover during the day (Gehrt and Riley, in press), it is possible that resource selection may differ between activity periods, especially regarding land-cover types associated with human activities. Therefore, we determined patterns of land-cover selection between activity periods for resident and transient coyotes, with the hypothesis that coyote selection for Residential and Urban Lands may increase during nocturnal hours when human activity declines. Because coyotes with home ranges composed largely of human development may be assumed to be attracted to human-associated land-cover types (given limited habitat patches), we further focused this analysis on coyotes with home ranges with a mix of natural and urban land use, and coyotes with highly urbanized home ranges (>50% combination of Residential and Urban Land types). Resident coyotes with home ranges located largely within natural fragments were censored from this analysis.

Conservation efforts are often focused on minimum levels of natural habitat required to maintain home ranges in urban landscapes. Therefore, we report the size of home ranges relative to the cumulative composition of natural habitat within the home range. We report the smallest fragment of natural habitat in which a coyote associated with a pack maintained a territory for at least a full year. Likewise, we report the cumulative proportion of natural habitat within annual home ranges with a particular focus on the minimal amount used by resident coyotes.

Table 1.—Annual home-range estimates (km^2) for radiocollared coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area during 2000–2006, estimated with 95% minimum convex polygon. Home-range estimates are partitioned by age–sex class within social categories, except that males and females are pooled in the juvenile class.

Category	Age–sex group	*n*	$\bar{X}$	*SE*
Resident	Adult female	22	4.80	0.66
	Subadult female	11	5.17	0.98
	Adult male	29	5.46	0.58
	Subadult male	22	4.32	0.68
	Juvenile	24	2.53	3.08
Transient	Adult female	9	18.92	4.82
	Subadult female	14	34.67	5.91
	Adult male	15	23.70	3.92
	Subadult male	2	30.47	18.64

Nuisance coyotes.—We identified marked coyotes as nuisances if >1 human resident registered complaints (typically phone calls to an animal control agency) concerning an individual animal, or if the complaint of an individual resident resulted in control action against a coyote. In essence, the public identified a nuisance coyote rather than us. Unfortunately, our sample size of nuisance coyotes was not sufficient for analyses of resource selection.

Results

We captured and radiocollared 181 coyotes (including 17 adult females, 41 subadult females, 28 female pups, 28 adult males, 40 subadult males, and 27 male pups). We recorded 25,509 locations, yielding sufficient numbers of locations to estimate 182 annual home ranges, including multiple estimates for some individuals. We initially estimated 118 annual home ranges for residents and 40 home ranges for solitary transients. Because some individuals were monitored for multiple years, we reduced the number of home ranges to 84 residents (22 adult females, 11 subadult females, 29 adult males, and 22 subadult males). Individual coyotes appear in the analyses more than once if they graduated from one age group to another, or if they shifted from transient to resident or vice versa. Twenty-four annual home ranges were calculated for pups, which are presented for reference but are not included in analyses because we assumed they were still associated with adults.

Home-range size.—Annual home-range estimates for resident coyotes (Table 1) were similar by sex ($F = 0.03$, *d.f.* = 1, 80, $P = 0.86$) and age ($F = 0.61$, *d.f.* = 1, 80, $P = 0.44$) classes with no interaction ($F = 0.89$, *d.f.* = 1, 80, $P = 0.35$). Similarly, differences in annual home-range estimates for transient coyotes among sex and age classes were not significant (all $P > 0.12$; Table 1). However, mean ($\pm$ *SE*) annual home ranges of transient coyotes ($\bar{X} = 26.80 \pm 2.95$ km^2) were larger ($t = 12.6$, *d.f.* = 122, $P < 0.001$) than

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Table 2.—Seasonal home-range estimates (km^2) for resident, radiocollared coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area, 2000–2006. Home ranges were estimated with 95% minimum convex polygon.

Season	Age	Sex	*n*	$\bar{X}$	*SE*
Breeding	Adult	Female	22	4.40	0.44
		Male	31	3.89	0.39
	Subadult	Female	4	2.72	0.94
		Male	10	3.79	0.74
Pup-rearing	Adult	Female	27	4.17	0.60
		Male	36	4.00	0.39
	Subadult	Female	7	5.70	2.01
		Male	12	2.80	0.58
Dispersal	Adult	Female	20	4.47	0.54
		Male	27	4.73	0.40
	Subadult	Female	5	6.04	1.43
		Male	10	3.00	0.50

those of resident coyotes ($\bar{X} = 4.95 \pm 0.34$ km^2), with home ranges of transients ranging up to 98 km^2. Home-range size for resident coyotes did not vary among seasons ($F = 1.02$, *d.f.* = 2, 210, $P = 0.36$), or between age ($F = 2.63$, *d.f.* = 2, 210, $P = 0.11$) and sex ($F = 2.17$, *d.f.* = 2, 210, $P = 0.14$) classes (Table 2).

Home-range composition and land use.—Home ranges of resident coyotes were typically associated with natural habitats, and in many cases these were home ranges that were almost completely encompassed within large habitat fragments (Fig. 2). In these cases, boundaries of coyote home ranges followed the borders between parks and surrounding development. However, some coyote home ranges varied considerably in the composition of natural habitat, with concomitant variability in the composition of Urban Land and Residential land use (Fig. 3). Unlike home ranges of residents, home ranges of transients were not composed exclusively within natural fragments, although Natural land cover still dominated the other land-cover categories (Fig. 3).

Home-range size of residents was positively ($r = 0.38$, $n = 84$, $P < 0.001$) related to the amount of human-related development within the home range (Fig. 4). However, home-range size also varied substantially among coyotes with home ranges composed almost exclusively of Natural or Undeveloped areas. Thirty-seven annual home ranges were located nearly exclusively (>95%) within single fragments of Natural land use, and ranged in size from 0.92 km^2 to 11.1 km^2. The smallest contiguous Natural fragment to exclusively occupied a coyote pack was 247 ha. Larger fragments of Natural habitat typically had multiple pack territories within them.

In contrast to those home ranges associated with Natural land-use patches, there also were 24 annual home ranges of residents that were composed of little (<10%) Natural land use. Eight percent of annual home ranges had no (0%) measurable patches of Natural land use within them.

Third-order selection.—Resident and transient coyotes showed similar patterns of land use within annual home ranges (Fig. 5), with both classes of coyotes using Natural areas heavily. Similarly, selection of land-use types within home ranges was nearly identical between coyote classes (Fig. 5). In both cases, coyotes selected Undeveloped and Other categories most (the 2 highest-ranked categories), and avoided Urban Grass, Residential, and Urban Land as the lowest-ranked categories (residents: $F = 10.49$, *d.f.* = 7, 89, $P < 0.001$; transients: $F = 8.18$, *d.f.* = 7, 19, $P < 0.001$). Coyotes avoided urbanized areas either by restricting their movements to boundaries of Natural habitat fragments or by focusing their activities within series of smaller patches of undeveloped areas within home ranges (Fig. 6).

Selection by season.—Resident coyotes also exhibited selection of land-use types within seasonal home ranges (all $P < 0.001$), and there was no difference in the pattern of selection among seasons (2-way ANOVA interaction term season × land-use: $F = 1.21$, *d.f.* = 14, 96, $P = 0.28$). Undeveloped, Other, and Water were the most-selected categories in each season, and the 3 land-use categories associated with humans, Urban Grass, Urban Land, and Residential, were avoided (Table 3).

Selection by sex.—Male ($n = 56$) and female ($n = 40$) residents exhibited selection of land-use types within annual home ranges (males: $F = 5.68$, *d.f.* = 7, 50, $P < 0.0001$; females: $F = 6.37$, *d.f.* = 7, 33, $P < 0.0001$), and their patterns of selection were similar across years (2-way ANOVA interaction term sex × land-use class: $F = 0.36$, *d.f.* = 7, 63, $P = 0.92$). In both cases, Undeveloped and Other were the highest-ranked categories (used greater than expected), and Residential, Urban Grass, and Urban Land were the 3 lowest-ranked categories, in each case with selection scores indicating avoidance.

Selection by activity period.—Rankings of land-use selection by coyotes remained generally consistent between diurnal and nocturnal periods (Fig. 7). Transient coyotes ($n = 14$) selectively used land-use categories during both periods (diurnal: $F = 6.12$, *d.f.* = 7, 7, $P = 0.014$; nocturnal: $F = 4.51$, *d.f.* = 7, 7, $P = 0.032$). For both activity periods, the 3 top-ranked land-use types were Water, Undeveloped, and Other. These were relatively strongly selected for during the diurnal periods, with Water the most selected (Fig. 7). For both periods, Residential was strongly avoided, along with Urban Grass during diurnal periods, and Urban Land during nocturnal periods.

We partitioned resident coyotes into those with home ranges composed of >50% urban matrix (urban home ranges) and those with highly urbanized home ranges (high-urban home ranges). Coyotes with urban home ranges ($n = 41$) had significant selection during diurnal ($F = 7.64$, *d.f.* = 7, 34, $P < 0.001$) and nocturnal ($F = 14.12$, *d.f.* = 7, 34, $P < 0.001$) periods, and the ranking order was identical for both periods. Undeveloped, Other, and Water were the 3 top-ranked categories, in each case reflecting positive selection, and Urban Grass, Residential, and Urban Land the lowest-ranked categories, in each case indicating avoidance (Fig. 7).

Coyotes with high-urban home ranges ($n = 9$) did not exhibit significant selection by activity period (diurnal: $F = 7.86$, *d.f.* = 7, 2, $P = 0.12$; nocturnal: $F = 3.83$, *d.f.* = 7, 2, P

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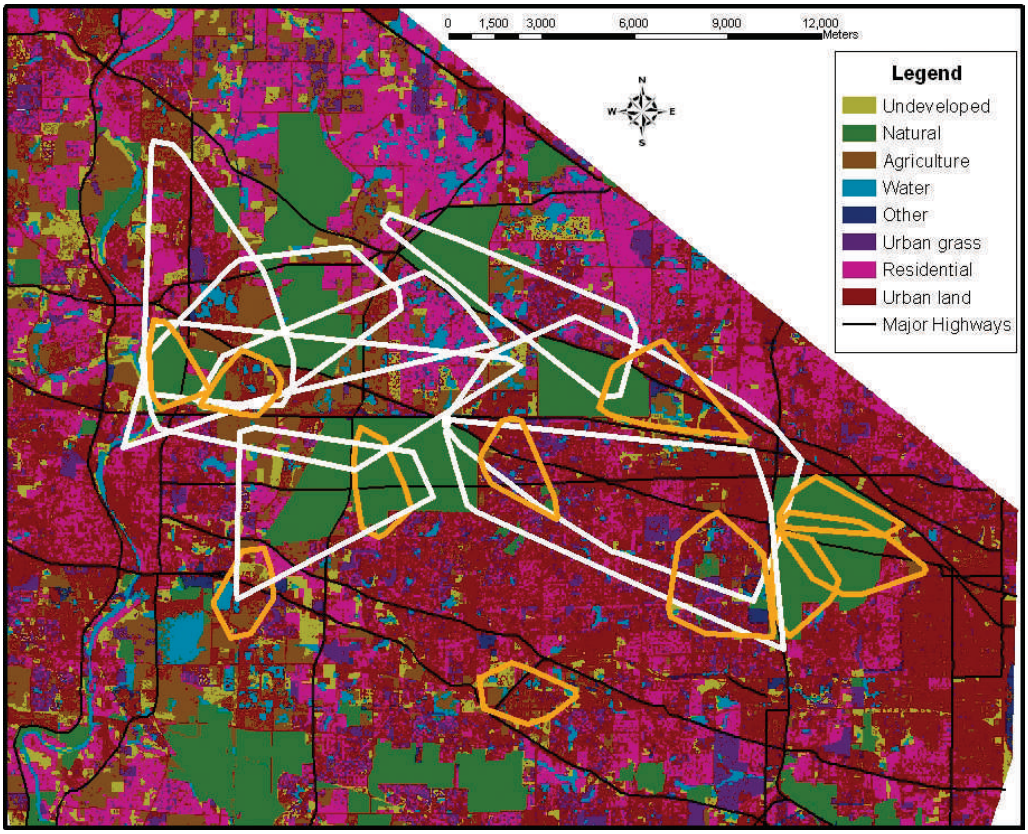


Fig. 2.—Distribution of annual home ranges of resident (yellow lines) and transient (white lines) coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area during 2004.

= 0.22). However, the lack of significance may be the result of small sample size, because there were relatively strong selection scores, with Undeveloped and Water as the 2 top-ranked categories in both periods and Urban Grass, Residential, and Urban Land the lowest-ranked categories for both periods (Fig. 7).

Nuisance coyotes.—We identified 7 radiocollared coyotes that generated complaints from the public or were killed during control efforts (Table 4), which comprised 4% of the radiocollared sample. Nuisance coyotes were represented by a range of sex–age classes. Four coyotes had dispersed from their original territories, with 1 becoming a resident and the rest transients at the time of removal. Overall, 3 coyotes were residents and 4 were transients at the time of conflict (Table 4). Two coyotes (adult males 2 and 3) were nuisances immediately upon being radiocollared. Only coyote 3 was known to possibly attack domestic animals and also was the only suspected alpha male as a nuisance (based on visual observations with a reproductive female); coyote 3 was in good health, rested during the day in a large patch of natural habitat, and moved into developed areas at night. Four coyotes were in poor health at the time of conflicts, including 3 afflicted with mange (they were not known to create a conflict before mange infections). In all cases they were observed near houses during the day, which they apparently used for food or shelter (2 were known to attempt to use dens under decks). One of these (coyote 76) was monitored for nearly 4 years without incident, until she developed a severe mange infection. Two coyotes in good health at the time of conflict were an adult (coyote 78) that was shot while located near runways at O'Hare International Airport and a juvenile (coyote 154) that was increasing his use of developed areas in response to feeding by people before a collision with a vehicle (other members of the pack continued to avoid developed areas).

Discussion

Home-range size can be an important indicator of resource distribution and abundance (Gittleman and Harvey 1982), and also may correlate with population density. Thus, comparisons of home-range size between urban and rural landscapes can provide important insights into the ecology of carnivores in urban areas. At the landscape level, small home ranges can be an indicator of high population densities (Andelt 1985; Fedriani et al. 2001) in either urban or rural areas.

Are urban home ranges smaller than rural home ranges?—Our estimates of annual and seasonal home-range sizes for resident coyotes are smaller than winter (median 27.0 km^2) or summer (median 16.8 km^2) home ranges reported for residents in the agriculturally dominated landscape of rural Illinois (Gosselink et al. 2003). Similarly, Atwood et al. (2004) observed smaller home ranges for coyotes in suburban areas. Likewise, there is a trend for home ranges of red foxes, a

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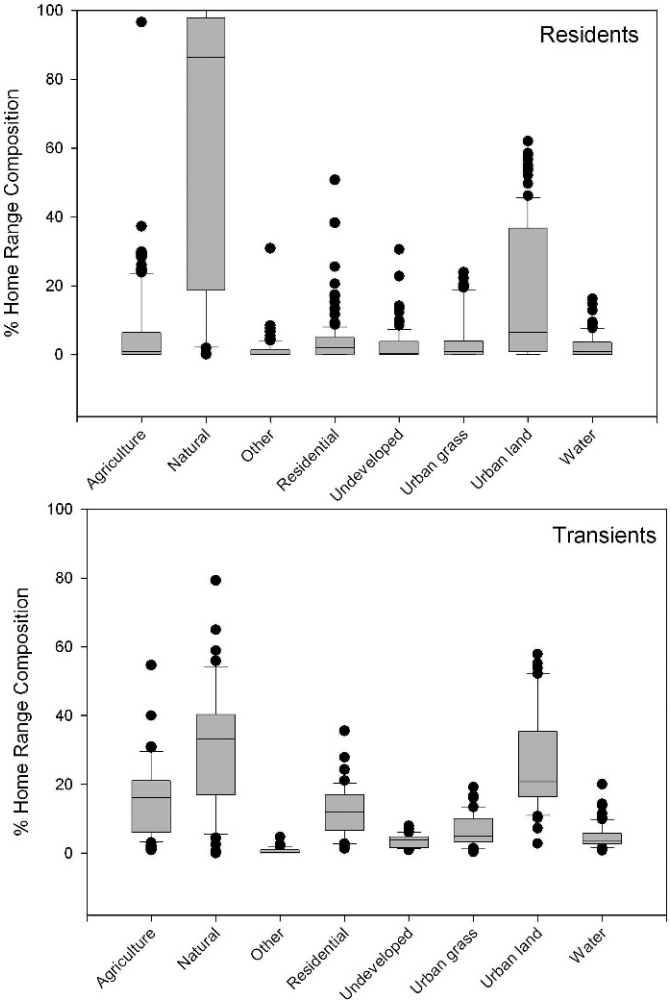


Fig. 3.—Box plots of composition of annual home ranges by land-use category for resident and transient coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area, 2000–2006. Horizontal lines represents the mean, the box represents the standard deviation, 95% confidence intervals, and points outside confidence intervals.

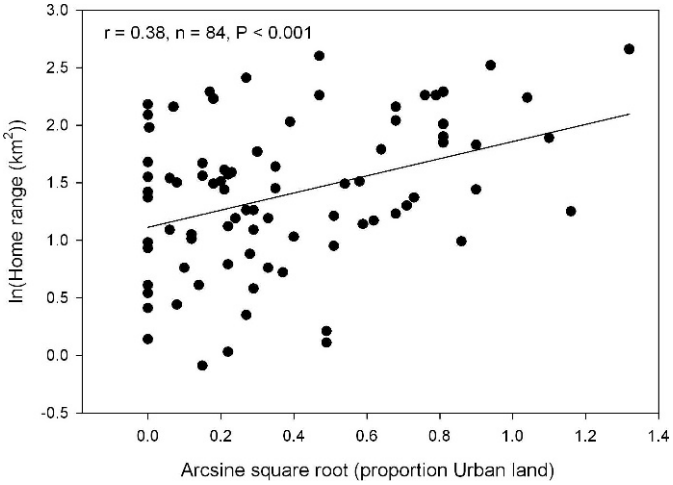


Fig. 4.—Relationship between annual home-range size (95% minimum convex polygon) and proportion of the home range composed of urban land use (combined Residential, Urban Grass, and Urban Land) for radiocollared coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area.

synanthropic species, to decrease with urbanization (Cavillini 1996; Goszczyński 2002).

Although comparisons across studies suggest a general trend for smaller home ranges to occur in urban landscapes, at the local scale habitat fragmentation resulting from urbanization may cause coyotes to increase home-range size to meet daily needs (Riley et al. 2003). The positive relationship between urban land use and home-range size in our study is consistent with this argument, but contradicts previous studies. Within the Los Angeles, California, area, Tigas et al. (2002) did not observe an increase in home-range size with increased urban fragmentation, but their study had a small sample size, and Riley et al. (2003) found a positive, but nonsignificant, relationship between home-range size and urban development from the same area.

Although we documented a positive relationship between urban composition in the home range and home-range size, we also documented considerable variation in home-range size regardless of the composition of home ranges. Likewise, coyotes in Tucson, Arizona (Grinder and Krausman 2001), and urban red foxes in Great Britain (Doncaster and Macdonald 1991; Soulsbury et al. 2007) also exhibit considerable variation in home-range size. It appeared that the size and shape of resident home ranges in our Chicago-area study were simultaneously affected by the juxtaposition of resources, fragmentation, and human activities. For example, the home-range boundaries of many resident coyotes conformed to the boundaries of natural areas, probably reflecting the dramatic small-scale gradients typical of urbanization. However, other resident coyotes maintained home ranges that spanned such gradients, and individual variation among coyotes in response to development and human activities was apparent.

The upper range of home-range sizes of transients in our study was similar to that from urban and rural studies, although our mean size was relatively smaller than those reported for other areas (Cape Cod, Massachusetts—115 km^2 [Way et al. 2002], and Tucson—105 km^2 [Grinder and Krausman 2001]). Our relatively smaller mean may reflect the considerable individual variation in the way coyotes leave territories and their movements across the heavily developed landscape in our study area. Also, our long-term monitoring of individuals allowed us to identify when individuals separated from their original territories and entered a transient phase, regardless of the size of the area of their movements. In any event, it is clear transients are capable of maintaining large home ranges in highly urbanized landscapes.

Does home-range size vary with sex, age, or season?—Our findings that home ranges were similar in size among different sex and age groups and seasons are generally consistent with previous studies. Urban and rural studies of coyotes have been mixed when assessing sex differences in home-range size (see Bekoff and Gese 2003; Laundrè and Keller 1984). For example, in the same Los Angeles study, Tigas et al. (2002)

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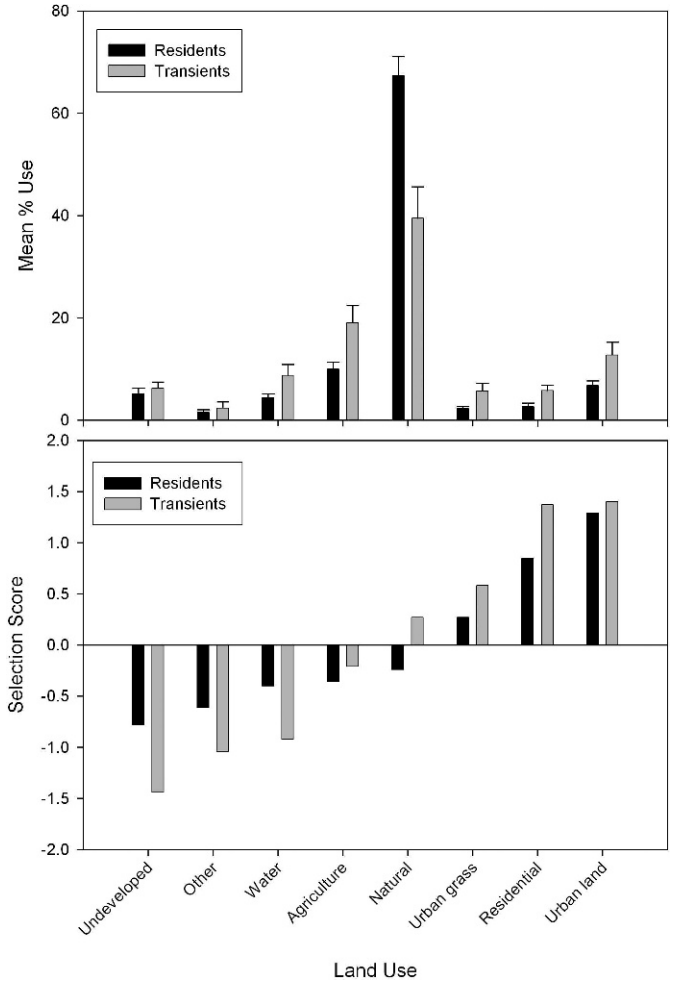


FIG. 5.—Use and selection of land-use types by radiocollared coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area, 2000–2006. Selection score represents mean difference in ranks between use and availability within the home range (Johnson's [1980] T-bar), with negative scores representing selection for, and positive selection scores representing avoidance.

reported females with larger home ranges than males, whereas Riley et al. (2003) found that home ranges of males were larger than those of females. As in our study, home-range size was similar between sexes for coyotes in Tucson (Grinder and Krausman 2001).

Few studies of urban coyotes have assessed seasonal variation in home-range size, but coyotes in Tucson also exhibited consistency in home-range size across seasons (Grinder and Krausman 2001). Some studies from rural areas have reported seasonal differences (Bekoff 1982; Gese et al. 1988), including in Illinois (Gosselink et al. 2003), whereas others have not (Andelt 1985).

Are coyotes attracted to human-associated areas?—We found no evidence that resident or transient coyotes, in general, were attracted to human-associated areas within home ranges, regardless of age, sex, season, or activity period, despite considerable individual variation in home-range compositions. Developed land-use types were consistently the lowest-ranked habitats and selection scores indicated avoidance. Even coyotes with home ranges primarily composed of developed areas maintained a consistent avoidance of areas associated with humans. Previous studies of urban coyotes have either documented use of residential areas in proportion to availability (Gibeau 1998; Grinder and Krausman 2001; Way et al. 2004), or avoidance of residential or other developed land-use types (Bogan 2004; Quinn 1997).

Foxes in urban areas have been observed to restrict their use of residential areas to nocturnal hours (Harrison 1997; Saunders et al. 1997), and some have suggested that coyotes do the same (Quinn 1997). In contrast, we did not observe a temporal shift in selection of developed areas in our study, even for coyotes with highly urbanized home ranges. However, avoidance does not imply that coyotes did not use developed areas. We were able to visually observe resident and transient coyotes with highly urbanized home ranges passing through residential and commercial areas at night to reach isolated habitat patches with no natural corridors, but they did so quickly and these movements did not result in high levels of use in our monitoring data. Indeed, it is likely these coyotes would be removed by control efforts if they did not move quickly and covertly through these areas during the night. In contrast to most coyotes, 1 of the nuisance coyotes in our study resided in an urban natural area during the day and foraged in an adjacent residential area at night.

What kinds of land cover are selected by coyotes?—We did not assess 2nd-order selection in our study, but it was notable that many coyote home ranges largely comprised protected areas in the form of Natural land use or areas protected from development, which also was typical of coyotes in other urban areas (Grinder and Krausman 2001; Riley et al. 2003). However, as with coyotes in Tucson (Grinder and Krausman 2001), there was considerable variation in home-range composition among coyotes, ranging from home ranges that were composed exclusively of single large patches of Natural land use to home ranges that did not include any patches of Natural land use.

Although Natural land cover was consistently in the middle of selection rankings with use by coyotes near that of availability, this was undoubtedly affected by apparent 2nd-order selection by coyotes that resulted in many home ranges with large proportions of this land-use type. The importance of natural habitat patches was reflected by the high level of use exhibited by most coyotes and diets dominated by food items associated with natural areas (Morey et al. 2007). Although natural patches appear to serve as cover and provide food items for coyotes, it is important to note that the vast majority of properties associated with natural habitats in our study area were public, with resulting heavy use by humans. For example, the Ned Brown Forest Preserve in our study area is typical of most Cook County forest preserves, in which the approximately 15-km^2 area receives between 1 and 3 million human visitors annually (Gehrt 2004), and is used for multiple purposes including hiking, biking, picnicking, and as exercise areas for pets. Thus, natural areas that might represent refuge from people in other systems provide only limited respite from

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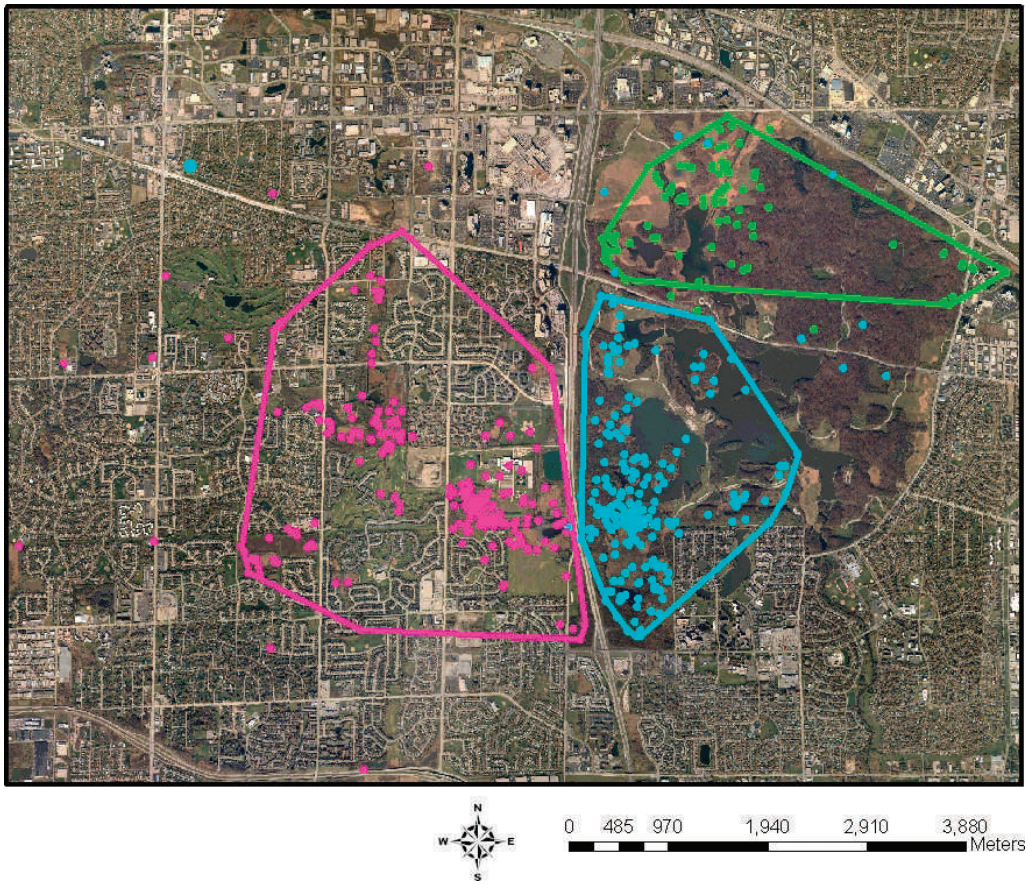


Fig. 6.—Variability of landscape use among urban coyotes (*Canis latrans*), as illustrated by patterns of use within annual home-range boundaries for 3 resident coyotes during 2004 in the Chicago, Illinois, metropolitan area. Each color represents the locations and 95% minimum convex polygon of a resident coyote from 3 territories. Each coyote exhibits avoidance of developed areas, despite considerable differences in territory composition.

people in the Chicago metropolitan area. Indeed, it could be argued that some of the public natural areas have human activity on as high a level as traditional developed areas, especially during warmer months. Coyotes in these areas are still exposed to people and pets, and vice versa, on a consistent basis, but nevertheless have more escape cover than in developed areas. Even within large urban natural parks, coyotes typically avoid areas or trails with high human activity (George and Crooks 2006).

Table 3.—Seasonal land-use selection within home ranges by radiocollared coyotes (*Canis latrans*) in the Chicago, Illinois, metropolitan area (2000–2006). Land-use categories are ranked in order of selection, with 1 representing the most-used category relative to availability, and 8 the least-used relative to availability. Selection scores represent the mean difference in ranks between use and availability among land-use types (Johnson 1980). A negative selection score reflects preferred categories, whereas positive values reflect avoidance.

	Breeding		Pup-rearing		Dispersal	
Land use	Ranking	Score	Ranking	Score	Ranking	Score
Undeveloped	1	−1.07	1	−1.00	1	−1.11
Other	2	−0.94	2	−0.99	2	−1.10
Water	3	−0.50	3	−0.64	3	−0.44
Agriculture	4	−0.19	4	−0.44	4	−0.40
Natural	5	−0.14	5	−0.13	5	−0.17
Urban Grass	6	0.50	6	0.50	7	0.32
Residential	7	0.83	7	0.81	6	0.16
Urban Land	8	1.51	8	1.89	8	1.85

The land-cover types with consistently high selection rankings and significant selection scores within home ranges were Open, Undeveloped, and Water. Undeveloped, in particular, was used for cover and foraging habitat, and was particularly important for those coyotes with little or no natural habitat in their home ranges. This land-cover type is most easily characterized as small patches that are typically too small to develop into buildings, and often serve as buffers between developments or roads. Open areas also serve multiple purposes for coyotes, especially when golf courses or cemeteries maintain small patches of habitat that provide cover. The Water category was most typically represented by small water-retention ponds near developments. When coyotes used these types of areas, they usually had emergent vegetation such as cattails, rushes, or *Phragmites* that provided cover for coyotes, especially during the day. We also observed coyotes frequently using these areas during winter, possibly for insulation from wind and low ambient temperatures. Unfortunately, we are unsure as to their value for prey species.

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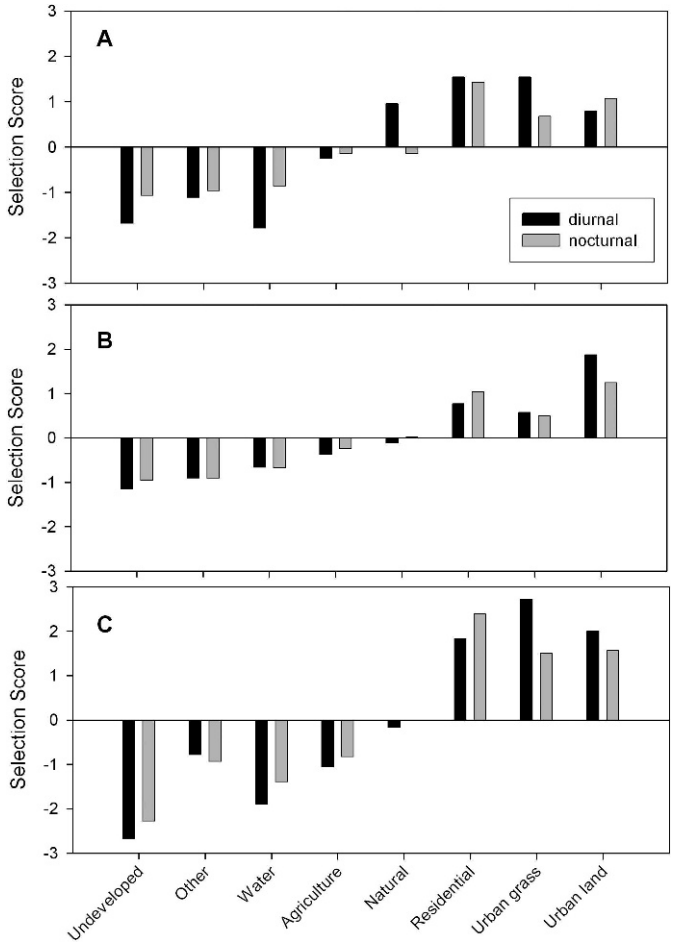


FIG. 7.—Selection of land-use classes within home ranges by coyotes (*Canis latrans*) during diurnal and nocturnal hours: A) transients ($n = 14$), B) residents with mixed land-use types ($n = 41$), and C) residents with highly urbanized home ranges ($n = 9$). Selection scores represent differences between mean rankings of use and availability (Johnson 1980). Negative scores indicate a higher use ranking than available ranking for a land-use type, and vice versa for positive scores. Coyotes were monitored during 2000–2006 in the Chicago, Illinois, metropolitan area.

However, we frequently observed coyotes hunting small mammals in Undeveloped patches, especially easements along major roadways.

The patterns of landscape use and selection we observed for radiocollared coyotes were consistent with diet studies in our study area, in that food items associated with natural areas, rather than anthropogenic foods, dominated the diet across the landscape (Morey et al. 2007). Further, coyotes did not use developed habitat associated with human food within large natural fragments. The high levels of human use within the natural areas in our study area typically resulted in readily available refuse near garbage cans and dumpsters, which were used heavily by raccoons (Bozek et al. 2007; Prange et al. 2004). Yet, coyotes residing in these areas did not exhibit an attraction to these areas within their territories (Gehrt 2004) and consequently human-related foods rarely occurred in their diets (Morey et al. 2007). Thus, the relatively heavy use of natural areas by coyotes was not a result of the availability of rich clumps of anthropogenic foods that occur in those areas.

Given that some studies using track stations have indicated that coyotes have a threshold of fragmentation beyond which they are absent (Crooks 2002; Randa and Yunger 2006), we were surprised to observe coyotes maintaining home ranges in areas with limited or no natural habitat. In each case these were stable home ranges that were maintained for 1 or more years, and in each case these were apparently associated with packs because other coyotes were observed with radiocollared individuals. Some of these packs were located in downtown or industrial areas, including some of the most heavily developed portions of our study area, in addition to occasional transients. It is important to note that we were unable to trap for coyotes in completely urbanized areas, and could only document that use once radiocollared coyotes moved into those areas. However, we frequently observed unmarked coyotes traveling with radiocollared individuals and litter-rearing in these areas. Indeed, we were aware of coyotes residing in portions of the inner core of the city of Chicago. To some degree our results contradict predictions, derived from track stations, that coyotes in the Chicago area will decline in occurrence as urbanization continues to convert rural lands to urban development (Randa and Yunger 2006). Attempts to determine coyote presence with track stations and artificial substrates may underestimate the presence of coyotes (Harris and Knowlton 2001).

Nuisance coyotes.—We are unaware of previous descriptions of the frequency and characteristics of nuisance coyotes in an urban area. Coyotes of various sex and age classes became nuisances, and in nearly all cases either disease or feeding by residents was involved. The relatively low

TABLE 4.—Characteristics of nuisance coyotes (*Canis latrans*) in the Chicago, Illinois, region, 2000–2006. Monitoring period refers to the length of time between initial capture and last location or terminal capture. Status includes individuals that dispersed from group territories and were subsequently transients (Disp. Tran.) or residents (Disp. Res.) at the time of capture.

Coyote no.	Sex	Age	Monitoring period	Status	Condition	Fate
2	Male	Adult	25 March 2000–24 April 2001	Transient	Fair–poor	Disappeared
3	Male	Adult	30 March 2000–31 May 2000	Resident	Good	Road-killed
76	Female	Adult	25 October 2002–8 October 2006	Disp. Res.	Poor, mange	Euthanized
78	Male	Adult	30 October 2002–10 January 2005	Disp. Tran.	Good	Shot at airport
93	Female	Adult	3 April 2003–16 January 2004	Disp. Tran.	Poor, mange	Euthanized
154	Male	Pup	12 August 2004–20 October 2004	Resident	Good	Road-killed
156	Male	Pup	24 August 2004–28 December 2004	Disp. Tran.	Poor, mange	Shot by homeowner

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proportion of radiocollared coyotes that subsequently became nuisances is consistent with the general pattern of avoidance of human-related areas. Indeed, if those with health issues and encroaching on airports are excluded, the proportion of radiomarked coyotes that became nuisances was low (2 of 181) during our study. Only 1 of the nuisance coyotes, a presumed alpha male, was reported attacking and killing domestic animals.

Conclusion.—Our results can be summarized into 3 primary observations. First, in a landscape dominated by human development, natural habitat was used heavily by coyotes. Second, despite the importance of natural habitat for coyotes, some individuals are capable of maintaining territories in portions of the landscape with minimal or no natural areas and elevated human activity. Third, coyotes consistently demonstrated avoidance of areas associated with humans, regardless of their sex, social status (resident or transient), the activity period, or the amount of urban development within their home ranges. Our interpretation of coyotes avoiding human-related areas also is supported by a shift in activity to nocturnal periods and a lack of human-related foods in the diet.

It was clear that coyotes were using a variety of strategies to exploit the landscape while avoiding people, with some limiting their use exclusively to natural patches, and others with a mixture of land-use types. However, coyotes were consistent in apparently avoiding human activities despite home ranges located in areas with nearly complete development, which created a paradox of use and avoidance of developed land-use types. Future research should further explore the limitations of urban landscapes for coyotes, including the influence on survival and reproductive rates in different parts of the urban landscape, but our results demonstrate that coyotes represent a medium-to-large carnivore capable of exploiting areas of intense development while largely managing to avoid people and conflicts.

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