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Is the Urban Coyote a Misanthropic Synanthrope? The Case from Chicago

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Coyotes appear to be one of the few mammalian carnivores that occur in urban areas, although their true relationship with urbanization remains poorly understood. We summarize results from a long-term study of the urban ecology of coyotes in the Chicago metropolitan area to determine the degree of synanthropy for this species and discuss the subsequent management implications for human-coyote conflicts. Local population densities were slightly higher, and survival rates for pups were five times higher compared to rural populations. In contrast to demographic patterns, behavioral responses to urbanization, including home range size, avoidance of developed land cover, activity budget, and diet, were not consistent with synanthropy, even for coyotes located in the urban matrix. We discuss the management implications of the paradoxical relationship coyotes have with people and cities.

Keywords
Canis latrans, Chicago, coyote, density, diet, home range, Illinois, survival, synanthrope

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INTRODUCTION

Wildlife species vary in their responses to urban areas, with some avoiding urbanization while others are synanthropic (Johnston 2001; Withey and Marzluff 2008), in that they appear to thrive in urbanized landscapes. As a group, the Carnivora have been largely persecuted by humans, either for perceived or real conflicts, so it is not surprising that only 14% of terrestrial Carnivora species are associated with urban areas (Iossa et al. 2010). Further, given their unique requirements as top predators, large members of this group seem to have a strong negative association with human densities and metropolitan areas (Woodroffe 2000; Iossa et al. 2010), while some smaller species appear to benefit from life in cities (Prange et al. 2003; Gehrt 2004). However, more information is needed on the urban ecology of many species of this group to better understand the variability in their responses to urbanization and subsequent conservation and management implications.

Synanthropy may be manifested through demographic or behavioral processes (Table 1). In general, one would expect a synanthropic species to exhibit enhancement of one or more demographic characteristics, such as density, reproduction, or survival. For example, survival of kit foxes (*Vulpes macrotis*) may be elevated in urban landscapes (Cypher 2010), and populations of raccoons in urban parks may reach much higher densities than occur in rural settings (Riley et al. 1998; Gehrt 2003; Prange et al. 2003). Behavioral patterns may include selection for parts of the landscape associated with human activities (e.g., residential, commercial areas), or more specifically utilization of anthropogenic resources related to denning or food (e.g., raccoons [*Procyon lotor*] Prange et al. 2004; red foxes [*Vulpes vulpes*] Baker and Harris 2008; Soulsbury et al. 2010). Species may be attracted to human activity, especially if it is associated with food. Conversely, a species that exhibits spatial or temporal avoidance of humans or their activities, or whose survival or reproduction is negatively associated with urbanization, could be characterized as a misanthrope (Table 1).

The coyote (*Canis latrans*) has recently emerged as a resident in many metropolitan areas following a remarkable range expansion across much of North America (Laliberte and Ripple 2004) . It is an interesting species within the carnivore guild because it is often the largest member present in such systems and functions as a top predator (Crooks and Soule 1999), is capable of killing domestic animals and people (Howell 1982; White and Gehrt 2009), and its presence often elicits strong reactions from the public (Miller et al. 2001). The recent appearance of the coyote in urban systems begs the question: should it be considered a synanthrope, in which it thrives in urban landscapes, or a misanthrope, in which it is actually negatively affected by urbanization? Research to date has provided mixed results as to whether coyotes are a true synanthropic species. For example, some studies have suggested that coyotes respond negatively to the urban landscape (Crooks 2002; Randa and Yunger 2006), whereas others have reported a variety of responses to developed areas (Quinn 1997a; Gibeau 1998; Grinder and Krausman 2001; Riley et al. 2003; Way et al. 2004; Gehrt et al. 2009). However, these studies have varied in methods, sample size, and location of the study with respect to the larger metropolitan area (Gehrt and Riley 2010).

Table 1. Predictions for selected demographic and behavioral responses to urbanization for mammalian wildlife species.

	Predictions	
Characteristics	**Synanthrope**	Misanthrope
Demography		
Density	High	Low
Reproduction	High	Low
Survival	High	Low
Behavior		
Home range size	Small	Large
Landscape use	Attracted to human use areas	Avoid human use areas
Activity Patterns	Positive or neutral response to human activity levels	Avoid peak human activity levels
Diet	Dominated by anthropogenic foods	Dominated by 'natural' foods
Potential for human conflicts	High	Low

This question of whether the urban coyote is a synanthrope or a misanthrope has important practical implications. The probability for conflict, and associated management strategies, can be properly evaluated once we have a better understanding of the urban ecology of coyotes, much like an understanding of the ecology of coyotes has aided management of livestock predation (Knowlton et al. 1999; Blejwas et al. 2002).

For the past decade, we have been monitoring the coyote population in the Chicago metropolitan area to provide a better understanding of how coyotes respond to urbanization and relationships to people and other wildlife in urban systems. Although our study is still on-going, we synthesize our results during the period 2000-2006, and additional monitoring from 2007, as they relate to this basic question of how do coyotes respond to urban systems? We focus on population densities, survival, home range size, landscape use and selection, activity patterns, and diet. In some cases we revisit published results, in other cases we report unique findings. We also compare our results to published parameters from previous studies conducted in rural landscapes, given that no portion of our study area could be classified as rural. Our overall objective is to present an urban portrait of this species and eventually demonstrate the relevance of urban ecological characteristics to management and the mitigation of conflict between urban coyotes and humans.

METHODS AND MATERIALS

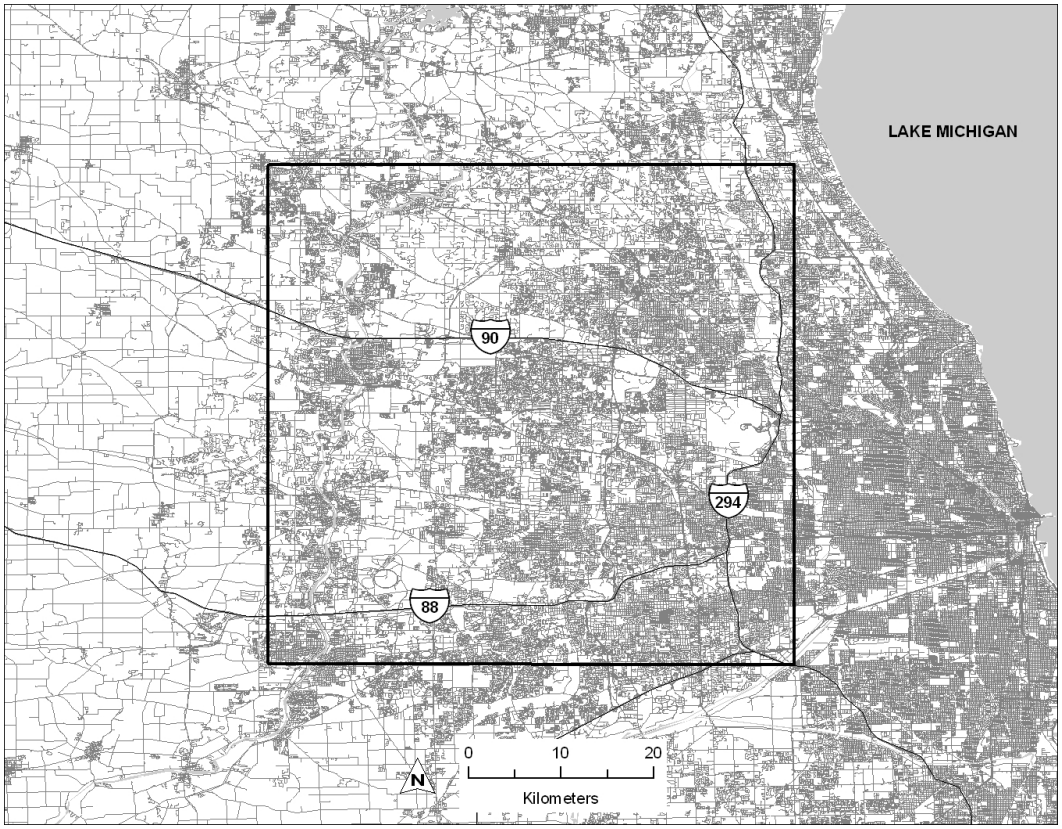
Study Area

The Chicago metropolitan area includes >260 municipalities and a cumulative human population exceeding 9 million, making it one of the largest urban centers in the United States. General land cover across the six counties encompassed by the metro area in 1997 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) have been highly fragmented for some time, first by agriculture in the early 1800s, and more recently through urbanization. Continued development creates a dynamic landscape, with patches of habitat disappearing under development activities and urbanization continuing to consume outlying agricultural lands.

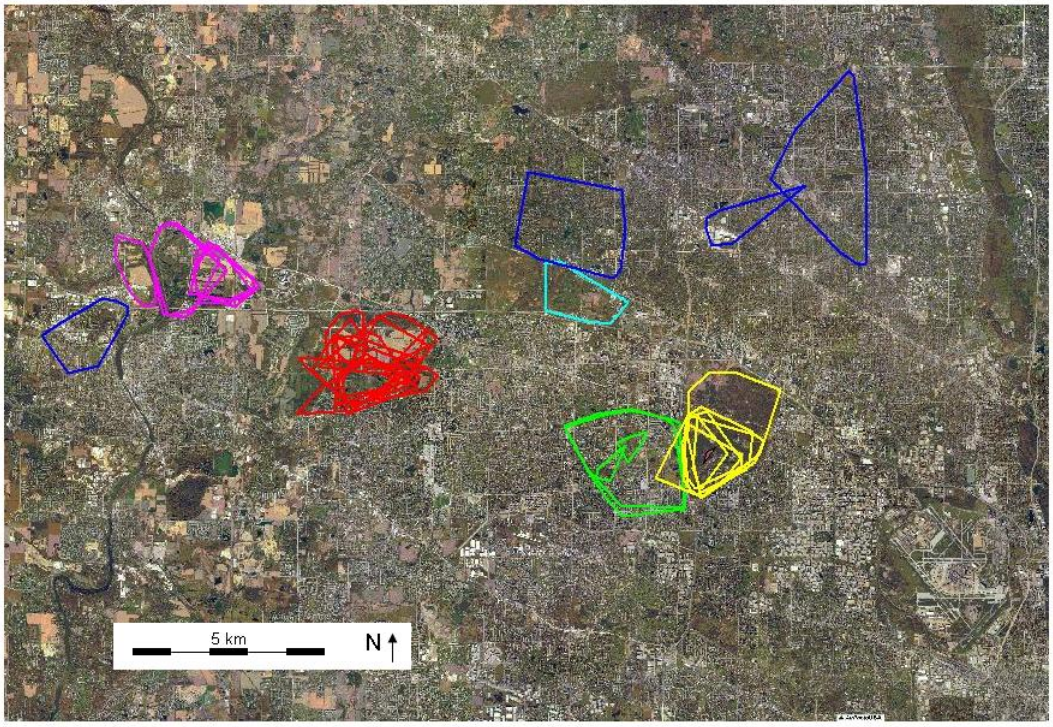
Our fieldwork was largely focused in the northwestern portion of the metro area, including O'Hare International Airport (Figure 1). The scope of the study area was determined by the cumulative area of locations of radiocollared, resident coyotes, which spanned approximately 1,173 km^2. It is important 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 (Gehrt and Riley 2010). 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 (source: Illinois Department of Transportation). For comparison, statewide road densities for Midwestern states range from 0.065 to 0.189 km/km^2 (2000 Bureau of Transportation Statistics). Landscape composition within the study area was comprised of the following land use types: agriculture (14%), natural habitat (13%), residential (20%), urban land (including commercial/industrial use, 43%), and other land covers (10%).

Figure 1. The Chicago metropolitan area and overall study area where trapping and radiotelemetry was focused. Figure from Gehrt and Riley 2010.



Although our monitoring occurred across much of the metropolitan area, it was necessary to focus our trapping efforts in public or private parks. These areas included 5 foci (Figure 2): the Ned Brown Forest Preserve (NB), Poplar Creek Forest Preserve (PC), Max McGraw Wildlife Foundation (MM), Schaumburg Village (SCH), and a portion of the Highland Woods Forest Preserve (HW). The areas of 3 sites (NB, PC, MM) were determined by the boundaries of the preserves because the resident coyotes largely restricted their movements to the preserves, whereas the boundaries of the other sites (SCH, HW) were determined by the perimeter of the coyote territories. We estimated densities and diets for coyotes residing within these areas. Thus, each of these sites is briefly described below.

Figure 2. Distribution of resident coyote home ranges in 2006. Home ranges associated with the MM area are in pink, PC in red, HW in light blue, SCH in green, and BW in yellow. Single resident home ranges are in dark blue. O'Hare International Airport is in the bottom right corner.



Study sites NB and PC were open to the public and received considerable recreational use in the summer. Site NB was located 5 km west of Chicago O'Hare International Airport and was surrounded by medium-density residential and high-density commercial areas, and was bordered on two sides by 8-lane highways. PC was a forest preserve bounded by medium-density housing, a commercial area, and an 8-lane highway. Although these sites were protected from development, human use of these sites was intensive. For example; NB received 1.5 million visitors/year, mostly during non-winter months (Prange et al. 2003; Gehrt 2004). Major uses of the forest preserves included picnicking, hiking and biking, and refuse was prevalent during warm months.

Site MM was a private natural area and hunting and fishing preserve. The property was adjacent to a gravel pit and areas of public use that included 2 small amusement parks. Private property in the center of MM included a commercial strip with a restaurant and small shopping plaza, and a small residential area. Site HW was defined by coyote territorial boundaries, and included a portion of the forest preserve and the adjacent city of Palatine. Site SCH consisted of a human population of 75,400. It was 14.4 km from the city of Chicago and surrounded by 6 cities (population range: 23,100 [Roselle] to 49,500 [Hoffman Estates]). Primary land uses within this area was medium-density residential and commercial use. Habitat fragments included small city parks, 2 golf courses, 4 small natural areas and a water treatment plant.

The coyote was observed in the Chicago metropolitan area only sporadically through most of the 20th century, and active predator control programs removed coyotes on sight until the 1970's. During the 1990s, there was a dramatic increase in the number of sightings and reports of conflicts (Gehrt 2004).

Live capture

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 live trapped with padded foothold traps and cable restraint devices. Upon the capture of an unmarked individual, the coyote was usually transported to a laboratory area and immobilized with an injection of Telazol. Coyotes were marked with uniquely-numbered plastic eartags (NASCO Farm & Ranch, Fort Atkinson, Wisconsin) and fitted with VHF radio collars (Advanced Telemetry Systems, Isanti, Minnesota, USA). We weighed each coyote, 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 during the night or early morning. Our trapping and handling protocols were approved by Ohio State University's Institutional Animal Care and Use Committee (ILACUC#2003R0061).

Radiotelemetry

Our radiotelemetry methods were described in detail by Gehrt et al. (2009), and are briefly described here. We obtained radiolocations for coyotes by visual observations, triangulation (with program LOCATE II (Pacer, Truro, Nova Scotia, Canada), or by circling the animal's location with a truck-mounted antenna and record their location directly with a Global Positioning System (GPS) unit. The latter was possible when coyotes moved into the urban matrix and the road system allowed us to closely follow animals. Coyote locations were recorded to the nearest meter using the Universal Transverse Mercator (UTM) grid system.

Our typical monitoring schedule involved obtaining single diurnal locations 2-3 times per week, and conducting tracking shifts at night in which we focused on a group of coyotes and obtained sequential locations at 60-120 minute intervals for 5-6 hrs during

the night. Mean (±SD) error for test transmitters was 108 ±87 m via triangulation (Morey, 2004).

Density estimates

We estimated local densities of coyotes for sites that we trapped intensively across years (NB,PC,MM,SCH,HW). We obtained the number of radiocollared coyotes using the sites for all or portions of the year and constructed 2 estimates: a lower estimate that only included year-round residents, and a higher estimate that is a combination of year-round residents and those coyotes that used the site for part of the year. Often the latter group consisted of coyotes that were residents that began to move beyond the local site, often as they transitioned to transient status. We did not capture all residents in these areas, so the minimum known alive should be considered a conservative population estimate. The area used to estimate densities was either park boundaries (for park sites) which encompassed the coyote home ranges of multiple packs, or the pooled home range boundaries of the residents for sites not restricted to large parks. We report numbers for 2004-2006 because our trapping efforts and number of radiocollars were greatest in those years.

Survival estimates

We estimated annual survival of coyotes with the staggered entry modification to the Kaplan-Meier survival estimator (Pollock et al. 1989). Survival distributions were determined by month. Annual periods extended from April to the following March each year for subadults and adults, and from July to the following March for juveniles. Coyotes that disappeared or dispersed from the study area were removed from the analysis during the month they disappeared. We assumed that survival probabilities were independent among individual coyotes, and that survival probabilities were constant during monthly intervals.

Home range estimates

We used the Home Range Extension (Hooge and Eichenlaub 1997) for ArcView 3.2 Geographical Information System (GIS) software (Environmental Systems Research Institute, Redlands, California, USA) to plot 95% minimum convex polygon (MCP) home-range estimates. 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 more than one season within an annual period). However, for transient coyotes we used a lower minimum number of at least 30 locations because of the difficulties associated with monitoring coyotes with large home ranges in the metro area, such as locating telemetry signals, and because solitary individuals sometimes dispersed and truncated our time to acquire locations. We classified a coyote as a resident if it used one unique area for ≥1 biological season and was observed with another coyote, and a transient if it maintained a home range that overlapped multiple resident territories or was not observed associating with other coyotes for more than one season (Gese et al. 1988). Resident home ranges 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.

Gehrt et al. (2009) created a land-use type coverage with 28.5 m resolution from 1997 Chicago Wilderness/NASA Landsat Thematic Mapper images for use in ArcView GIS 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). Residential, Urban grass, and Urban Land were the land cover classes most associated with human activity.

Gehrt et al. (2009) assessed coyote selection of land cover types at the third order of selection (i.e., within the home range) by comparing the rankings of use versus availability for resource components using the individual as the unit of measurement (Johnson 1980). Selection is determined by a test for a significant deviation from an equal distribution with a multiple comparison procedure (Waller and Duncan 1969).

Activity

During radiotracking in 2000-2002, we classified coyote locations as active or inactive based on signal modulations. Once we obtained a bearing for a location, we listened to the signal for 30 sec. If the signal varied during this period, it was classified as active; alternatively, a lack of signal modulation resulted in a location classified as inactive. We pooled data within hourly blocks and qualitatively compared the proportion of locations classified as active between diurnal and nocturnal periods.

Diet

Here we review the diet analysis reported by Morey et al. (2007). In brief, scats were collected during 2000-2002 from fixed routes located in four sites (NB, PC, SCH, MM) within our larger study area. Diet items were presented as frequencies of occurrence in the scats. We synthesize Morey et al.'s results and present here for comparison across sites in light of the additional information in this paper.

RESULTS

During 2000-2006, we captured and radiocollared 181 coyotes, including 17 female adults, 41 female subadults, 28 female pups, 28 adult males, 40 subadult males, and 27 male pups at the time of radiocollaring.

Population Density
Mean minimum population densities pooled across sites ranged between 0.8 and 2.1 coyotes/km^2 across years (Table 2). At the local site level, densities ranged between 0.4 and 3.5 coyotes/km^2. There was a trend for the site (SC) with the highest level of development to have the lowest densities.

Survival and Mortality
Annual survival ranged between 0.58 for subadult females and 0.70 for adult females (Table 3); however, there were no significant (all P's > 0.1) differences between demographic groups.

We recorded 68 mortalities of radiocollared coyotes, of which 62% died from collisions with vehicles, 18% were shot, 10% died from mange, and 10% died from other causes. The mortalities in the other category included a juvenile that died from emaciation and the cause of death for the rest (n = 6) could not be determined. Some coyotes suffering from extreme mange were shot, but these cases were classified as mortalities caused from mange because we deemed the disease to be the ultimate cause of mortality that caused the animal to be euthanized. Individuals in the shot category were either killed as nuisances, as part of legal harvest, or illegally poached.

Table 2. Minimum densities (coyote/km^2) of coyotes by study site during 2004-2006 in the Chicago metropolitan area. Densities were estimated from the number of radiocollared coyotes using the area (N) for at least a portion of the year. For simplicity, landcover types for each site are combined into two primary types: 1) natural (Nat) which represents the combined percentages of Natural, Agriculture, Undeveloped, Water, and Other categories, and 2) urban (Urb) which represents the combined percentages of Residential, Urban Grass, and Urbanized.

	Area	Landcover		2004		2005		2006	
Site	**(km^2)**	**%Nat**	**%Urb**	**N[a]**	**Density**	**N**	**Density**	**N**	**Density**
PC	14	100	0	10-14	0.7-1.0	15-20	1.1-1.4	15-19	1.1-1.4
NB	6-11	100	0	8-11	0.7-1.0	7-9	1.2-1.5	7-9	1.1-1.5
MM	5	95	5	11-14	2.4-3.0	9-16	2.0-3.5	5-7	1.1-1.5
HW	3-8	54	46	6-9	0.8-1.2	6-11	1.9-3.4	2-5	0.5-1.3
SCH	6-11	25	75	5-8	0.4-0.7	4	0.7	4-5	0.4-0.5
Average					**1.0-1.4**		**1.4-2.1**		**0.8-1.2**

[a] Smaller number represents the number of residents that remained on the site during the year; the larger number represents the residents combined with other coyotes that used the area for a portion of the year, some of which were residents that became transients.

Table 3. Annual survival estimates, (*S*), for age-sex classes of coyotes during 2000-2006 in the Chicago metropolitan area, Illinois, USA.

Category	N	Deaths	Missing	*S*	95% CI
Adult female	52	11	8	0.70	0.57-0.83
Adult male	86	26	15	0.59	0.48-0.70
Subadult female	46	11	12	0.58	0.43-0.73
Subadult male	41	9	6	0.63	0.48-0.78
Juvenile female	26	5	1	0.61	0.45-0.77
Juvenile male	22	6	1	0.61	0.42-0.81

N is the sample size for the demographic category.
CI is the confidence interval.

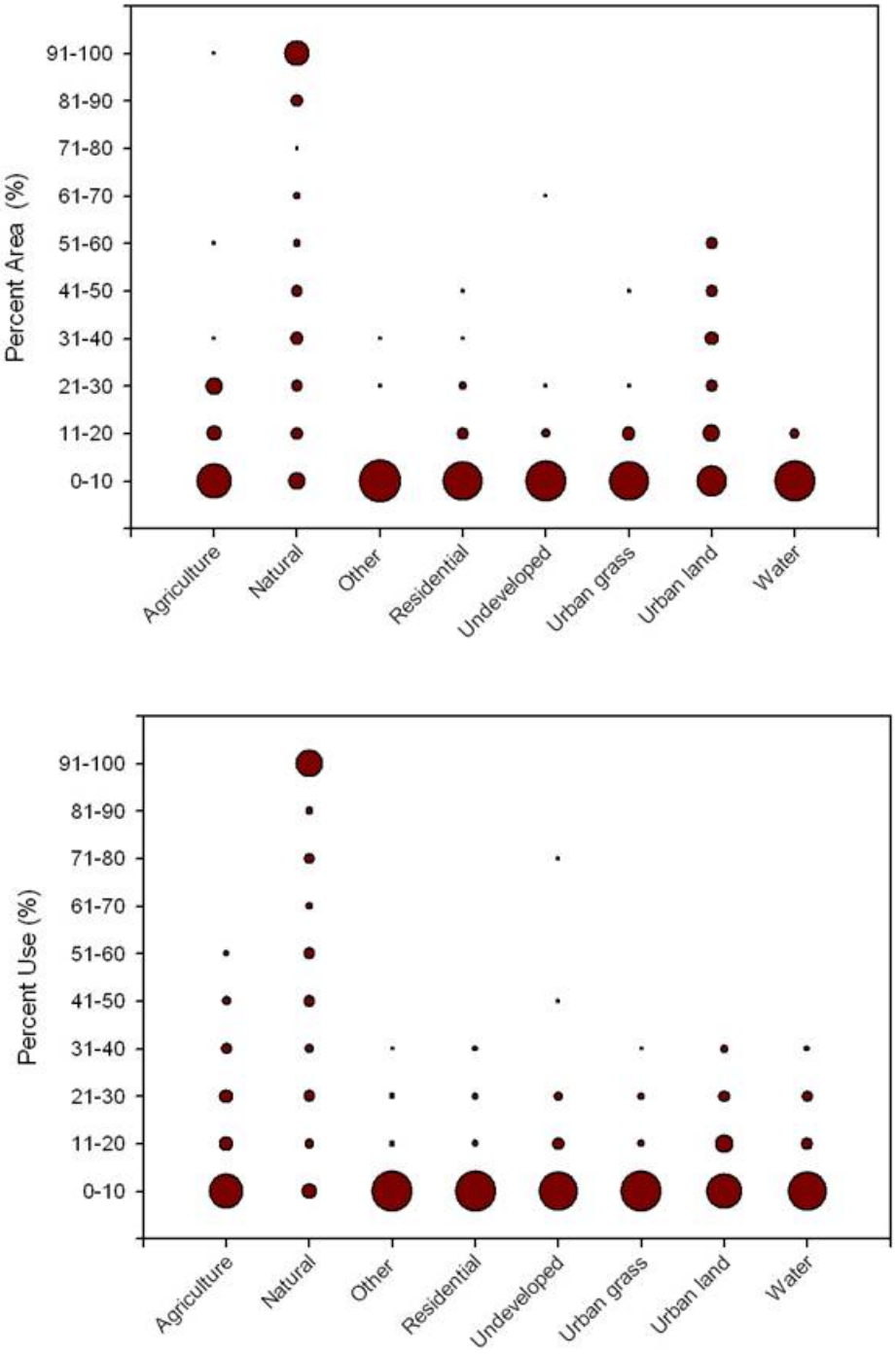
Home range size and habitat selection

Gehrt et al. (2009) used 25,509 locations to estimate 182 annual home ranges. Because some individuals were monitored for multiple years, this reduced the number of home ranges to 84 residents (22 adult females, 11 subadult females, 29 adult males, 22 subadult males) and 40 transients (9 adult females, 14 subadult females, 15 adult males, and 2 subadult males). Home range size was similar among age-sex groups for both residents and transients. Mean (±SE) annual home ranges of transient coyotes ($\bar{x}$ = 26.80 ±2.95 km^2) were larger (t = 12.6, df = 122, P < 0.001) than those of resident coyotes ($\bar{x}$ = 4.95 ±0.34 km^2), with transient home ranges ranging up to 98 km^2.

Some coyotes restricted their movements completely within urban parks, whereas others had home ranges located completely in the urban matrix with very little available natural habitat (Figure 3). There was a trend (r = 0.38, n = 84, P < 0.001) for home range size to increase with an increase in urban land cover within the home range. However, there was considerable variation in home range size even in the same types of land cover. Home ranges located completely within protected parks or habitat fragments ranged in size from 1.15 to 8.85 km^2, and those home ranges composed of >70% urban development ranged in area between 6.38 and 16.85 km^2.

Patterns of habitat selection at the third order scale (i.e., within the home range) were consistent across status (resident and transients), season, gender, and activity periods (day or night). In each case, selection was significant and land cover categories most associated with human activity (residential, urban grass, and urban use) had selection scores consistently indicating avoidance (Table 4). Conversely, land cover classes associated with water, undeveloped patches, and other were selectively used across classes. Resident coyotes were further partitioned into those with urban home ranges (10-50% composed of a combination of residential, urban grass, and urban land) and high urban home ranges (>50% developed). For both groups, the same patterns of habitat selection occurred, with consistent avoidance for each of the human activity land cover categories (Gehrt et al. 2009).

Figure 3. Composition of coyote home ranges and frequency of use of land cover types within home ranges in the Chicago metropolitan area 2000-2006. Size of the bubble reflects the relative number of coyotes that occurred in the % composition or % use categories.

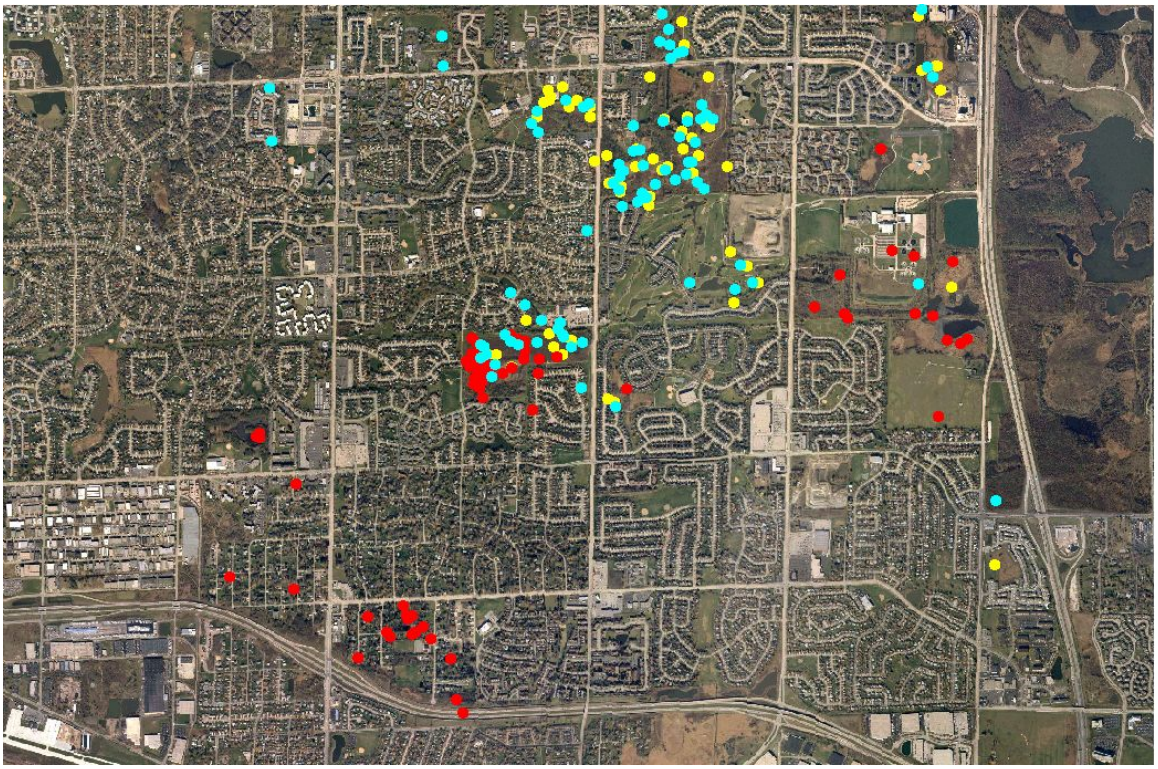


The pattern continued in 2007, in which seven coyotes had home ranges with <10% natural habitat fragments and 14 coyotes had home ranges located largely (>85%) within natural fragments, but strong avoidance of developed areas. The following illustrates the typical pattern of landscape use for those coyotes living in the urban matrix. In 2007, coyote 266 had an annual home range that was 6.6 km^2, of which nearly half (47%) was urban land and 22% was residential (Figure 4). Natural habitat comprised only 3% of the home range, and undeveloped was 6%. However, percent use was only 8% for urban land, 19% residential, 55% for undeveloped land and 8% use of the limited small natural fragments. This coyote was born and reared nearby (also completely in the urban matrix), and he shared part of his home range with his parents (Figure 4).

Table 4. Overall summary of land cover selection for coyotes in the Chicago metropolitan area 2000-2006 (from Gehrt et al. 2009). Land cover categories are: Undeveloped (U), Other (O), Water (W), Agriculture (A), Natural (N), Urban grass (UG), Residential (R), and Urban land (UL). Ranking order was determined from selection scores derived from Johnson's ranking method (Johnson 1970), and reflect the level of selection for, or avoidance of, land cover categories. For heuristic reasons, we have presented the rankings that reflected avoidance with negative scores (which is opposite from Johnson [1970]). The order of ranking represents the relative difference between use versus availability.

		Selection ranking							
Class	**Category**	**U**	**O**	**W**	**A**	**N**	**UG**	**R**	**UL**
Status	Resident	1	2	3	4	5	-6	-7	-8
	Transient	1	2	3	4	5	-6	-7	-8
Season	Breeding	1	2	3	4	5	-6	-7	-8
	Pup-rearing	1	2	3	4	5	-6	-7	-8
	Dispersal	1	2	3	4	5	-7	-6	-8
Gender	Male	1	2	3	4	5	-6	-7	-8
	Female	1	2	3	4	5	-6	-7	-8
Activity	Diurnal	1	2	3	4	5	-6	-7	-8
	Nocturnal	1	2	3	4	5	-6	-7	-8
Home range	Urban	1	2	3	4	5	-6	-7	-8
	High Urban	1	2	3	4	5	-6	-7	-8

Figure 4. Radiolocations of coyote 266 (red) and his parents (mother is yellow, father is blue) during 2007 in Schaumburg, Illinois.



Activity

We determined activity for a subset of 5,290 locations. Patterns of activity revealed that coyotes were largely active at night, although there was some activity throughout the 24-hr period (Figure 5). Frequency of active locations was consistently <20% during diurnal hours (800-1600), while frequency of active locations was consistently >70% during most nocturnal hours (1900-200).

Diet

Diet analysis was conducted on 1,429 coyote scats collected from the following four sites: NB, PC, SSCH, MM. There was considerable variation across sites and seasons (see Morey et al. 2007 for details), but the general pattern was that small rodent (*Microtus* spp, *Peromyscus* spp) was the most common diet item in all seasons and sites (Table 5). Other common food items included deer (*Odocoileus virginianus*), fruit, eastern cottontail (*Sylvilagus floridanus*), and a general bird category. These top food items varied among sites ($\chi^2_{12} = 535.15$, $P < 0.001$; Morey et al. 2007). In contrast, relatively low frequencies of occurrence were observed for human-associated food items combined with domestic cat, although there was a difference in frequency for these diet items among sites ($\chi^2_3 = 72.46$, $P < 0.001$), with the highest occurrence in SCH (Table 5).

Figure 5. Patterns of activity for radiocollared coyotes in the Chicago metropolitan area, where bars represent the frequency of active locations and dots/line represents the number of locations recorded by hour. Data collected during 2000-2002.

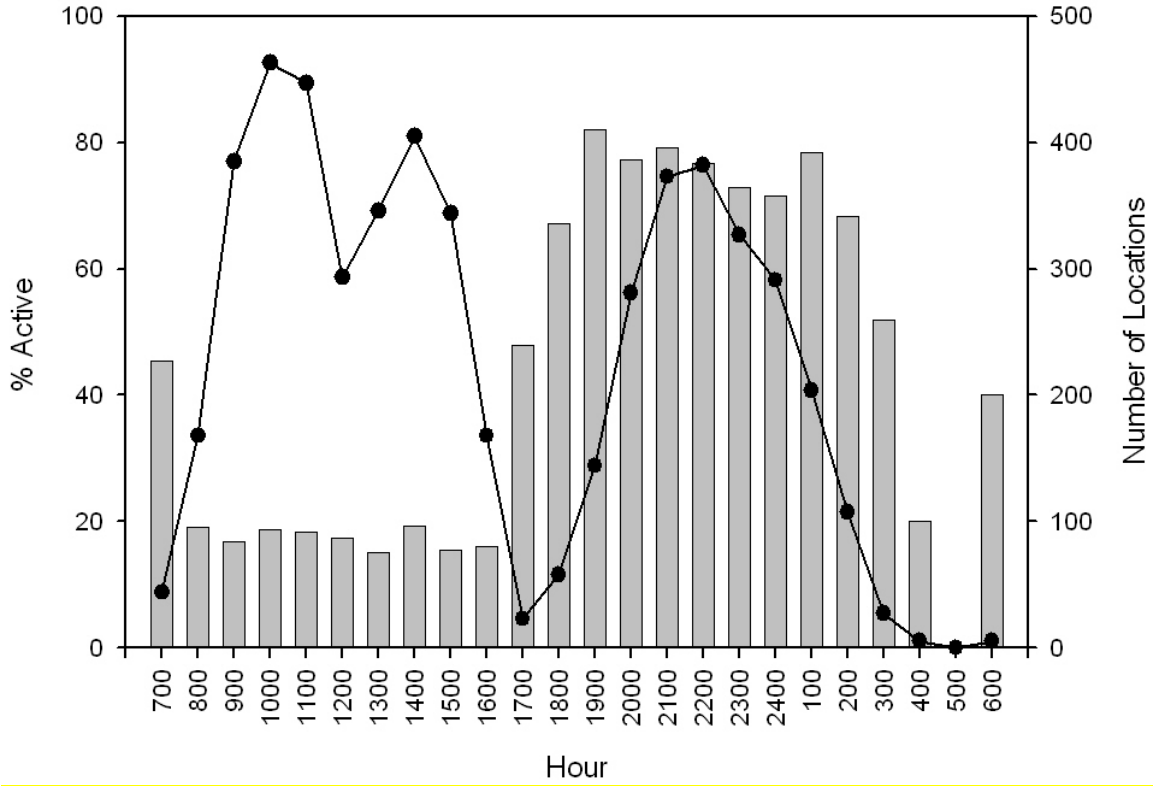


Table 5. Frequencies of occurrence (%) for selected diet items in coyote scats collected during 2000-2002. Complete list of diet items in Morey et al. (2004).

	Study Site				
Diet Item	**NB**	**PC**	**MM**	**SCH**	**Total**
Small rodents	74	37	28	31	**42**
Deer	17	35	14	10	**22**
Fruit	8	12	44	31	**23**
Rabbit	10	28	9	25	**18**
Bird	4	5	33	8	**13**
Anthropogenic	2	3	1	11	**2**
Cat	1	0	0	7	**1**
No. Scats	**325**	**535**	**419**	**150**	**1429**

DISCUSSION

A synthesis of our results from the Chicago metropolitan area produces a portrait of an animal that appears to benefit from the urban landscape through enhanced survival and possibly elevated population densities, while also exhibiting strong spatial and temporal avoidance of humans by consistently avoiding developed portions of the landscape and shifting activity patterns to nighttime hours.

Demographic Characteristics

There are few published density estimates for urban coyote populations, nevertheless, there appears to be a trend toward higher densities in response to urbanization, but not dramatically so. Bekoff and Gese (2003) reported coyote densities from 12 different non-urban studies and from various times of year, ranging from 0.1-0.9 coyotes/km^2 with an extreme fall estimate of 1.5-2.3 coyotes/km^2 (Knowlton 1972). Using a combination of genotypes and capture rates, Fedriani et al. (2001) reported densities of 2.4-3.0, 1.6-2.0, and 0.3-0.4/km^2, for 3 sites on the outskirts of Los Angeles, California. More extensive radio-tracking of coyotes in these same areas yielded minimum density estimates of 0.21 coyotes/km^2 in the fragmented areas and 0.53 coyotes/km^2 in the contiguous natural areas adjacent to urbanization (Gehrt and Riley 2010). Our density estimates are conservative; given this, it appears that densities in our sites were generally high compared to rural settings. We have also been able to estimate densities using visual sightings of collared and uncollared coyotes for some local sites, and these estimates have ranged 2-6 coyotes/km^2 (Gehrt 2004). In these cases, we simply took the largest number of coyotes observed simultaneously by research staff or the public for a particular coyote group in a year, and scaled the estimate by the territory size of the group for that year. These estimates should also be regarded as conservative as it is unlikely that all residents of the area are observed at one time; in any case, densities in urban habitat fragments are quite high. But, coyote densities in the urban matrix were relatively low (compared to those in natural habitat fragments in our study area), suggesting that coyotes may find the urban matrix more challenging than large habitat fragments.

Our adult survival estimates were similar to estimates for coyotes in rural Illinois (59%, Van Deelen and Gosselink 2006), but our survival estimate for juveniles was approximately five times higher than the 13% survival rate reported for rural juveniles (Van Deelen and Gosseilnk 2006). Rural Illinois, like most of the midwestern United States, is a landscape dominated by row-crop agriculture, and hunting of coyotes occurs year-round without any regulatory constraints such as bag limits. Given intensive hunting and trapping pressure, coyote vulnerability is magnified in a landscape that undergoes a major loss of cover (agricultural crops) during substantial parts of the year (Van Deelen and Gosselink 2006). Large metropolitan areas contrast with the larger rural landscape by affording protection from exploitation as well as the extensive seasonal loss of habitat via harvest of crops.

The difference in survival rate between rural and urban juvenile coyotes is of note regarding population growth and the possibility that large metropolitan areas may serve as source populations for the larger Midwestern landscape. Survival rate is an important

mechanism in coyote population dynamics, and previous population models suggested a constant survival rate >50% across age classes would indicate $\lambda > 1$, even if other compensatory factors exist (i.e., smaller litters, low proportion of females breeding). For example, given conservative population parameters 36% of females breeding and a mean litter size of 4.3, a constant survival rate of only 39.1% is needed to maintain a stable population (Sterling et al. 1983). Similarly, population modeling by Knowlton (1972) for stable rural populations in Texas predicted a 33% survival rate of young to 1 year of age was sufficient to maintain population levels given a 60% annual survival rate for adults. Thus, the coyote population in the Chicago metropolitan area, with a relatively high juvenile survival rate, is likely experiencing positive growth or is serving as a source population with the annual production of excess individuals. In any case, survival data suggests synanthropy, at least in the Midwest.

Behavioral Characteristics

Home range size can be an important indicator of habitat quality or the distribution of resources, and synanthropic species tend to have relatively smaller home ranges in urban rather than rural settings (e.g., raccoon, Prange et al. 2004, red fox Iossa et al. 2010; Soulsbury et al. 2010). Mean home range size for coyotes in the Chicago area was relatively small compared to more rural studies, which is typical of most other coyote studies (Atwood et al. 2004; Gehrt and Riley 2010). For example, home range sizes for coyotes in rural Illinois (Gosselink et al. 2003) were much larger than the mean for residents in our study. However, the relationship appears to be more complex when patterns of variation in home range size are considered within the urban system. First, there was a considerable range among individuals, even for those using similar parts of the landscape (e.g., exclusive to natural fragments). Second, coyotes residing in the urban matrix had larger home ranges than those located within large parks. The larger size reflects avoidance of developed areas and a need to travel greater distances to use suitable patches of the landscape. To some degree, the contrasting trends in home range size between macro- and microscales reflects the paradoxical relationship coyotes have with urbanization.

Likewise, coyote selection for land cover types contradicts synanthropy. Coyotes in our study exhibited strong selection for certain landscape cover types, with consistent avoidance of those parts of the landscape most associated with human activity regardless of how we partitioned the data. Strategies for avoidance differed among individuals, but generally involved restricting movements to large blocks of natural fragments and avoiding the urban matrix altogether, or moving quickly through developed areas at night to forage or rest in patches of habitat (Gehrt et al. 2009; Gehrt and Riley 2010).

A consistent observation among virtually all urban coyote studies is a shift toward nocturnal activity for coyotes residing in urban areas (Atkinson and Shackleton 1991, Quinn 1997a, Gibeau 1998, Grinder and Krausman 2001, Tigas et al. 2002, Riley et al. 2003). Similarly, in urban parks coyotes also avoid areas and time periods with high human activity (George and Crooks 2006). Exceptions to these trends may involve coyotes that have become habituated to human activities or have been infected with a disease such as mange (Gehrt 2006; Gehrt et al. 2009).

Food habit studies of coyotes in urbanized areas have typically reported diets dominated by small mammals (e.g., rodents, lagomorphs; MacCracken 1982; McCune et al. 1995; McClennen et al. 2001; Bogan 2004). The low prevalence of anthropogenic foods in the diets of coyotes in our study area contrasts with the 40-60% prevalence reported for red foxes in Great Britain (Harris 1981), and the likely prevalence for raccoons in our study area and other cities (Gehrt 2004). Other studies of diets of coyotes in metropolitan areas have also reported a positive relationship between the frequency of anthropogenic items in the diet and proximity of coyotes to development (Quinn 1997b; Fedriani et al. 2001). However, it is important to note that human foods (including pet food) only constituted 11% of the diet in a landscape heavily dominated by development. It is further notable that the use of human foods was also quite low in the large parks (NB, PC) that had tremendous levels of human activity and presence of refuse (Gehrt 2004), despite their technical classification of natural land cover. Thus, there was clearly resistance to utilize human-related foods by coyotes.

Relevance for Management: A Case Study

The importance of ecological characteristics in the management of coyote conflicts is illustrated in the following case study. We captured and radiocollared a 16.25 kg, adult male coyote during the first year of the study (March 31, 2000). Subsequent observations revealed it was paired with an adult female, and that this was likely an alpha male. The animal was captured within NB, and his daytime locations were restricted to the preserve. At night, most of his locations occurred in the adjacent residential community. We observed him crossing the road bordering the preserve within an hour post-sunset. His presumed mate (not radiocollared), however, was never observed crossing the road and was never seen with him in the neighborhoods.

Over the next two months, complaints emerged of cats and other domestic animals disappearing or otherwise likely killed by a coyote. By the end of May, the city began negotiations with a nuisance trapper to remove the coyote(s) using the area. At the same time, the city began an education campaign to educate residents about coyotes and to deter wildlife feeding. On May 31, 2000, the coyote was killed while crossing the road and trapping was never implemented. This was, in essence, a specific removal of a problem individual, even though the removal was serendipitous.

During the period of conflict, we became aware of one resident purposely feeding coyotes and other animals. Following the removal of the problem coyote, the city cited the resident repeatedly until they quit feeding wildlife. Thus, there was a comprehensive program to selectively remove a problem individual, an education program to prevent future conflicts, and enforcement for those residents that did not cooperate.

Following the 'removal' of the original alpha male, another male apparently took his place by October and we eventually captured this individual in February 2001. This was a 16-kg adult male, and subsequent genetic analysis would reveal that he had alpha status as he fathered litters. In the subsequent years, this coyote in addition to other residents rarely moved into the adjacent developed area (Appendix 1). During the period 2001-2007, individual coyotes were never located outside the preserve more than 4% of the time. Pooling across individuals and years, we recorded 3063 locations, of which 19

(<1%) were located in the developed area. It is important to note that there were no physical barriers to crossing the road and moving from the preserve to the neighborhood; at this location, the forest preserve is bounded by a narrow, 2-lane road with only light, residential traffic. This road did not represent a physical barrier to coyote movements, as coyotes from other areas in our study regularly crossed roads with much higher traffic volumes. There were no complaints of missing pets during this time.

This case study illustrates the effectiveness of a specific removal of a nuisance animal combined with an educational program to deter wildlife feeding. The removal of one coyote resulted in coexistence for at least seven years, despite a resident coyote population continuing to persist in proximity to people. Unfortunately we did not radiocollar the nuisance coyote prior to his conflicts, therefore we cannot confirm the cause and effect of the wildlife feeding by a human resident. However, our experience in other areas during the course of the study suggests that wildlife feeding was likely a precursor to the nuisance behavior.

What were the ecological/behavioral parameters relevant here? 1) The vagility of transients, even in a heavily urbanized landscape, results in the replacement of resident coyotes following removal, 2) most coyotes avoid areas of human use if possible, 3) coyotes are capable of finding natural prey in urban fragments, and 4) human behavior (through wildlife feeding) can change the inherent avoidance coyotes exhibit toward people and likely contributes to the probability of conflict. Thus, targeted removal of problem individuals may be more effective than a general removal of the local coyote population at reducing damage and complaints, given that most coyotes avoid human use areas and are not relying on anthropogenic foods. This strategy is similar to that for livestock depredation by coyotes (Blejwas et al. 2002). However, removal programs must be accompanied by education programs directed at human behavior, particularly regarding intentional or accidental feeding of wildlife. This case study suggests that a selected removal, joined with efforts to prohibit feeding of coyotes, can have an effect that lasts for years.

Our results for coyotes in the Chicago metropolitan area reveal a dichotomy between behavioral and demographic responses to urbanization, in which the urban coyote appears to be behaviorally misanthropic (e.g., strong spatial and temporal avoidance of people) but demographically synanthropic (e.g., elevated survival and density, possibly reproduction). This unique combination has likely played an important role in the success of coyotes in urban areas, given that coyotes are often considered nuisances and removal efforts initiated when coyotes are seen by the public, often in the absence of damage. However, as coyotes continue to expand into urban areas, more research is needed on other life history parameters of urban coyotes, and especially from other metropolitan areas to determine if these characteristics are consistent across cities.

SUPPLEMENTAL MATERIAL

Distribution of coyote locations during 2000-2007. Each color represents a different individual for that year, but not necessarily the same individual between years. These figures are available with this article at Cities and the Environment Journal (www.catejournal.org).

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Appendix 1. Locations of resident coyotes from the south side of the Ned Brown Forest Preserve and the percentage of locations recorded outside the preserve in adjacent residential and commercial areas.

Year	Coyote identification	Total locations	Number of locations outside preserve	Percentage (%) of total locations outside preserve
2000	3	52	28	54.8
2001	32	129	0	0.0
2001	25	37	0	0.0
2002	32	621	5	0.8
2002	27	620	0	0.0
2002	76	140	1	0.7
2002	77	136	4	2.9
2002	80	57	1	1.8
2003	32	22	0	0.0
2003	80	83	1	1.2
2003	77	121	0	0.0
2003	76	142	0	0.0
2004	110	39	1	2.6
2004	107	221	0	0.0
2005	182	60	0	0.0
2005	178	149	1	0.7
2005	223	13	0	0.0
2006	178	115	1	0.9
2006	223	114	2	1.9
2006	235	82	0	0.0
2007	223	53	2	3.8
2007	220	48	0	0.0
2007	278	61	0	0.0