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Stanley D. Gehrt

Ohio State University, Columbus, OH, USA

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ECOLOGY OF COYOTES IN URBAN LANDSCAPES

STANLEY D. GEHRT, School of Environment and Natural Resources, Ohio State University, Columbus, OH, USA, and Max McGraw Wildlife Foundation, Dundee, IL, USA

Abstract: Coyotes (*Canis latrans*) have become common in many metropolitan areas across the United States. Recent research has focused on the urban ecology of coyotes to better our understanding of how they exist in urbanized landscapes. I summarize findings from a variety of ecological studies of coyotes in or near metropolitan areas, and focus on three areas of coyote ecology: survival rates, home range/activity, and food habits. Most studies have reported relatively high survival rates (annual $S = 0.62 - 0.74$), with vehicle collisions often a common cause of mortality. Size of coyote home ranges (mean home range sizes among urban studies ranged 5 - 13 km²) generally exhibit a negative trend with urbanization when compared to rural studies, but this is complicated by a trend within urban landscapes in which coyote home ranges tend to increase with fragmentation and development. Studies have consistently reported a decrease in diurnal activity with human use areas. Although coyotes in some areas avoid human use areas, they are nevertheless frequently in close proximity to people. Coyote food habits in urbanized areas are similar to rural areas, in which mammalian prey and vegetation (i.e., fruit) comprise most of the diet; however, there is a trend toward more anthropogenic items from more developed areas. The relatively small home-range sizes and high survival rates suggest coyotes are successful in adjusting to an urbanized landscape.

Key words: *Canis latrans*, coyote, diet, home range, survival, urbanization

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INTRODUCTION

The coyote (*Canis latrans*) has become established in an increasing number of metropolitan areas across the United States, and in most of these areas it represents the largest carnivore maintaining residency near people. As is noted in other papers in this symposium, their role as top predator in these systems often leads to interesting relationships with people, including conflicts (Gehrt 2004, Timm et al. 2004). Because the coyote dramatically expanded its geographic distribution in the last century (Bekoff and Gese 2003), the phenomenon of coyotes living in urbanized landscapes is a relatively recent occurrence

in much of this new range. Because of its mystique among the general public, dramatic range expansion, opportunistic behavior, and role as a top predator in most North American metropolitan areas, the coyote is arguably one of the most controversial carnivores in urban landscapes.

Although the coyote is one of the most studied canids in North America (Bekoff and Gese 2003), our understanding as to what extent the coyote becomes successful in urbanized landscapes remains limited. Compared to the amount of research devoted to coyotes in more natural, or rural landscapes, there has been a paucity

of research on coyotes in urban areas. This is partly a function of the difficulty and cost of successfully conducting research on coyotes in cities, but it is also true that there was little need for urban studies of coyotes in cities throughout much of its range more than 20 years ago. Consequently, coyote behavior in urbanized areas, and the ensuing relationship between coyotes and people, is frequently interpreted through media reports or where complaints occur. However, it is important to understand the ecology of coyotes in urban areas to place conflicts in context and determine the efficacy of various management strategies.

To better understand how coyotes respond to urbanization, I summarize the findings of coyote studies in a variety of urban systems. I focus specifically on survival/cause-specific mortality, movement and activity patterns, and food habits because these ecological characteristics have been reported most frequently in the urban coyote literature, and because of their implications for human-coyote conflict.

SCOPE OF REVIEW

I surveyed published literature, theses, and my own research (described below) for comparisons and consistencies across areas. In most cases I restricted the review to studies that used radiotelemetry techniques, except for diet studies. Comparisons among studies must be considered with caution as researchers have used different techniques for data collection and analysis, and studies have varied considerably in sample sizes and have occurred in landscapes with dramatically different levels of urbanization (Table 1). Because of the small number of available studies, I have not attempted to restrict the review to those with identical methods or even similar landscapes. Indeed, published studies have varied considerably in the size of the metropolitan area and the level of development within the study area (Table 1). Unfortunately, many studies do not specifically report the level of development within their study areas, but inspections of study area figures indicate that they differ considerably and this may explain variations in results among studies.

Table 1. Location, associated human density, and sample size for select radiotelemetry studies of urban/suburban coyotes, illustrating the variation in urbanization and sampling intensity among studies.

| Metropolitan area | State | Human density (people/mi ²) ^a | No. radiocollared | Source |
|-------------------|---------------|--|-------------------|--------------------------------|
| Tucson | Arizona | 92 | 19 | Grinder and Krausman 2001a, b |
| Los Angeles | California | 2,344 | 13 | Tigas et al. 2002 |
| Los Angeles | California | 2,344 | 66 | Riley et al. 2003 |
| Cape Cod | Massachusetts | 561 | 11 | Way et al. 2002, 2004 |
| Albany | New York | 563 | 21 | Bogan 2004 |
| Chicago | Illinois | 5,684 | 150 | Morey 2004, Gehrt unpubl. data |

^aHuman density is estimated by US Census Bureau data (2004) for the primary county in the metropolitan area; it is not necessarily the density of people within the specific study area but provides a measure of the variation in intensity of development of the larger landscape among studies.

Diet studies generally have used similar analytical techniques, primarily scat analysis, but they have differed in sample size and spatio-temporal extent of the sampling. Similarly, radiotelemetry studies have differed in sample size and spatio-temporal designs. Where possible, I report annual home ranges but the model used to construct home range estimates varies.

Cook County Coyote Project: In addition to published research, my survey includes research my colleagues and I have conducted on coyotes in the Chicago metropolitan area (Gehrt 2006). Using standard livetrapping and radiotelemetry techniques, we have been monitoring the coyote population since March 2000, and this project is currently on-going. Briefly, the Chicago study differs from many previous studies in that it is located well within the urban matrix, as opposed to the edge of the metro area, urban development dominates the landscape, and natural habitat only exists in relatively small fragments. The area encompassed by radio locations of resident coyotes is 1,168 km², has a paved road density of 6.11 km/km², and is comprised of the following land use types:

agriculture (14%), natural habitat (13%), residential (20%), urban land (including commercial/industrial use, 43%), and other (10%). Detailed descriptions of the study area and our methods are provided in Morey (2004).

ECOLOGICAL CHARACTERISTICS

Survival

Annual survival estimates for coyotes in the Tucson and Los Angeles areas were similar (Table 2), ranging from 0.71 to 0.74 across studies (Grinder and Krausman 2001a, Riley et al. 2003, Tigas et al. 2002). In the Chicago area, annual survival estimates ranged from 0.53 to 0.68 (mean = 0.62) during a six-year span (2000-2005), all sex-age groups combined (Gehrt, unpublished data). These survival estimates across studies are relatively high when compared to some rural estimates, particularly populations exposed to hunting and trapping, and are in contrast to an annual survival estimate of 0.20 for coyotes in the Albany, New York area (Bogan 2004).

Table 2. Annual survival estimates and annual home range sizes (km²) from radiotelemetry studies of coyotes in urban areas. Sample sizes include total number of radiocollared coyotes (N) in the study, and sample size (n) for home range estimates (this is usually a subsample of the total number of animals radiocollared).

| Metro Area | N | Survival | HR size (n) | Source |
|-------------------------|-----|----------|-------------|------------------------------|
| Tucson, AZ | 19 | 0.72 | 13 (13) | Grinder and Krausman 2001a,b |
| Lincoln, NE | 1 | - | 7 (1) | Andelt and Mahan 1980 |
| Lower Fraser Valley, BC | 13 | - | 11 (13) | Atkinson and Shackleton 1991 |
| Los Angeles, CA | 86 | 0.74 | 5 (40) | Riley et al. 2003 |
| Cape Cod, MA | 11 | - | 30 (5) | Way et al. 2002 |
| Los Angeles, CA | 13 | 0.71 | 3 (13) | Tigas et al. 2002 |
| Albany, NY | 21 | 0.20 | 7 (17) | Bogan 2004 |
| Chicago, IL | 150 | 0.62 | 5 (109) | Gehrt, unpubl. data |

Many urban survival studies reported vehicle collisions as a common cause of mortality, and this seems to be a cost to living in urban areas. Mortality as a result

of vehicles represented 35 to 50% in Albany, Tucson, and Los Angeles, whereas it represented 62% ($n = 68$) of the deaths in the Chicago area. The higher vehicle

mortality rate for the Chicago area may be a reflection of the heavily urbanized landscape, and the number of roads coyotes must cross regularly, relative to other studies. Interestingly, the Albany study that reported a low annual survival rate also reported a relatively high rate (43%) of hunting mortality (Bogan 2004), which is not a common activity in urban areas and may reflect differences in study area location relative to the metropolitan area.

Home Range and Related Behavior

I surveyed 9 studies reporting annual home range estimates for resident coyotes from 8 urbanized areas (Table 2). There was a range in mean home range estimates from 3 to 30 km². The mean of 30 km² for Cape Cod is more than twice as large as the next largest mean home range size, which may be a product of a highly developed landscape or a different approach to estimating home ranges (Way et al. 2002). If the mean for Cape Cod is excluded as an outlier, urban home ranges across studies had a grand mean of 7.3 km². There is a trend for mean home range estimates from urbanized populations to be smaller than for rural populations, although there is overlap. Published home range estimates of resident coyotes from rural areas in the review by Bekoff and Gese (2003) ranged from 3 to 42 km², with a grand average of 17.5 km². This grand average is larger than that for urban studies and suggests a trend exists for smaller home ranges to occur in urban landscapes, despite similar range distributions in home range size. Similarly, Atwood et al. (2004) reported a negative relationship between home range size and anthropogenic development in Indiana. 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.

In contrast to the trend in home range size between urban and rural studies, at the local scale within metropolitan areas some studies have found a positive relationship between home range size and the amount of development within the home range (Riley et al. 2003). Within the Chicago area, there is a positive relationship ($r^2 = 0.40$, $P < 0.001$) between the amount of developed property in the home range and home-range size, but there is also considerable variation in home range size not explained by that relationship (Figure 1). This suggests that while coyotes are capable of living within the urban matrix, it may come as a cost in needing a larger home range to meet energetic requirements (Riley et al. 2003), or may reflect an avoidance of developed habitat.

Urban coyote populations consist of solitary, nonterritorial individuals in addition to the residents that maintain relatively smaller territories. However, few studies have reported movements and associated behavior for solitary coyotes, likely because of the large areas of their movements and dispersal. The few reports of solitary coyotes suggest that, like rural populations, the typical home range size of solitary coyotes is quite large (90-100 km², Grindler and Krausman 2001b, Way et al. 2002). Mean home range size for solitary coyotes in the Chicago area was 32 km² (n = 26), with a maximum size of 101 km². Solitary coyotes may move across the landscape and use habitats differently than resident coyotes, but little is known about their behavior. This paucity of information is unfortunate, because solitary coyotes may represent an important component for urban population dynamics and management implications.

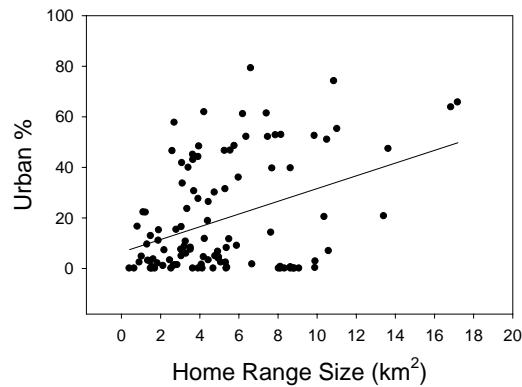


Figure 1. Relationship between annual home-range size and proportion of home range encompassing urban land use for coyotes in the Chicago metropolitan area, 2000-2005. Home ranges were estimated using the 95% minimum convex polygon model for coyotes with a minimum of 50 locations in a year.

Activity Patterns

Virtually all studies that have reported on coyote activity in urbanized landscapes have been consistent, with an increase in nocturnal activity with the level of development or human activity within the home range (Atkinson and Shackleton 1991, Quinn 1997a, Gibeau 1998, Grinder and Krausman 2001b, McClennan et al. 2001, Tigas et al. 2002, Riley et al. 2003, Morey 2004). Coyotes typically reduce their activity during the day as a result of living in close proximity to people. Given the strong consistency in this behavior across studies and metropolitan areas, exceptions to this nocturnal pattern would seem to be good indicators of habituation in coyotes, and a precursor to conflict.

At least two benefits to coyotes may result from nocturnal behavior. Coyotes can more easily avoid humans during nighttime because people may have more difficulty observing them or less human activity occurs at night. Also, traffic volumes are usually lower during nocturnal hours than during daytime, and this may allow coyotes to cross roads more easily at night. Given that a major mortality factor is often collisions with vehicles, a shift to nocturnal activity may be particularly important to survival in urban landscapes.

Habitat selection

Habitat or land use selection has been evaluated for coyote populations in Tucson, Los Angeles, Seattle, and Chicago metropolitan areas (Quinn 1997a, Grinder and Krausman 2001b, Tigas et al. 2002, Morey 2004), among others. Although coyotes may maintain territories within the urban matrix, there is a trend among studies for coyotes to avoid developed areas, such as residential areas, within the home range (Quinn 1997a, Riley et al. 2003, Morey 2004), or to use residential/developed areas in proportion to their availability (Gibeau 1998, Grinder and Krausman 2001b, Way et al. 2004). However, there is some ambiguity regarding this behavior as coyote use or avoidance of developed areas may vary seasonally (Grinder and Krausman 2001b) or time of day, with an increase of urban use during the night (Tigas et al. 2002). Perhaps higher resolution data from GPS collars will shed more light on the complexities of coyote response to developed habitat.

Food Habits

Dietary studies of coyotes in urbanized areas have typically reported diets dominated by small mammals (e.g., rodents, lagomorphs, Table 3). Comparisons across studies indicate variability in the frequency

of human-related food in the diet. For example, human-related foods ranged in frequency from 2 to 35% in studies summarized in Table 3, with most occurring below 20%. Interestingly, one of the lowest frequencies of human-related food occurred in the diet for coyotes in the Chicago area, where scats were collected from an area of relatively high urbanization and human use. Coyotes in that study had access to refuse, but nevertheless primarily consumed prey or vegetation (Gehrt 2004). The lack of refuse in the diet, despite its availability, was supported by radiotelemetry data that

determined coyotes were not focusing their movements around refuse areas (Gehrt 2004). The urban area for the study from Los Angeles contained a large trash dump (Fedriani et al. 2001), which likely affected the frequency of human-related food in that study, and the studies from the Tucson and San Diego areas were relatively small in scale. More dietary studies with careful sampling designs spanning various areas within metropolitan landscapes are needed to clarify diets of coyotes in the city.

Table 3. Diet studies from scat analysis for suburban/urban coyotes, and frequency of occurrence (expressed as %) for selected diet items. Cat refers to domestic cat.

| Study Site | No. scats | Diet Items (%) | | | | Source |
|-----------------|------------------|----------------|--------|-----|---------------|------------------------------|
| | | Leporid | Rodent | Cat | Human-related | |
| San Diego, CA | 97 | 14 | 8 | 2 | 17 | MacCracken 1982 |
| Los Angeles, CA | 250 ^a | 15 | 40 | 1 | 16 | Fedriani et al. 2001 |
| Tucson, AZ | 667 | 32 | 28 | 1 | 35 | McClure et al. 1995 |
| Chicago, IL | 1,429 | 18 | 42 | 1 | 2 | Morey et al. 2007 |
| Albany, NY | 274 | 40 | 14 | <1 | <1 | Bogan and Kays, unpubl. data |

^aThis sample is from the most urbanized site in their study.

Although comparisons among studies are somewhat ambivalent regarding use of anthropogenic foods, within-study comparisons have yielded consistent patterns of increasing frequencies of human-related foods with proximity to residential areas. Studies in Los Angeles, Chicago, and Seattle metropolitan areas collected scats along urban gradients, and each study reported higher frequencies of anthropogenic items in the diet in more urbanized areas (Quinn 1997b, Fedriani et al. 2001, Morey et al. 2007). For example, Fedriani et al. (2001) reported 24% occurrence of anthropogenic foods in a residential area, whereas that frequency was only 0-3% in a rural area. Fedriani et al. (2001) and Morey et al. (2007) also found a relationship between local urbanization and

diet breadth, reflecting the flexible foraging behavior of coyotes (Bekoff and Gese 2003).

Coyote predation on pets is a major contributor to human-coyote conflicts, but domestic cat or dog are consistently found in low frequencies in dietary studies (Table 3). The highest published frequency of occurrence for domestic cat in the coyote diet was only 13% for an urban area in Washington State (Quinn 1997b). This indicates that coyotes may not always consume cats or dogs that are killed by them, and that coyotes in urban areas are not dependent on pets for food.

CONCLUSION

It is important to note that my review is of urban coyote studies that, to my

knowledge, focus on the general coyote population and not necessarily of nuisance coyotes, or coyotes in conflict with people. The picture that emerges is of an animal that largely avoids people, either temporally or spatially, even while living in close proximity to them within the urban landscape. This is in sharp contrast to the picture of coyotes drawn from only media accounts that necessarily focus on human-coyote incidents.

The trend toward smaller home-range size in urbanized areas, coupled with relatively high survival, suggests that coyote populations are successful at establishing resident populations at high densities in close proximity to people. Despite their relative tolerance to urbanization (Crooks 2002) and ability to establish territories encompassing developed areas, many coyotes still avoid areas of high human use, even within the territory. This tendency to avoid people by shifting to nocturnal activity and possibly avoiding developed habitats at the local scale is likely closely tied to diet, and is consistent with a low frequency of human-related food over large areas. These results suggest that there are behavioral characteristics in coyotes that can result in minimizing conflicts with people, but that human actions can affect coyote behavior in negative ways. In particular, the opportunistic nature of coyotes may cause them to take advantage of anthropogenic foods, which may alter their tendencies to avoid people (Baker and Timm 1998, Gehrt 2004, Timm et al. 2004). Thus, effective management strategies that emphasize public education may be especially effective in preventing coyote-human conflicts.

Although some interesting patterns are beginning to emerge from ecological studies of urban coyotes, there is still the need for more research in metropolitan areas with different population densities and patterns of development. Urban/suburban

studies of coyotes have varied substantially in sample size, have often been located on the fringes of the larger metropolitan areas, and variations in the reported behavior of coyotes (such as use of developed habitat) may be a function of the location of the study area with respect to the city, sample size. Diet studies are extremely important for understanding conflicts and coyote behavior, yet they are often conducted on a small scale or suffer other limitations. In particular, diets need to be compared between coyotes residing in urban areas with and without nuisances. These comparisons need to consider spatial and temporal variations in prey abundance and coyote/human behavior (Morey et al. 2007). With recent technological advancements in radiotelemetry, current and future research will be able to provide a high resolution view of coyote movements across developed landscapes. This technology is now underway in research projects located in the New York metropolitan area (P. Curtis, pers. comm.), Tucson, Arizona (Shannon Grubbs, pers. comm.), St. Petersburg/Tampa, Florida (Melissa Grigione, pers. comm.), and the Narragansett Bay Coyote Study, Rhode Island. It is important that research continues to expand to additional metropolitan areas with different levels and patterns of development to gain a more complete understanding of how coyotes respond to urbanization, and the implications for coexistence and conflict between humans and coyotes in the city.

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