

Coyote Ecology and Conflicts with Humans across the Urban-Wildland Gradient: Identifying the Potential Impacts of Changing Land Use

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Abstract

Conflicts between humans and coyotes (Canis latrans) vary across the urban-wildland gradient. As the human population becomes more concentrated in urban centers and land use types succeed from wildland to rural to suburban to urban, the nature of conflicts will change. It is essential for the coexistence of humans and coyotes to understand coyote ecology (i.e. foraging habits, home range sizes, habitat selection, etc.) within these different environments to inform wildlife managers as to how a changing landscape will effect coyote survival and human-coyote conflict into the future.

In wildland areas, coyotes have been accused of negatively impacting availability of deer (Odocoileus spp.) for recreational hunting. Eastern coyotes have been documented to exhibit larger body size and a greater dependence on white-tailed deer (O. virginianus) in recent years, however, deer-coyote dynamics appear to be largely unexplored. Similarly, the effects of secondary contact between coyotes and wolves (C. lupis, C. lycaon, C. rufus) in wolf reintroduction areas is largely unstudied. This is perhaps due to the dominant theory that wolves historically excluded coyotes and will likely do so again in areas where they have been reintroduced. This theory, however, does not account for convergence in prey base in wolves and eastern coyotes, or possible effects of hybridization on interspecific interactions.

In rural environments coyotes have long been persecuted for depredation of sheep. Depredation management has had little benefit for the sheep industry to date, and the efficacy of economic subsidies should be further investigated and compared to other management strategies. There has also been little investigation into whether increased dependence on deer has an effect on livestock depredation. Depredation rates should be compared between larger eastern coyotes which have incorporated deer as a significant portion of their diet and smaller western coyotes.

The study of coyote ecology in suburban and urban environments is a relatively new but growing field. Its importance is only increasing as the United States continues to urbanize. Studies conducted thus far indicate that coyote populations have been able to not only survive, but to expand and thrive in many suburban and urban environments. Understanding the impact of such urbanization on coyotes is critical from a management perspective. Coyotes have been known to attack domestic pets and, on rare occasions, humans. Such encounters will likely only increase if coyotes continue to adapt to living in developed areas. More studies on coyote population dynamics and structure in suburban and urban environments are needed to make informed management decisions in the future.

Introduction

Human-wildlife conflicts have been a long standing issue in several sectors, but most prominently in agriculture. Perhaps the most controversial of these impacts has been the conflict between predators and livestock production, leading to policy innovation and the creation of entire governmental departments, such as the USDA's Wildlife Services, for management implementation purposes. Many of these predators are large species with charismatic qualities: bears, wolves, mountain lions, and coyotes most notably. In more recent history, NGOs have contested traditional management practices in the interest of preserving large predators for their intrinsic and ecological value. As landscape use changes with expanding zones of urbanization, it is intuitive that the nature of human-wildlife conflicts will also change. It is of interest to evaluate and predict these changes to implement preemptive management strategies to minimize future conflicts. This paper intends to review the existing literature the coyote (*Canis latrans*) across an urban to wildland gradient. Due to an abundance of literature and the capacity for coyotes to adapt and thrive in variable landscapes, they provide an excellent starting point to begin assessing wildlife management frameworks into the future.

The Urban-Wildland Gradient

The urban-wildland gradient is a term that is commonly used to refer to the continuum of development density from urban centers to surrounding undeveloped areas. Several sub-categories are identified within this gradient:

Urban – high density areas of human habitation. The U.S. Census Bureau defines urban areas as having a high density core of more than 386 people per km² and surrounding census blocks containing at least 193 people per km².

Suburban – lower density areas of human habitation surrounding urban areas,

Exurban – remote developments associated with urban areas but geographically dissociated,

Rural – very low density areas that are unincorporated/not associated with a municipality, defined by the Census Bureau as all areas that are not urban, and

Wildland/Natural Areas – areas lacking human development.

Many of the studies reviewed in this paper do not provide quantitative definitions of these sub-categories. Because the boundary between urban and suburban categories remains undefined, they are treated as a single designation in this review. Little information exists on exurban interactions and will be excluded from this review.

Coyote Ecology and Management History

Prior to European colonization, coyotes were primarily restricted to the plains regions of North America and arid portions of southern Texas and Northern Mexico (Parker, 1995). Today, they are ubiquitous across the continent. Small mammals (primarily rodents and lagomorphs) and large ungulate young and carrion are the most important food sources for coyotes (Berger et al., 2007; Fedriani et al., 2001).

Coyotes have a variable social structure that Pryah (1984) indicated was a function of four classes of social condition: 1) den-breeders, 2) den-non breeders, 3) transients, and 4) dispersers. The breeding pair is dominant in the pack, and are referred to as the alpha individuals. Non-breeders are generally offspring of the alpha pair that did not disperse after reaching maturity. Dispersal appears to be dependent on food availability and inter/intraspecific competition (Patterson et al., 2001; Pryah, 1984; Messier and Barrette, 1982). Atwood (2006) found that habitat type and proximity to anthropogenic activity also played a significant role in coyote group size – forest edges are thought to support larger groups because they contain high prey density and provide abundant refuge. While coyotes are often outcompeted by wolves, they have been documented to exclude wolves from a carcass where the coyotes outnumber the wolves (Merkle et al., 2009). Interestingly, coyotes east of the Mississippi River are thought to have hybridized with eastern wolf populations, resulting in significantly larger body size than western populations,

(Stronen et al., 2012). This larger body size may contribute to an ability to take down larger game and compete with wolves where the coyotes maintain large pack sizes.

Following government sponsored predator eradication programs in the early 20th century, coyotes expanded their range into areas where they had previously been excluded by apex predators such as wolves (*Canis spp.*) and mountain lions (*Puma concolor*) (Berger et al., 2007). Today, coyotes are found from southern Canada to Central America from coast to coast in almost every habitat type (Ripple et al., 2012). Two principle hypotheses exist to explain this dramatic range expansion. The first theory is centered on the extirpation of gray wolf (*Canis lupus*) populations from much of the country by the mid-20th century. Wolves and coyotes are interference predators, and coyote population densities are often inversely related to wolf densities (Berger and Gese, 2007). The elimination of the top predator in the east may have paved the way for coyote migration by removing their principle competitor. The second theory is based on the idea that human alteration of the landscape through logging activities has created additional coyote habitats (Gompper, 2002). While these landscape changes were detrimental to other carnivore species and contributed to the extirpation of wolves, coyotes were able to adapt to and thrive in these altered landscapes. It is likely that the combination of the removal of apex predators and the clearing of land facilitated population expansion throughout the country.

Coyote habitat use is primarily restricted by anthropogenic activity and development rather than by vegetative community. Kays et al. (2008) found that forested habitats with an open under-story were utilized just as often as the grassland habitats in which coyotes evolved. Likewise, in the arid west, little difference in habitat type has been associated with coyote density. Fedriani et al. (2001) found substantially higher densities of coyotes associated with urban environments; however this is attributed to anthropogenic supplementation of the food supply and increased water supply. Despite the increased densities observed in urban areas, coyotes spend the majority of their time in natural patches such as parks, open space, and riparian corridors – only moving through developed areas at night when human activity is minimal (Reily et al., 2003).

Wildland Environment

Habitat Preference

Coyote expansion out of the plains regions was greatly facilitated by clearing of forest habitat and elimination of larger predators (Parker, 1995). Abandoned farms provided early seral stage forest and edge habitat with high prey diversity, and it is thought that such habitats provided a pathway for eastward coyote expansions (Parker, 1995). Landscape use models and field data show a preference for similar early seral stage forest habitats fringing rural areas in New York, and timber harvest areas in West Virginia (Kays et al., 2008; Crimmins et al., 2012). There is evidence that coyotes existed in the western United States prior to European settlement (Sacks et al., 2004); however they still show a preference for highly heterogeneous habitat structure characterized by open to sparse canopy in these regions, including scrubland and juniper woodland in southeastern Colorado (Gese, 1988), and salt bush scrub in the interior coast ranges of California (White et al., 1995). This pattern is seen again in tropical forest regions such as western Mexico where coyotes have been shown to prefer areas cleared for grazing (Hidalgo-Mihart et al., 2006). It is hypothesized that coyotes colonized tropical areas of Mexico and Central America following European land clearing activity for agriculture (Parker, 1995). Preference for heterogeneous and early seral stage habitats may be due to availability of preferred prey, which is consistently rodents, lagomorphs, and deer across most habitat types (Gese et al., 1988; Hidalgo-Mirhart et al., 2006; White et al., 1995).

Home Range Size

Resident coyotes maintain significantly smaller home range sizes than transient animals (often by 7-8 times), and females generally have smaller home ranges than males within both groups (Gese et al.,

1988). Home ranges (95%MCP) have been measured at $4.3 \pm \text{km}^2$ and $42.8 \pm 17.7\text{km}^2$ ($\mu \pm \sigma$) for male resident and transient coyotes respectively in Mesquite Scrub habitat in south Texas, $11.3 \pm 5.8\text{km}^2$ and $106.5 \pm 27.7\text{km}^2$ in Juniper-Piñon Woodland in southeastern Colorado, $4.1 \pm 0.7\text{km}^2$ and $49.3 \pm 12.3\text{km}^2$ for prairie with interspersed woodland in Kansas, and $20.61 \pm 5.4\text{km}^2$ (only two transients observed with 82 km^2 and 107 km^2 home range sizes) in early successional forest habitats in North Carolina (Andelt, 1985; Gese et al., 1988; Kalmer and Gipson, 2000; Schregost et al., 2007).

Home ranges have been shown to vary in size depending on time of year, with smaller home ranges observed during the pupping season (Andelt, 1985). Variation in territoriality and home range size may be related to increasing foraging efficiency to feed immobile pups (Messier and Barrette, 1982). Home range has also been shown to vary with prey density; however variation is limited by territorial boundaries and encounters (Patterson and Messier, 2001).

Population Density and Social Structure

Coyotes typically maintain relatively low densities in wildland areas ($0.3 - 1/\text{km}^2$) (Andelt, 1985; Fedriani et al., 2001). Social structure has not been shown to vary significantly from other land use categories, but eastern coyotes have been documented chasing single wolves (*Canis lupus*) from a carcass where the coyotes outnumber the wolf (Merkle et al., 2009). As wolves recolonize areas occupied by coyotes there may be selective pressure for larger coyote pack size.

Foraging Habits

Eastern coyotes have been documented to have significantly larger body size than western coyotes (Way et al., 2007). Hypotheses for this include increased dependence on larger prey has led to larger body size, and larger size is the direct result of hybridization with eastern timber wolves (*Canis lycaon*). There is support that the former may be the primary driver as wolf packs dependent on white-tailed deer (*Odocoileus virginianus*) often have smaller sized members than packs which prey on larger game like elk (*Cervus elaphus*) (Way et al., 2007).

Management Issues and Strategies

Human wildlife conflict in wildland areas is primarily concerned over competition between hunters and coyotes for wild game. In the northeast, white-tailed deer is a principle component of the coyote diet (Parker, 1995; Kays et al., 2007). Larger coyotes adapted to taking larger game will have secondary effects in the rural environment. As preferred habitats are often early seral stage/edge/disturbed, many coyote packs live in proximity to rural environments. Larger pack hunting coyotes may be better able to take larger livestock in addition to sheep. Furthermore, coyotes in packs have been documented to actively exclude transient/dispersing wolves from deer kills in Montana where wolves have been re-introduced (however wolves in groups of two or more often killed coyotes during disputes over a kill) (Way et al., 2007). Eastern timber wolves have been shown to have smaller body size in eastern Canada where large game such as elk and caribou (*Rangifer tarandus*) no longer exist (Schmitz and Lavigne, 1987). The driver for smaller body size is hypothesized to be dependence on smaller game, such as white-tailed deer (similar driver for larger body size in coyotes) (Schmitz and Lavigne, 1987). Areas of secondary contact may have dramatically different interactions from those documented historically between coyotes and wolves. McVey et al. (2013) showed red wolves (*C. rufus*) and coyotes exploiting similar prey bases in North Carolina. Several explanations for red wolf and coyote coexistence in this environment have been given, such as high abundance of mutual prey base and differential exploitation of other resources – but territorial interactions were neither described nor accounted for. If larger coyotes are indeed able to compete with smaller wolves, there would be implications for wolf reintroduction efforts (e.g. target wolf packs with larger average body size for relocation into areas where elk are still present in viable numbers, or reintroduce large game in conjunction with wolves). Such interactions are likely variable among differing species.

Rural Environment

Habitat Preference

Rural landscapes tend to be highly heterogeneous and attract an abundance of small mammalian prey which are principle components of the coyote diet. Similarly, such habitats are preferred by deer, which have become a primary source of prey for coyotes in eastern North America. Conversion of old growth forest and dense vegetation types to pastoral land attracts coyotes as it results in an increased density of prey items. This has resulted in depredation conflicts, particularly involving sheep in rural environments.

Home Range Size

Coyote home ranges often contain both rural and wildland land use types, as they prefer heterogeneous and edge habitats (Kays et al., 2008). Atwood (2006) found that size and distribution of refuge patches and movement corridors was positively correlated with territory size ($R^2 = 0.76$, $p < 0.0001$) – smaller refuge patches that were farther apart were associated with larger territory size. However, this study area was located in rural Indiana, and may reflect a hostile environment where refuge is a more important habitat element than food availability (e.g. coyotes shot on site). Such human-coyote dynamics would result in large variability in territory size depending on the social perception of coyotes locally, type of cultivation (e.g. sheep versus corn production), and cultivation intensity and extent (which directly affects size and dispersion of refuge habitat elements).

Population Density and Social Structure

Coyote population density and structure is primarily affected by whether and what sort of depredation programs are in place. Alpha pair coyotes (particularly the males) are often the culprits of depredation events – particularly where breeding range overlaps with livestock production (Mitchel et al., 2004; Blejwas et al., 2006). Reduction of population density through depredation programs has been documented to result in larger litter size (Knowlton, 1972). Lower coyote density results in reduced intraspecific competition for small mammalian prey – therefore more prey per capita is available. Atwood (2006) found that aggregated resource patches (encompassing both refuge and prey elements) supported significantly larger pack sizes (5.2 ± 0.47 individuals; $\mu \pm SE$) than more dispersed resource patches (2.2 ± 0.24 individuals; $\mu \pm SE$). Further information is needed on the specific weight refuge has on pack size compared to prey abundance. However lower coyote population density due to depredation management would result in both more refuge and prey per capita and would allow for larger pack sizes in contiguous refuge habitat fringing rural areas. This contrasts with a previous study by Messier and Barrette (1982) who found that pack size is related to delayed dispersal of young due to increased foraging efficiency, increased social bonding during the mating and pup-rearing seasons, and/or lack of unoccupied habitats. Atwood's data suggests there is more weight to the forage aspect of this hypothesis, but other effects are still unclear. More information is needed on the relationship between resource type and availability, pack size, and individual dispersion in rural environments.

Foraging Habits

Coyotes living in rural environments have similar prey preferences to those occupying other habitat types; however, depredation is a salient management issue where home ranges overlap with livestock management areas. Alpha pair coyotes (particularly the males) have been shown from salivary DNA samples taken from sheep carcasses to be the primary culprits of depredation events (Blejwas et al., 2006). Predation on sheep has been associated with late spring and summer seasons when pups are still present, but the small mammal prey base is diminished. Castrated alpha males were shown to maintain authority in the pack, but did not predate on sheep as frequently – indicating sheep predation is related to providing for pups from a reliable and relatively abundant food source (Mitchell et al., 2004).

Management Issues and Strategies

Coyotes have been accused as a major contributor to the decline of sheep production in the United States over the past 100 years; however predator control efforts have been shown to have no significant effect on sheep production –market forces may provide a better explanation for the decline in U.S. sheep production over the last 100 years (Berger, 2006). Despite this, depredation management has dominated primary literature. Wolves were the historic target for depredation management, and were extirpated from the majority of their range through active depredation programs and loss of habitat and large ungulate prey (Berger, 2006). Conversely, coyotes do very well in habitats that have been disturbed by human activity due to dependence on smaller prey which cohabitate with low density human development. This, combined with the high reproductive rate of coyotes, makes them highly resistant to the same management programs which were successful against wolves (Berger, 2006). Strategies ranging from any combination of “shoot-on-site”, trapping, denning, and poisoning have proven to be only temporarily effective in reducing coyote populations, if at all. Pitt et al. (2001) produced a population model for coyotes that indicated that a population could recover within 1 year unless it was reduced by at least 60%. Even populations reduced by as much as 90% recovered within 5 years if there was no continued eradication effort (Pitt et al., 2001). As coyote populations become sparser, more effort is needed to capture the remaining individuals – making 100% eradication an unfeasible prospect for government sponsored programs (Berger, 2006). Furthermore, aggregated U.S. Wildlife Services data on litter size in Texas suggests that low density populations under active depredation management produced litters of 6-7 (6.9) pups on average, whereas only 4-5 (4.3) pups were produced on average in unmanaged areas (standard deviation not reported, sample sizes were 21 and 63 respectively) (Knowlton, 1972). Lack of efficacy for coyote depredation management programs indicate subsidy programs for livestock production may be a better use of government funding (Berger, 2006). Further studies are needed to compare differences in the efficacy of subsidy versus other better studied alternative management programs. More detailed studies on the effect of population density on litter size would be valuable to corroborate Knowlton’s work, and establish whether regional differences exist.

Urban/Suburban Environment

Habitat Preference

While the habitat fragmentation associated with human development has been documented to be detrimental to many vertebrate species, generalist predators with a wide niche breadth are often capable of maintaining healthy populations in disturbed habitats (Gehring and Swihart, 2003). Generalist species, such as coyotes, are typically highly mobile, able to exploit a variety of habitat and food resources, and capable of using edge habitats. These characteristics allow them survive in fragmented landscapes comprised of decreased patch sizes, increased edge to interior habitat ratios, higher patch isolation, and variable patch connectivity (Saunders et al., 1991). Several studies have examined the ability of coyotes to exploit the extensively fragmented landscapes of suburban and urban environments. In a study of coyotes in the Chicago metropolitan area, Gehrt et al. (2009) found considerable variation in habitat selection by individual coyotes, with some coyotes exclusively occupying a single patch of natural land (habitats protected from development but exposed to human use), and others occupying patches comprised completely of developed areas. Overall, however, coyotes were found to significantly prefer “open” (golf courses, cemeteries), “undeveloped” (patches too small for development or that form buffers between developments), and “water” (retention ponds with emergent vegetation) habitat categories. Each of these categories provides cover, while undeveloped areas also provide foraging opportunities. Grindler and Krausman (2001a) similarly found a great deal of variation in the habitat preferences of coyotes in Tucson, though their home ranges included more than 30% natural, park, and residential patch types, likely due to the availability of food and cover that these offer. Meanwhile, several studies conducted in areas with large tracts of undeveloped land have shown that coyotes may avoid developed landscapes when undeveloped patches are available. Along an urban to rural gradient beginning in Chicago, coyotes were observed exhibiting a preference for less developed landscapes (Randa and Yunger, 2006). Coyotes

were found in 6 of 18 urban sites, and in 18 of 29 rural sites. Similarly, in Seattle, coyotes were found to primarily inhabit forested areas bordering residential areas (Quinn, 1997). The studies that have been conducted on coyote habitat use thus far appear to suggest that while coyotes are certainly capable of occupying highly developed areas, they exhibit preference towards less developed habitat patches, whether these are small fragments located within suburban or urban areas, or more substantial rural patches fringing developed areas.

Home Range Size

The relationship between home range size and urbanization appears to be inconclusive at this point. Atwood et al. (2004) found that in west-central Indiana, coyotes inhabiting areas with greater human-development density and high traffic volume roads had home range sizes that were much smaller than those of coyotes in rural areas. They hypothesized that the smaller home range size in urban areas may be due to increased food availability. Conversely, Gese et al. (2012) found that coyotes in developed areas maintained home ranges that were twice the size of those in less-developed areas. The authors suggest that this result is due to the resource dispersion hypothesis, which is based on the idea that animals inhabiting dispersed patches require larger home ranges in order to meet their basic needs (MacDonald, 1983).

Similar to trends identified in wildland and rural environments, transient coyotes maintain significantly larger home range sizes than resident coyotes. In Chicago, Gehrt et al. (2009) found that the mean (\pm SE) home range sizes of transient coyotes (26.80 ± 2.95 km²) are significantly larger than those of resident coyotes (4.95 ± 0.34 km²). Grindler and Krausman (2001a) noted a similar trend among urban coyotes in Tucson, though the average home range sizes of coyotes in their study were substantially larger: 105.2 ± 37.9 km² and 12.6 ± 3.5 km² for transients and residents, respectively. Home range size in urban environments may also vary seasonally. In central Tucson, home range size was highest during the breeding season and lowest during the dispersal season (Grubbs and Krausman, 2009). However, several other studies, such as Gehrt et al. (2009) and Grindler and Krausman (2001a), found no such correlation between seasonality and home range size. Additional studies examining temporal variations in the home range size of urban coyotes are needed to attain more conclusive results.

Population Density and Social Structure

Few studies have published density estimates of urban coyote populations. However, based on those that have been done, there appears to be an overall positive relationship between the occurrence of coyotes and urbanization (Gehrt et al., 2011). Ordeñana et al. (2010) found that coyote occurrence increased with proximity to and intensity of urbanization in southern California, indicating an overall positive response of coyotes to urbanization. However, the authors were not able to identify individuals, so these results do not represent coyote abundance or density. Fedriani et al. (2001) found coyote population density to be highest in the most developed portion of the study area (2.4-3 individuals per km²), and lowest in the least developed area (0.3-0.4 individuals per km²). The highest estimated coyote population density published to date was calculated at the interface of suburban Tucson and Saguaro National Monument in Arizona, where densities were estimated to range from 3.2 to 4.6 individuals per km² (McClure et al., 1996). Considering that a density of 2 coyotes per km² was thought to only be achievable in extremely favorable environments (Knowlton, 1972), the relatively high densities estimated by Fedriani et al. (2001) and McClure et al. (1996) appear to demonstrate that suburban and urban environments are highly suitable for coyotes. This is likely due to the ability of coyotes to exploit urban food sources, such as garbage, pet food, and cultivated fruit. However, there may be a tolerance threshold for urbanization. In Chicago, coyote density was found to be lowest (0.4-0.7) in the area of highest development (75% urban) (Gehrt et al., 2011). Furthermore, coyote numbers have been found to decline in urban environments in which habitat fragments were too small or isolated (Crooks, 2002). Therefore, suburban/urban coyotes still require sufficient natural habitat patches to persist in these environments. Fringe habitats containing a matrix of developed and undeveloped patches, such as the Tucson/Saguaro National Monument study

area, allow coyotes to exploit the resources of both habitat types and therefore may represent ideal conditions that allow coyote populations to thrive.

Several studies have found that annual survival rates, an important mechanism of coyote population density, are higher for urban coyotes than rural coyotes. Survival rates in Chicago, Los Angeles, and Tucson range from 58% to 74% (Gehrt et al., 2011; Tigas et al., 2002; Riley et al., 2003a; Grindman and Krausman, 2001b), while survival rates in Albany, New York were found to be 20% (Bogan, 2004). Interestingly, Gehrt et al. (2011) estimated an adult survival rate of coyotes in Chicago similar to that of adult coyotes in rural Illinois (59%); however, a survival rate of 61% was calculated for urban juveniles, which was five times that of rural juveniles. The authors suspect that coyotes are more vulnerable in rural environments due to the year-round, limitless hunting and trapping of coyotes in the state. In this respect, metropolitan areas can provide protection to coyotes from exploitation by humans. Concerning mortality, it may be expected that urban coyotes would be at greater risk for being struck by cars or ingesting toxins such as rodenticides. However, Riley et al. (2003a) found no association between vehicle deaths or poisoning and urban association for coyotes. While humans are indeed the greatest threat to coyote survival in urban areas, rural coyotes are also exposed to risks of vehicle collisions, poisoning, hunting, and trapping.

Foraging Habits

The urban coyote diet is typically dominated by small mammals, such as rodents and lagomorphs. Deer carrion and plant material also constitute significant portions of diets in urban environments. However, urban coyotes consume a greater proportion of food from anthropogenic sources, such as garbage and domestic fruit, than do rural coyotes (Fedriani et al., 2001). Dependence on human-associated food items by urban coyotes has been found to vary between studies, ranging from 1.9% (Morey et al., 2007) to 35% (McClure et al., 1995) to 40.9% (Shargo, 1988). Morey et al. (2007) found that the occurrence of human-associated foods in scat was greater during the pup-rearing and dispersal seasons, which also coincide with periods during which people are more active outdoors. Increased outdoor recreation is thought to result in more garbage available in parks and open space for coyote forage (Morey et al. 2007). Coyotes occupying sites with the highest levels of human development have also been found to have the greatest dietary diversity (Fedriani et al., 2001). The utilization of a diversity of food sources may help coyotes persist in urban areas and explain the positive relationship between coyote population density and urbanization. Domestic cats have also been found to comprise between 6% and 13.6% of suburban and urban coyote diets (Quinn, 1997; Shargo, 1988; Morey et al., 2007). Coyote predation on household pets can raise significant alarm among residents and result in the implementation of coyote management strategies.

Management Issues and Strategies

Traditional coyote management strategies that are commonly implemented in rural environments, such as hunting and lethal trapping, may not be feasible in areas of dense human population. Furthermore, suburban and urban residents may be less accepting of lethal control methods. In a survey of Denver residents, Wittmann et al. (1998) found that the majority of respondents viewed lethal methods negatively, unless the consequences of human-coyote interactions were severe. Respondents agreed coyotes should not be killed if seen in an open space (73%), a residential area (62%), or in a person's yard (57%). However, lethal response became more acceptable if the coyote injured a pet (62%), killed a pet (67%), or carried a disease that posed a risk to humans (86%).

Understanding the public's perceptions of coyotes and their preference for lethal or nonlethal control methods will assist wildlife managers in selecting appropriate management strategies that minimize controversy. Referred to as wildlife acceptance capacity (WAC), this approach to wildlife management is useful for assessing how the public will react to a particular management decision (Decker and Purdy, 1988). The incorporation of public opinion is a primary objective of the adaptive impact management

strategy (AIM) introduced by Riley et al. (2003b). AIM focuses on integrating the fundamental objectives of stakeholders (in urban/suburban environments, this would be the general public) into the decision-making process to identify the most appropriate management strategy. By engaging stakeholders in wildlife management, there is a greater likelihood that stakeholders will accept the chosen management approach (Enck et al., 2006). However, WAC varies among constituency groups, challenging managers to balance the views of multiple groups (Decker and Purdy, 1988).

Both lethal and nonlethal predator control techniques have been used in suburban and urban areas to deal with nuisance coyotes. For example, following the first fatal attack on a human in 1981, padded offset-jaw leg-hold traps were set within a 0.8 km radius of the attack site. Shooting was also used as a secondary method in limited areas within the target zone. Over a period of 80 days, 55 coyotes were trapped or shot within the zone. Lethal techniques were also paired with a massive public education initiative aimed at informing citizens on how to avoid attacks, hazing strategies, and the risks imposed by coyotes (Baker, 2007). Governments are often reluctant to implement lethal control methods, fearing media and citizen backlash, or litigation from animal welfare groups (Timm et al., 2004). Shooting in particular has limited feasibility in densely populated areas.

Because people in suburban and urban environments often engage in activities that inadvertently attract coyotes, such as keeping household garbage, pet food, and fruit trees in yards; public education programs can play an integral role in reducing human-coyote interactions in these environments. Marin County, California and Vancouver, British Columbia are two examples of communities that have implemented successful coyote coexistence programs centered on proactive public education (Fox, 2006). Intentional wildlife feeding has also been cited as leading to attacks, and some cities and municipalities have imposed bans on wildlife feeding; however, such regulations are difficult to monitor and enforce (Timm et al., 2004). Hazing and aversive conditioning techniques offer a nonlethal alternative by attempting to alter coyote behavior. Techniques include shooting starter pistols, pellet guns, and blasting air horns, and have had varying degrees of success. Unfortunately, they are often implemented too late and only temporarily impact coyote behavior (Timm et al., 2004; Baker, 2007).

Whether addressing the issue of nuisance coyotes in rural or suburban/urban environments, the ability to directly target problem coyotes can determine in large part the success of control programs. Gehrt (2004) suggests that the removal of non-problem coyotes may simply lead to their replacement by other members of the local coyote population. Furthermore, local extirpation of coyotes is not cost-effective, and can lead to direct and indirect effects along trophic cascades, such as an overabundance of rodents. Control methods should therefore attempt to be selective toward problem coyotes, though this is a difficult task (Mitchell et al., 2004).

Summary and Recommendations for Future Studies

The coyote is a highly adaptable species that has continued to expand its numbers and distribution despite 200 years of persecution by humans. Regional variants, such as the eastern coyote, have become apparent with differing body size, pack size, and prey types (Way et al., 2007; Kays et al., 2008). Their ability to adapt to changing environments is likely to result in significant changes in the frequency, degree, and very nature of human-coyote conflicts as habitats are transformed from wildland to rural to suburban/urban. Hybridization with other large canids and access to larger prey in eastern North America have generated coyotes that may interact in rural and suburban/urban environments differently than what has been previously documented in observations of its western counterpart. Based on this review of the existing literature, further studies are needed in the following areas for anticipation and management of human-coyote conflict into the future:

- 1) Coyote-wolf hybridization: Endangered wolf populations may face genetic dilution as significant proportions of populations become hybridized with coyotes. Such hybridization has been identified as a conservation concern for the red wolf. More information as to what conditions facilitate coyote-wolf interbreeding and the rate at which such events occur would be helpful for wolf preservation.
- 2) Eastern coyote-wolf interactions: Current information shows that wolves are mostly able to outcompete coyotes for food where wolf reintroduction programs have been implemented and in areas of secondary contact in contracted wolf ranges. However, coyotes have been documented chasing wolves off from a kill where coyotes outnumber wolves. Coyotes are also not being excluded on a regional scale in these areas – rather they are occupying habitats that are of lower quality for wolves (e.g. early successional forests and grassland habitats). Assessment of how coyotes and wolves interact in today’s highly fragmented landscape would provide insight into how to manage wolves into the future as well as to whether habitat type was the primary means by which wolves were historically able to restrict coyotes to the prairies and shrub-lands of the Midwest and southern United States.
- 3) Larger-body size/coy-wolf hybrid interactions with livestock: As larger sized eastern coyotes become more dependent on deer, the impacts to livestock are unclear. Further study is needed to determine whether coyotes preying primarily on deer are more or less likely to depredate livestock.
- 4) Effect of larger scale habitat fragmentation on coyotes: More in depth examination is needed as to the effect refuge habitat loss has on coyote group size and social structure. Current evidence suggests that smaller, more dispersed habitat fragments result in larger home range size; however, determinants of pack size are less clear (some studies suggest prey density, others prey body size, and still others habitat saturation).
- 5) Suburban/urban coyote ecology: While coyotes are a well-studied species, the majority of previous research has focused on coyote ecology in rural and wildland environments. The need to understand coyote behavior in urban areas has only arisen within the last 30 years. Suburban/urban coyote ecology therefore is still a relatively young field of study, and the need for understanding coyotes in these environments continues to grow. The majority of studies that have been conducted on coyote ecology in suburban/urban landscapes have focused on cities in the western United States, such as Los Angeles, Denver, and Tucson. Western coyote populations are well-established and therefore have been the subject of much study. However, coyotes are ubiquitous throughout the country today, and major gaps exist in our knowledge of suburban/urban coyote ecology in eastern states in particular.
- 6) Contemporary suburban/urban coyote population density estimates: The majority of studies documenting coyote population density in suburban/urban environments are at least a decade old. Knowlton (1972) is one of the most frequently cited studies on coyote density. Additional studies should be conducted on coyote density in multiple suburban and urban settings, to determine whether densities in these environments have changed over time. This would provide an improved understanding of whether coyotes are continuing to adapt to urbanization. Furthermore, while the results of several studies suggest that coyote density increases with urbanization, there appears to be a threshold tolerance for coyotes. Determining this threshold would have significant impact on our understanding of the ability of coyotes to continue to thrive in developed areas, and provide insight into how they will be affected by expanding urbanization in the future.

- 7) Suburban/urban coyote population structure: Virtually no studies have focused on coyote population structure in suburban and urban environments. In rural landscapes, aggregated patches generally support larger pack sizes; therefore, as habitats become more fragmented with increased development, population structure and group dynamics may change. Changes in population structure may also result in changes in foraging habits and home range sizes, for example, and are therefore an important component of suburban/urban coyote ecology.
- 8) WAC is a relatively new concept and further study into the public perception of predators is critical to shaping wildlife conservation and management policy.

With the above information, more informed management decisions will be possible as shifts in land management continue into the future. This will have important consequences for canid diversity in North America, as well as for shaping depredation policies (e.g. subsidies may be more effective than active depredation efforts) and canid conservation and management efforts.

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