Research Paper

More dogs less bite: The relationship between human–coyote conflict and prairie dog colonies in an urban landscape

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HIGHLIGHTS

- We assess human–coyote conflicts in an urban landscape.
- We explore the role of black-tailed prairie dog colonies in impacting conflict.
- Rates of coyote conflict were highest near habitat fragments where prairie dogs were absent.
- Prey availability may influence human–carnivore conflicts in urban areas.

ARTICLE INFO

ABSTRACT

Human–coyote conflict in urban environments is an emerging concern throughout the U.S., but specific factors that influence rates of conflict remain largely unknown. We explored a possible link between coyote conflict rates and the distribution of black-tailed prairie dogs, a highly interactive species, in an urban landscape. Overall, rates of coyote conflict appeared elevated in proximity to undeveloped land, but these rates were highest near habitat fragments where prairie dogs were absent, and 15–45% lower within 400 m of fragments colonized by prairie dogs. Multivariate analyses comparing conflict points to random points generated in the same area also revealed that smaller and younger habitat fragments were associated with greater levels of conflict. However, the effect of nearby habitat fragments lacking prairie dogs was at least as strong as the effect of fragment area, a factor known to influence coyote distribution. We propose several possible explanations for reduced human–coyote conflicts on or near prairie dog colonies, including colonies acting as more preferred foraging habitat than backyards or neighborhoods, and changes in human behavior near colonies. Inter-species dynamics are rarely investigated in urban systems, and our study provides a first look at potential interactions between two politically controversial but ecologically important species. We suggest that future studies evaluate the impact of prey availability on human–carnivore conflicts to determine whether conservation of prey species may represent a valuable management strategy in urban areas.

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1. Introduction

Cities were created to produce resources and opportunity for people around the world, but increasingly do so for wildlife species as well (Adams, 2005; Chace & Walsh, 2006; Forman, 2008; Magle, Hunt, Vernon, & Crooks, 2012; Mayer, 2010). While species diversity in urban areas can be reduced, species that are able to adapt to these altered landscapes often become quite abundant, sometimes attaining densities higher than those recorded in undeveloped areas (Magle et al., 2007; Prange, Gehrt, & Wiggers, 2003; Riley, Hadidian, & Mansky, 1998). Many urban species provide tangible benefits (e.g., pollination, Mendes, Balmer, Kaethler, & Rhoads, 2008), and the natural areas that attract wildlife are esthetically pleasing and can increase property values (Bolitzer & Netusil, 2000; Waddell & Moore, 2008). Unfortunately, when humans and wildlife share urban space, negative interactions can occur, including incidents of animal-vehicle collision (Forman, et al., 2003), damage to lawns and landscaping (Urbanek, Allen, & Nielsen, 2011),

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transmission of zoonotic disease (Bradley & Alitzer 2007), and animal attacks on pets, and rarely, people (Curtis & Hadidian, 2010; Gehrt & Riley, 2010; Poessel et al., 2013).

Many small and medium-sized carnivores thrive in urban areas, particularly those with generalist diets and opportunistic behavioral patterns (Crooks, 2002; Gehrt, Riley, & Cypher, 2010). Coyotes (*Canis latrans*) exemplify this archetype, and have become increasingly common in cities across North America (Gehrt & Riley, 2010; Gehrt, Anchor, & White, 2009; Poessel et al., 2013). While the majority of coyotes never create conflict (e.g. risks for pets and humans, Gehrt et al., 2009; Poessel et al., 2013), a subset of animals do create problems, particularly through attacks on pets (Grubbs & Krausman, 2009; Poessel et al., 2013; Timm, Baker, Bennett, & Coolahan, 2004). While rare, these incidents can negatively impact human safety and well-being, and have become a management priority (Lukasik & Alexander, 2011; Poessel et al., 2013). Variations in foraging behavior, human activity patterns, and territorial behavior with other species have all been suggested as explanations for the spatio-temporal variability in human–coyote conflicts in urban areas (Lukasik & Alexander, 2011; Poessel et al., 2013). Coyotes in urban areas appear to consume largely natural prey but will also forage on human-associated food items (Lukasik & Alexander, 2012; Morey, Gese, & Gehrt, 2007). Examination of unexplored ecological factors such as abundance of natural prey may help elucidate the mechanisms behind the varied rates of human–coyote conflict observed in urban systems.

For carnivores in urban areas, human pets might represent 'sink prey', defined as prey that, if solely consumed by the predator, decreases the fitness of the predator (Simoni, 2012). As humans typically capture and kill carnivores that focus on pets or livestock as their primary food source, this foraging strategy is unlikely to be sustainable in the long-term. Thus, carnivores should avoid these sink prey species, but animals with no other options, as well as injured or inexperienced individuals, may still target human commensals such as pets or livestock. Under these conditions, we would expect the presence of natural prey resources to potentially reduce the rate of conflict between coyotes and human pets.

In the Denver, Colorado metropolitan area, black-tailed prairie dogs (*Cynomys ludovicianus*) represent an abundant prey species (Magle et al., 2007). Prairie dogs are able to persist in urban areas, with no apparent sign of nutritional (Magle, 2008) or genetic (Magle, Ruell, Antolin, & Crooks, 2010) instability, and the vast majority of colony extinctions occur only as a direct consequence of habitat destruction or colony eradication by humans (Magle, Reyes, Zhu, & Crooks, 2010). Urban prairie dogs are frequently exterminated to make way for development or due to concerns regarding plague and impacts to landscaping (Magle, Reyes, et al., 2010). In grassland ecosystems, prairie dogs function as highly interactive or keystone species (Miller, Ceballos, & Reading, 1994; Miller et al., 2000, 2007; Soulé, Estes, Berger, & del Rio Martinez, 2003; Soulé, Estes, Miller, & Honnold, 2005), increasing diversity and altering ecosystem dynamics due to their burrowing activities. In urban areas their ecological role is not as well understood; although they continue to modify vegetative communities (Magle & Crooks, 2008), they do not enhance bird diversity as they do in the wild (Magle, Salamack, Crooks, & Reading, 2012). Prairie dogs are an essential prey item for both aerial and terrestrial carnivores in natural systems, including coyotes (Lomolino & Smith, 2003; Shaughnessy & Cifelli, 2004; Shipley & Reading, 2006). In fact, it has been suggested that when prairie dog populations are reduced, coyotes reliant on that food source may turn to predation on livestock (Reeve & Vosburgh, 2006). However, it is not known whether the prairie dog's ecological role as prey is conserved in urban systems, or what impacts urban prairie dogs may have on carnivore distribution and behavior.

While coyotes do sometimes capture prairie dogs in the Denver area (Magle, personal observation), it is not known whether prairie dogs represent a significant part of their diet. Prairie dog colonies are visually obvious and persistent on the landscape, and in addition to the prairie dogs present, burrows provide habitat for other potential prey species (Hoogland, 1995), such as cottontail rabbits (*Sylvilagus floridanus*). Thus, colonies could represent a reliable food resource for coyotes. In addition, human activities may alter patterns of conflict near prairie dog colonies, for example if people who live in proximity to colonies keep their dogs on leash due to concerns of contracting plague (*Yersinia pestis*) from prairie dogs (Cully, Biggins, & Seery, 2006) or to prevent dogs from harassing wildlife, which also prevents resultant competitive interactions between dogs and coyotes.

Our goal was to test the hypothesis that prairie dog colonies would be associated with reduced rates of human–coyote conflict (e.g., risk to pets and humans, Poessel et al., 2013) in the Denver, Colorado metropolitan area. Using data on coyote conflicts (Poessel et al., 2013) and prairie dog colony distribution (Magle, Reyes, et al., 2010), our specific objectives were to: (1) determine whether the presence of prairie dog colonies was correlated with the rate of human–coyote conflict, (2) investigate whether this correlation, if present, was also measurable within spatial buffers beyond the bounds of the colony itself, and (3) Quantify the relative impact of prairie dogs on coyote conflict rates compared to other landscape factors known to impact the distribution of coyotes, such as habitat availability and habitat fragment area, age, and connectivity (Crooks, 2002).

2. Methods

2.1. Study area

Our research was conducted in and near Denver, CO, USA, a rapidly urbanizing area of approximately 2 million people embedded in a shortgrass prairie biome (Fig. 1). Our study area (368.4 km^2) contains portions of 4 counties and represents a gradient of urbanization (Magle & Angeloni, 2011; Magle & Crooks, 2009; Magle, Reyes, et al., 2010; Magle, Ruell, et al., 2010). Within this area, each potential habitat fragment (for coyotes and/or prairie dogs) was identified, and the presence of prairie dogs was recorded. A habitat fragment was defined as any plot of undeveloped land with an area of at least 1/4 ha that was not regularly landscaped or manicured by humans, and that was embedded in a dissimilar, human-modified urban matrix (Magle & Crooks, 2009). In 2002, there were 384 habitat fragments within this study area, 54 of which were colonized by prairie dogs.

2.2. Overview

We conducted our study in three steps. First, we began by restricting our available data to the existing study area. Then, to investigate the potential role of habitat patches, prairie dog colonies, and other characteristics of the landscape such as habitat area, age, and connectivity in driving the distribution of human–coyote conflict, we performed two separate spatial analyses: (1) a spatial assessment of rates of conflict in proximity to habitat fragments with and without prairie dog colonies, and (2) a multivariate analysis evaluating the relative influence of prairie dog colonies and other landscape variables on human–coyote conflicts.

2.3. Data preparation

Coyote reports were recorded by 22 state and local entities from January 2003 to June 2010 in a 7 county area around Denver, CO,
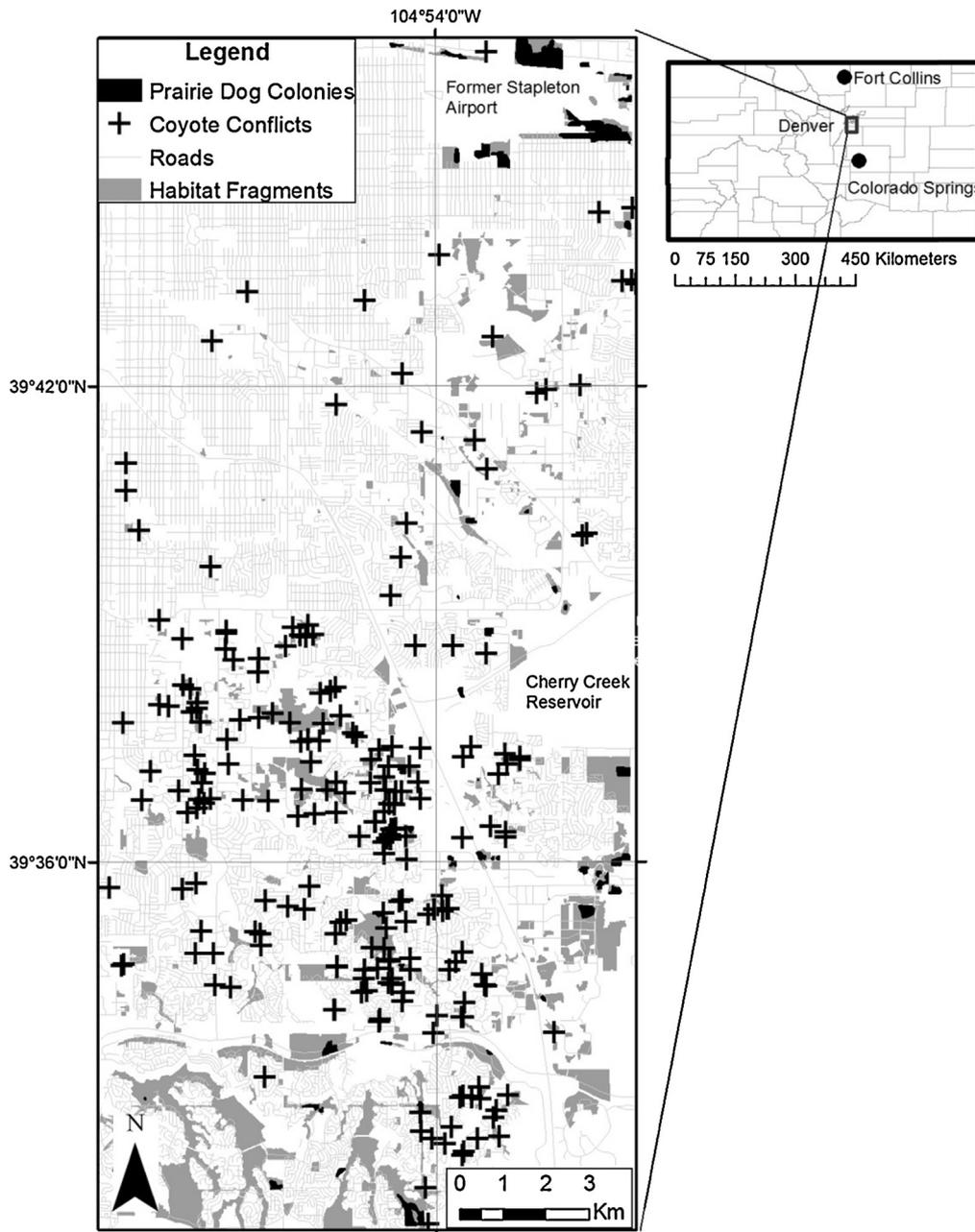
Fig. 1. Map of the study area, coyote conflicts, habitat fragments, and black-tailed prairie dog (*Cynomys ludovicianus*) colony distribution, as well as the relative position of the study area within the state of Colorado, USA.

USA. Most of the reports (93.8%) where the origin could be identified were made by citizens (details in Poessel et al., 2013). Briefly, the data include 510 conflict events, which were defined as incidents (conflicts that include baring teeth, growling, snarling, or stalking humans, 5% of all conflicts), and attacks on humans (3%) and pets (92%) by coyotes. The data, which include date and location, did not include simple observations of coyotes, or encounters between coyotes and humans that were unexpected but did not generate an incident.

To explore the potential interactions between the distribution of prairie dog colonies and the patterns of coyote conflicts, we reduced the 510 conflicts recorded (Poessel et al., 2013) to only the 230 located within the 368.4 km² study area where prairie dog distributions were known (hereafter 'study area', Magle & Crooks, 2009, Fig. 1). We were interested specifically in elucidating the separate effects of prairie dogs and available habitat on human–coyote

conflict. While prairie dog colonies are located within urban habitat fragments, coyotes are also potentially attracted to such undeveloped parcels (Gehrt & Riley, 2010), perhaps regardless of whether those fragments contain prairie dogs.

2.4. Spatial assessment of rates of human–coyote conflict

After determining the number of conflicts within the study area, we then calculated the background rate of conflicts/km² for the entire study area, including areas with no habitat and/or no conflicts. This background rate was then compared to the rate of conflicts/km² within undeveloped habitat fragments (regardless of prairie dog presence). In addition, we generated buffers around habitat fragments at distances of 25 m, 50 m, 75 m, 100 m, 200 m, and so on up to 1000 m, and determined the rate of conflicts/km² within the area encompassed by the undeveloped fragments and

their buffers. All overlapping buffers were dissolved together and were clipped to the extent of the study area. If habitat fragments have an impact on coyote conflicts, either positive or negative, this process allowed us to determine the zone of influence at which this impact can be measured. In addition, to specifically delineate the impact of prairie dogs, as opposed to potential habitat, we repeated this process using only those fragments that contained a prairie dog colony, and then only those fragments that did not. While these differences cannot be tested statistically because no replication exists (only one of each buffer type is calculated), they do provide a spatial depiction of the apparent role of prairie dogs and available habitat on coyote conflicts. We analyzed three different fragment types (those containing prairie dogs, those not containing fragment types, and both types combined) in order to separately assess the potentially confounded impacts of prairie dogs and available habitat, since prairie dog colonies were located only within habitat fragments.

2.5. Evaluating landscape factors influencing conflict

We used a logistic regression/model selection framework to further evaluate the specific effects of prairie dogs on coyote conflict rates, as well as to determine their relative impact compared to landscape variables. As there were 230 human–coyote conflicts within the study area, we created an equal number of randomly generated points within the same area for comparison (Burdett et al., 2010; Johnson, Nielsen, Merrill, McDonald & Boyce, 2006). These random points were spatially constrained only to the limits of the study area, and thus represent availability for conflicts, rather than absence of conflicts. Previous research shows that analyses of this type are relatively robust to potential contamination that results when random points overlap with actual events (Johnson et al., 2006). The proportion of random points within different land cover types closely matched (within 5%) the actual distribution of available land cover, indicating that these points adequately characterize variability within the study area. Our goal was to evaluate whether coyote conflicts tend to occur closer to, or further from, certain types of habitat fragments. Thus, for each of the conflict points within the study area, as well as the random points generated, we determined the distance to the nearest habitat fragment, to the nearest fragment containing prairie dogs, and to the nearest fragment not containing prairie dogs. We ran logistic regression models to determine which of these distance-to-fragment variables best predicted coyote conflict, with actual conflict points represented as '1' and random points depicted as '0'. We used Akaike's Information Criteria corrected for small sample sizes (AICc) to determine the best performing distance-to-fragment variable (Burnham & Anderson, 2002). We restricted models to only one variable since some distance-to-fragment variables were subsets of others, and therefore not independent. We then used the best performing distance-to-fragment variable in all subsequent analyses.

As an additional component to the analysis, we investigated the potential impacts of three biogeographic variables (habitat area, age, and connectivity) known to be important determinants of the persistence of wildlife in urban habitat fragments (Crooks, 2002; Magle & Crooks, 2009). Larger and more connected habitats are more likely to be discovered by dispersing organisms, and to receive new migrants for demographic and genetic stability, while older fragments (those isolated by development for a longer period) may be more susceptible to stochastic events and the long-term impacts of fragmentation (Crooks, 2002; Tilman, May, Lehman, & Nowak, 1994). These factors may be important, as coyotes that cannot discover or persist in certain habitat patches cannot be involved in human–coyote conflict in the vicinity. Thus, we also determined the fragment area, age, and connectivity for the nearest habitat

fragment to each coyote conflict and random point. Fragment area was measured using ArcGIS 9.3 (ESRI, Redlands, CA), and fragment age was determined by review of historical aerial imagery and county assessor records (details in Magle & Crooks, 2009). Researchers previously calculated 11 connectivity metrics of varying complexity for habitat fragments in this system (Magle, Theobald, & Crooks, 2009). The presence of multiple connectivity metrics in predictive models is problematic, both because metrics tend to be strongly correlated, and because interpretation of models comprised of multiple measures of connectivity is challenging. Thus, to select one metric for analysis, following Magle et al. (2009), we created 11 univariate logistic regression models to determine which best predicted the presence of nearby coyote conflicts, as compared to random points (Magle & Crooks, 2009; Magle et al., 2009). Each point, conflict or random, was assigned connectivity values from its closest fragment and the top performing metric was selected using AICc. We then used the selected connectivity metric as our measure of connectivity in subsequent analyses.

Finally, we generated multivariate logistic regression models with conflict/random point as the response variable. As predictor variables we used every possible combination (Doherty, White, & Burnham, 2012) of the terms for (1) best performing 'distance to fragment' metric, (2) best performing connectivity metric on closest fragment, (3) area of closest fragment, and (4) age (time since isolation) of closest fragment, with no interaction terms included. When total number of models are small, every possible combination model selection is increasingly seen as desirable (Doherty et al., 2012), and has the added advantage of creating a balanced model set, necessary for calculation of variable importance weights (Burnham & Anderson, 2002) and thus direct comparison of the importance of each independent variable. We tested for correlation between predictor variables prior to analysis, and excluded any variables with Pearson correlations above 0.70. We tested 16 total models, including an intercept-only model with no other predictor variables. The intercept-only model is presented for comparison to ensure that our tested terms have explanatory power. Before analysis, all variables were re-scaled to span from 0 to 1 to ensure comparability. We also calculated variable importance weights for each predictor variable by adding the weight of all models that contained that variable, and provide evidence ratios comprised of the ratio of Akaike weights, which indicate the strength of each model with respect to the top model (Burnham & Anderson, 2002). If prairie dogs impact conflict rates with coyotes, our top models should contain the terms for distance to prairie dog colonies, or distance to fragments not containing colonies. If instead coyote conflicts are most closely related to available habitat (independent of prairie dog presence), or to the presence of larger, more connected, or more recently isolated habitat, then we conclude that landscape factors are the main drivers of coyote conflicts in this urban landscape.

3. Results

3.1. Spatial assessment of rates of human–coyote conflict

As the study area was 368.4 km^2 and contained 230 conflicts, the background rate of coyote conflict was 0.61 conflicts/km^2. When evaluating rates of conflict within different types of habitat fragments, fragments lacking prairie dogs exhibited rates of conflict 22% higher (0.78 conflicts/km^2) compared to the background rate and 21% higher than fragments containing prairie dog colonies (0.62 conflicts/km^2) (Fig. 2). This elevated rate of conflict on fragments without prairie dogs peaked within buffers 25 m away from habitat fragments (at 1.06 conflicts/km^2) and then fluctuated around an elevated mean, eventually declining at buffers
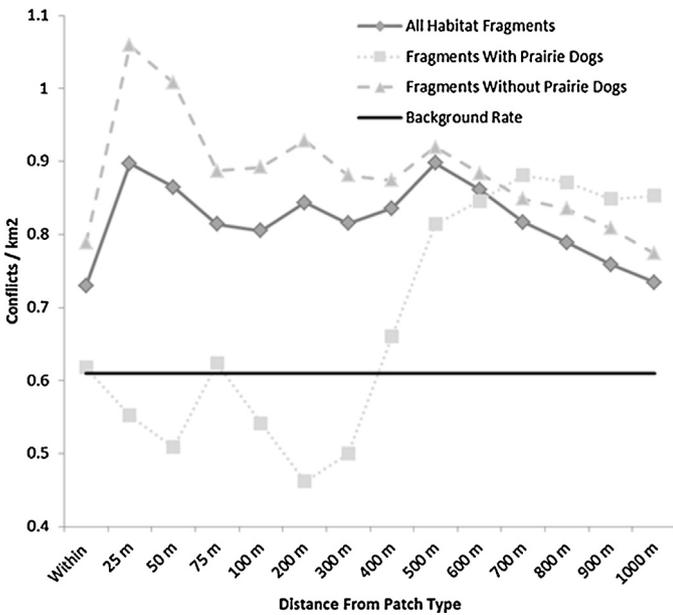
Fig. 2. Assessment of rates of coyote conflict (conflicts/km^2) within all habitat fragments, fragments containing and lacking prairie dog colonies, and within buffers created around fragments. The background rate represents the overall rate of conflict for the entire study area.

greater than 500 m (Fig. 2). Fragments containing prairie dogs were associated with conflict rates approximately equal to or below (range: 0.46–0.62 conflicts/km^2) the background rate until buffer sizes reached 400 m or greater, at which point they exhibited conflict rates similar to other fragment types (Fig. 2). These values are presented only for descriptive comparison and cannot be tested statistically, as each buffer has only one replicate.

3.2. Evaluating landscape factors influencing conflict

When evaluating which types of nearby fragments had the greatest impact on conflict distribution, the top model (AIC weight = 94%, over 15 times stronger evidence than for the next best model) contained distance to fragments lacking prairie dogs,

with conflicts more likely to occur near those sites (Table 1). No other model held more than 6% of the total model weight, indicating a high level of certainty that the top model contained the most explanatory power of those tested (Burnham & Anderson, 2002). Distance to fragments lacking prairie dogs was thus selected for inclusion in subsequent analysis. Of the 11 connectivity metrics tested previously (Magle et al., 2009), edge to edge distance to the nearest fragment performed best, followed closely by a similar metric representing centroid to centroid distance to a nearest fragment (Table 2). Thus, edge to edge distance was selected for inclusion in subsequent analyses.

When combining distance to fragments without prairie dogs with nearby fragment area, age, and connectivity in multivariate models, the four predictor variables were not strongly correlated, with age and connectivity of the closest fragment exhibiting a Pearson correlation coefficient of 0.55, and no other correlation between variables stronger than 0.36. The top performing model contained the terms for nearby fragment area, age, and distance to fragments without prairie dogs, with the second model containing all four variables (Table 3). All other models had evidence ratios >50, indicating little to no support from the data (Burnham & Anderson, 2002). Parameter estimates indicated a negative relationship between coyote conflict occurrence and nearby fragment area and age, as well as distance to fragments lacking prairie dogs (Table 4). Thus, coyote conflicts were more likely to occur (compared to random points) near smaller and younger fragments, and closer to fragments not containing prairie dogs. Variable importance weights indicated a relatively low value for fragment connectivity (Table 5), suggesting connectivity has a limited role in predicting coyote conflict rates.

4. Discussion

We provide evidence that, as we hypothesized, the distribution of prairie dogs in an urban landscape influences the distribution of human–coyote conflicts. Specifically, both a spatial assessment of rates of conflict in proximity to various habitat fragment types and a multivariate analysis evaluating the impact of a variety of landscape features suggest an association between coyote conflicts and prairie dogs in this system. Among habitat fragments, those containing prairie dogs were subject to the lowest overall rate of

Table 1
Results of AICc model selection procedure used to determine the best models predicting locations of coyote conflict based on distance to different types of habitat fragments near Denver, CO, USA. *K* refers to the number of parameters in a model +1.

Model	K	Delta AICc	Model weight	Evidence ratio	Beta estimate	95% CI (low)	95% CI (high)
Fragments without prairie dogs	2	0.00	0.94		−5.12	−6.62	−3.62
All fragments	2	5.49	0.06	15.7	−5.40	−7.08	−3.72
Fragments with prairie dogs	2	53.20	<0.01	2350.7	−1.22	−1.97	−0.47
Intercept only	1	61.66	<0.01	2771.2	0.68	0.38	0.97

Table 2
Results of AICc model selection procedure used to determine the best fragment based connectivity metric predicting nearby coyote conflict near Denver, CO, USA. *K* refers to the number of parameters in a model +1.

Model	K	Delta AICc	Model weight	Evidence ratio	Beta estimate	95% CI (low)	95% CI (high)
Nearest fragment–edge to edge	2	0.00	0.53		−1.83	−2.92	−0.74
Nearest fragment–centroid to centroid	2	0.64	0.39	1.38	−1.98	−3.17	−0.79
Nearest colony–centroid to centroid	2	6.47	0.02	25.38	−1.00	−1.78	−0.22
% of colonies within 2000 m	2	6.84	0.02	30.53	−3.67	−7.18	−0.16
% of colonies within 1000 m	2	6.97	0.02	32.66	−2.74	−5.25	−0.24
Nearest colony–edge to edge	2	7.92	0.01	52.40	−0.83	−1.56	−0.10
% of habitat fragments within 2000 m	2	8.45	0.01	68.39	1.02	0.07	1.98
% of colonies within 200 m	2	9.09	0.01	94.09	−2.34	−5.05	0.35
Intercept	1	10.97	0.00	241.07	0.03	−0.15	0.22
% of fragments within 200 m	2	12.51	0.00	521.52	0.37	−0.69	1.42
% of fragments within 1000 m	2	12.65	0.00	558.86	0.33	−0.79	1.44
T-stat	2	13.08	0.00	691.87	0.09	−1.77	1.96

Table 3
Results of AICc model selection procedure used to determine the best model used to predict nearby coyote conflict near Denver, CO, USA. Models were comprised of all possible combinations of the predictor variables: closest fragment area, closest fragment age, and fragment connectivity, as well as distance to nearby fragment without prairie dogs. *K* refers to the number of parameters in a model +1.

Model	K	Delta AICc	Model weight	Evidence ratio
Area, age, distance to fragment without prairie dogs	4	0.00	0.71	
Area, age, connectivity, distance to fragment without prairie dogs	5	2.04	0.25	2.77
Age, distance to fragment without prairie dogs	3	8.18	0.01	59.75
Area, connectivity, distance to fragment without prairie dogs	4	8.44	0.01	68.07
Age, distance to fragment without prairie dogs	3	8.54	0.01	71.53
Age, connectivity, distance to fragment without prairie dogs	4	10.56	0.00	196.25
Distance to fragment without prairie dogs	2	11.58	0.00	326.81
Connectivity, distance to fragment without prairie dogs	3	12.75	0.00	587.96
Area, age	3	39.79	0.00	4.37E + 08
Area, age, connectivity	4	39.94	0.00	4.70E + 08
Age	2	54.35	0.00	6.34E + 11
Age, connectivity	3	54.43	0.00	6.60E + 11
Area, connectivity	3	55.37	0.00	1.06E + 12
Connectivity	2	62.33	0.00	3.43E + 13
Area	2	69.81	0.00	1.44E + 15
Intercept	1	73.30	0.00	8.24E + 15

Table 4
Beta coefficients from top two models predicting distribution of coyote conflicts near Denver, CO, USA. Fragment area, fragment age, and fragment connectivity are calculated for the nearest habitat fragment to each conflict and random point.

Model	Parameter	Estimate	Standard deviation
Area, age, distance to fragment without prairie dogs	Area	−1.74	1.11
	Age	−1.68	1.08
	Distance to fragment without prairie dogs	−4.49	2.60
Area, age, connectivity, distance to fragment without prairie dogs	Area	−1.74	1.11
	Age	−1.70	1.09
	Connectivity	0.04	0.58
	Distance to fragment without prairie dogs	−4.50	2.61

conflict, while those lacking colonies exhibited the highest rates. The rate of human–coyote conflict associated with colonized fragments was much lower than for other habitat fragments in the study area, both within the fragments and up to 400 m away. To our knowledge, we are the first to directly investigate a link between a prey species and human–carnivore conflicts in an urban landscape. However, as we did not directly measure coyote predation rate on prairie dogs, the mechanism driving the relationship remains speculative.

Coyotes in urban systems tend to gravitate toward remnants of natural habitat (Gehrt et al., 2009; Riley et al., 2003). As such it is relatively unsurprising that rates of conflict increased in and near habitat fragments, which were comprised of undeveloped land, compared to the background level throughout the study area. Numerous studies have shown that coyotes and other carnivores in cities tend to be present in larger and more connected patches of natural habitat within urban boundaries (Crooks, 2002; Gehrt & Riley, 2010), and as such we anticipated higher rates of conflict near larger fragments. However, we actually detected a negative relationship between coyote conflict rate and the area of adjacent habitat patches, indicating conflicts were less likely to occur near larger fragments. We suspect that this is not due to a lack of coyotes in larger patches, but due to altered coyote or human behavior

Table 5
Variable importance weight for each of the predictor variables used to predict coyote conflict distribution in Denver, CO, USA. Weights are calculated by adding the model weights for each model that includes the given variable. High variable importance weight values indicate more explanatory power for that variable.

Variable	Total weight
Distance to fragment without prairie dogs	>0.99
Area	0.98
Age	0.97
Connectivity	0.27

within and near these patch types. For example, large patches (which in this system also typically exhibited the lowest levels of landscaping and trails) may have proportionally less edge habitat in which coyotes encounter humans and pets. In addition, larger fragments would tend to harbor more prey species (Brueste, Niemelä, & Snep, 2008; MacArthur & Wilson, 1967), which could in turn reduce conflict by providing alternate food sources for coyotes. A previous study in Calgary, Canada also found higher coyote conflict rates near smaller parks, and attributed the difference to reduced prey populations (Lukasik & Alexander, 2011). Habitat age was also an important predictor, with younger fragments (those isolated by urbanization for a shorter time) associated with higher rates of conflict. We suspect this is because younger fragments tend to be located at the urban fringe, closer to undeveloped areas, which might be more likely to harbor coyote populations. While landscape variables clearly have explanatory power for coyote conflicts in this system, in the multivariate analysis, the distance to habitat fragments lacking prairie dogs actually held the highest variable importance weight, indicating that it was at least as important as the other tested variables in predicting the distribution of coyote conflicts.

While the mechanisms behind the prairie dog–coyote dynamics in this system remain unclear, prairie dogs and associated organisms living in prairie dog colonies may be a food resource for coyotes and thus lessen energetic constraints that may cause them to attack humans and pets (Simoni, 2012). Coyotes are known to hunt on urban colonies and sometimes capture and consume individual prairie dogs (XXX masked for blind review, personal observation). Coyotes in urban areas typically focus their foraging efforts on natural prey items (Gehrt, 2004; Gehrt & Riley, 2010; Morey et al., 2007), and in this system prairie dogs and other prey associated with colonies are apparently fairly abundant, and are certainly extremely predictable, as colonies are visually apparent and cannot readily change location. While prairie dogs

use alarm call behavior and retreat to burrows to avoid predators such as coyotes (Hoogland, 1995), avoidance behaviors are not always successful, and alarm call behavior can be relaxed following repeated human exposure (Magle, Zhu, & Crooks, 2005). Coyotes are frequently observed (XXX masked for blind review, personal observation) waiting motionless above burrows before dawn, presumably to increase the odds of capture. Poessel et al. (2013) revealed that human–coyote conflict rates in this system are highest in winter and hypothesized this was due to changes in coyote and/or human behavior in winter. We offer another hypothesis to explain this pattern, that in winter prey populations on prairie dog colonies are at their lowest levels. Studies in other systems found differing (Lukasik & Alexander, 2011) or no (White & Gehrt, 2009) seasonal relationships, which could be attributed to differing prey patterns in those systems.

However, there are also other potential explanations for the patterns observed. Most of the conflicts in this system involved a coyote attacking a pet near a home, but of conflicts within open space areas, most involved unleashed dogs (Poessel et al., 2013). Humans who perceive a risk from coyotes or other wildlife may be less likely to let their animals roam freely, either in a yard or while on a walk. It is possible that people who reside near open space, particularly near prairie dog colonies, may be better informed regarding wildlife issues (George & Crooks, 2006; Milley, 2008), and thus may engage in behavior designed to avoid conflict such as securing pets, maintaining fencing, and not approaching or feeding wildlife. Similarly, prairie dog colonies may be seen as a hazard to pets due to concerns about both plague and injury when stepping in burrows (Lamb, Reading, & Andelt, 2006). Thus, conflicts may be reduced on prairie dog colonies simply because human residents prevent dogs from roaming free on those sites.

Coyote conflict data in this system should be interpreted cautiously due to the inherent limitations of the dataset. Coyote conflicts were largely self-reported by citizens and willingness to report incidents likely varies spatially, temporally, and with respect to attitudes of individuals toward wildlife (Poessel et al., 2013). The entities that collected the reports varied in the timespan over which data were collected and in the methodology used to compile information. Increasing media attention has likely increased the reporting rate over time, but whether rates of increase differ near habitat fragments of different types remains unknown. While previous research made use of a large database of coyote observations from this same area (Poessel et al., 2013), including visual observations of coyotes or their sign, we restricted our analysis to conflict data (human and pet attacks and aggressive incidents) as these data are expected to be less biased because of the severity of the interaction. It should also be noted that due in part to the relatively coarse spatial resolution of the conflict data, we were unable to assess local fine-scale landscape features such as the presence of shrubs and other cover features, drains, fences, and other factors that may influence the distribution of coyotes in an urban landscape.

5. Conclusion

Urban ecosystems are slowly becoming popular targets for research (Forman, 2008; Mayer, 2010; McDonald, Kareiva, & Forman, 2008). However, studies directly investigating interactions between species remain rare (Magle, Hunt, et al., 2012). To gain a complete understanding of the ecology of urban areas, it will be necessary to evaluate not only the component species, but the nature of the relationships between them. In addition, while wildlife management techniques such as population control, sterilization, exclusion, and translocation are relatively common topics in urban wildlife research, direct investigations into the human conflicts and property damage that those techniques are designed

to mitigate remain uncommon (Magle, Hunt, et al., 2012). Thus, our study is novel in directly investigating dynamics of a potential urban predator–prey dyad with respect to human–wildlife conflict. While not conclusive, our results suggest dynamics which, if verified in other systems and with other species, could have implications for management of human–wildlife conflict in cities worldwide. While certainly prairie dogs are not present in all urban centers, abundant prey species such as ground squirrels and rabbits may play a similar role in other systems.

The mechanisms that underlie the relationship between urban predators, prey, and human–wildlife conflict remain unclear and may be biological, sociological, or a combination of both. Dietary analysis of urban coyotes in this system as well as behavioral observations of movement would be needed to verify 'sink prey' dynamics (Simoni, 2012), in which coyotes with access to natural prey are able to fulfill foraging needs without resorting to investigation of yards and attacks on pets. Surveys of residents living in the area could shed light on whether the presence of prairie dogs influences human behavior and thus reduces conflict rates (Milley, 2008). Future studies that combine prey availability, human and pet behavior, predator dietary analysis, and conflict data would further elucidate how presence of prey species may serve to reduce conflict between carnivores and humans. If prairie dogs are confirmed to reduce rates of conflict in this landscape, strategic management of colony placement could be used as an urban wildlife management strategy. In some cases, conservation of urban prey may constitute a 'win–win' scenario (Rosenzweig, 2003), in which multiple wildlife species can be productively maintained within the world's most altered landscapes.

Acknowledgments

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