Effects of urbanization on the behaviour of a keystone species

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Summary

Habitat fragmentation and urbanization not only cause extirpation of species, but also alter the behaviour of species in human modified areas. We evaluated behavioural characteristics of the black-tailed prairie dog (*Cynomys ludovicianus*), a keystone species, in the urban landscape of Denver, CO, USA. Specifically, we investigated the proportion of vigilance, foraging, and social behaviour within a system of urban colonies that varied in area, degree of connectivity, and time since isolation. Overall, rates of vigilance were lower than are typically reported for black-tailed prairie dogs in grassland habitats. Colonies that were more isolated exhibited higher levels of vigilance, but colonies isolated for a longer period of time exhibited reduced vigilance. Thus, while urban stimuli may increase alertness in the most isolated colonies, we suggest that black-tailed prairie dogs might eventually adjust to these stimuli and relax their vigilance responses. Because behaviour varies based on age of fragments, we provide evidence that black-tailed prairie dog populations are responding to urbanization through behavioural changes that may be adaptive. The ability to understand how landscape-level factors influence black-tailed prairie dog behaviour provides important information about the response of keystone species to urban settings and can aid conservation and management efforts in fragmented systems.

Keywords: connectivity, habitat fragmentation, keystone, landscape ecology, prairie dog, urban habitat.

1. Introduction

Habitat fragmentation and urbanization are critical threats to biodiversity (Wilcove et al., 1998; Czech et al., 2000) that not only cause localized

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extinctions, but also alter ecological interactions, behaviour and fitness for those species that persist in or near urban environments (Marzluff, 2008). Acquisition of nature preserves for wildlife has been levelling off in recent years (Blair & Johnson, 2008), and as such the importance of anthropogenic landscapes for biodiversity conservation will only increase (Harveson et al., 2007; Chipman et al., 2008; Mayer, 2010). Behaviour is predicted to be one of the first traits to change in a modified environment (Plotkin, 1988; Wcislo, 1989; West-Eberhard, 1989; Riechert, 1993). Indeed, birds and mammals that remain in urban habitats often exhibit modified patterns of behaviour, including altered habitat selection and breeding patterns, modified communication signals, attraction to anthropogenic features and changes in social and anti-predator behaviour (e.g., Estabrook, 1999; Yeh & Price, 2004; Magle et al., 2005; Patricelli & Blickley, 2006; Wood & Yezerinac, 2006; Harveson et al., 2007; Chipman et al., 2008; Rodewald & Shustack, 2008; Valcarcel & Fernandez-Juricic, 2009).

Because anthropogenic impacts can alter behaviour in ways that may affect fitness and population persistence, the study of animal behaviour is now recognized to provide important insights into conservation (Buchholz, 2007; Caro, 2007; Angeloni et al., 2008). Understanding how wildlife in urban areas might modify their behaviour is useful in determining the extent to which animals can adapt to new stimuli and persist in human-modified landscapes, identifying which urban habitats are capable of supporting certain species, and delineating how urban ecosystems function (Marzluff et al., 2008).

The specifics of how animals respond behaviourally to urbanization, however, are still somewhat unclear, with existing hypotheses providing alternate predictions. For example, the risk-disturbance hypothesis (Frid & Dill, 2002) predicts that animals disturbed by novel stimuli such as humans, pets, and added levels of noise and light pollution in an urban environment may engage in vigilance and avoidance behaviour similar to those they would use in response to predators. These anti-predator behaviours are energetically costly, require time that could be used for other activities such as foraging (e.g., Festa-Bianchet, 1988; Bachman, 1993; Cawlishaw, 1997), and in some circumstances can limit survival and reproduction, thereby reducing population viability (Frid & Dill, 2002; Fernández-Juricic et al., 2003; Peters & Otis, 2005; Pauli & Buskirk, 2007). However, several hypotheses predict a decrease in vigilance of urban animals. Reduced populations of native predators in highly urban areas (e.g., Crooks, 2002) may lessen the vigilance behaviour of urban animals. Additionally, species frequently exposed to novel stimuli, including humans and associated anthropogenic disturbances, may habituate over time, showing overall decreased responsiveness (e.g., Whittaker & Knight, 1998; Frid & Dill, 2002; Taylor & Knight, 2003; Magle et al., 2005; Harveson et al., 2007; Stankowich, 2008; Knight, 2009). The ultimate outcome on animal behaviour may depend on the type, nature, and duration of urbanization. Thus, human stimuli in urban environments can have complicated effects on animal behaviour that are only beginning to be explored.

The unique characteristics of the black-tailed prairie dog (*Cynomys ludovicianus*, hereafter prairie dog) make it an excellent species to investigate the impacts of human-modified environments on animal behaviour. These burrowing rodents are highly social, and have clearly delineated anti-predator responses (Loughry, 1993; Hoogland, 1995), which are modified by human interaction (Adams et al., 1987; Magle et al., 2005). Prairie dogs live in social groups called coteries within which social interactions are common (Hoogland, 1995). Prairie dogs function as keystone (Miller et al., 1990, 1994, 2000, 2007; Forrest, 2005; Kotliar et al., 2006) and/or highly interactive (Soulé et al., 2003, 2005) species, and as such have the potential to impact numerous other species in their vicinity. The prairie dog plays a pivotal role in prairie and steppe ecosystems, acting as prey for a variety of predators, influencing soil mixing, primary production of plants, and landscape heterogeneity (Holland & Detling, 1990; Ceballos et al., 1999; Bangert & Slobodchikoff, 2000; Hoogland, 2006). Extermination programs, sylvatic plague (caused by the bacterium *Yersinia pestis*), agricultural expansion, and commercial and residential development have reduced prairie dog populations drastically (Miller et al., 1990; 1994; Kotliar et al., 1999; Proctor et al., 2006). Despite these threats, many prairie dog colonies persist in highly urban areas, which is unusual for keystone species (Magle & Crooks, 2008; Magle et al., 2009). Urban prairie dog colonies are known to differ from prairie dogs in relatively intact prairie, including differences in density (Johnson & Collinge, 2004; Magle et al., 2007), changes in seasonal individual condition (Magle, 2008), and modified interactions with other species and local vegetation (Lomolino & Smith, 2001, 2003; Magle & Crooks, 2008), though the specific mechanisms behind these changes remain unknown. Prairie dogs may also experience different predator communities in urban areas. Typical predators in prairie habitat, such as native mammalian carnivores (e.g., badger (*Taxidea taxus*), coyote (*Canis latrans*), swift fox (*Vulpes velox*)) and raptors (e.g., eagles and hawks), may be less prevalent or absent in smaller, more isolated urban habitat islands (e.g., Crooks, 2002; Faeth et al. 2005). Conversely, invasive predators such as domestic cats and dogs would be expected to be more common in urban areas and to have greater access to prairie dogs without venturing far from human habitation (Crooks & Soulé, 1999). Little is known about how behavioural patterns of prairie dogs may be modified in an urban environment, and the impact of behavioural changes on their long-term persistence and conservation.

We used focal animal sampling to evaluate behavioural characteristics of the black-tailed prairie dog within the highly urban landscape of Denver, CO, USA. Specifically, we investigated the proportion of vigilance behaviour, foraging behaviour, and social interactions within a system of urban colonies distributed along an urban gradient that varied in area, time since isolation (fragment age), and degree of connectivity. We generated predictions of responses to degree of urbanization based on existing behavioural theory and hypotheses. If the risk-disturbance hypothesis (Frid & Dill, 2002) has been fundamental in shaping behaviour in highly urban areas, we expected prairie dogs to display increased vigilance due to intensified anthropogenic disturbances on older, and more isolated urban fragments. Alternatively, we predicted that prairie dogs would exhibit lower rates of vigilance in highly urban fragments if habituation to repeated human disturbances (Whittaker & Knight, 1998; Knight, 2009) or reduced populations of primary native predators resulted in decreased responsiveness.

Given the demonstrated trade-off between vigilance and foraging (e.g., Festa-Bianchet, 1988; Bachman, 1993; Cawlishaw, 1997), we also predicted that foraging rates would vary inversely with vigilance across the gradient of urbanization. Additionally, as urban colonies may have reduced forage quantity (Magle & Crooks, 2008), we anticipated elevated rates of foraging on the colonies that were isolated for the longest periods of time. Finally, we predicted increased population densities and possible resource limitations in the smallest, oldest, and most isolated urban fragments would diminish cooperative social behaviour, as behaviour between conspecifics becomes more competitive (e.g., Parker & Nilon, 2008).

2. Materials and methods

2.1. Study area

In the summer of 2002 we used aerial photography maps to identify a section of the Denver Metropolitan area (13 × 29 km, approx. 374 km^2) spanning from downtown Denver south through Highlands Ranch (a southern suburb of Denver), isolating a gradient of increasing urbanization south to north (Figure 1). Denver is a rapidly urbanizing region located in a wider arid short-grass prairie biome. Within the study system prevalent plant species tended to be invasive and were dominated by field bindweed (*Convolvulus arvensis*). At the time of surveying, the southern boundary represented the outer edge of urban development. We performed a census that identified 384 habitat fragments within this study area. A 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 matrix. Habitat fragments in this study were located in residential, industrial, and commercial areas. Highway embankments were omitted due to inaccessibility to researchers. We used paved roads to delineate boundaries between habitat fragments. Recent genetic evidence from a subsample of colonies suggests reduced but measurable movement of prairie dogs among fragments (Magle et al., 2010a).

Consequently, it is possible that prairie dogs from one site might visit the other if separated only by one paved road, but detailed data on prairie dog movement and population dynamics would be needed to verify these events. Given that the urban roads in our study experienced high traffic volumes and were a known source of prairie dog mortality (pers. obs.) and in order to maintain consistency in the study, prairie dog burrows separated by roads were considered separate colonies and prairie dog burrows located on the same fragment were considered part of the same colony. All fragments were verified via field reconnaissance, and characterized as colonized or not colonized by prairie dogs. In 2002, 54 habitat fragments were occupied by prairie dogs.

2.2. Prairie dog behavioural observations

Between July 2003 and August 2004, we collected behavioural data from urban prairie dog colonies, categorizing behaviours using an ethogram (Bekoff

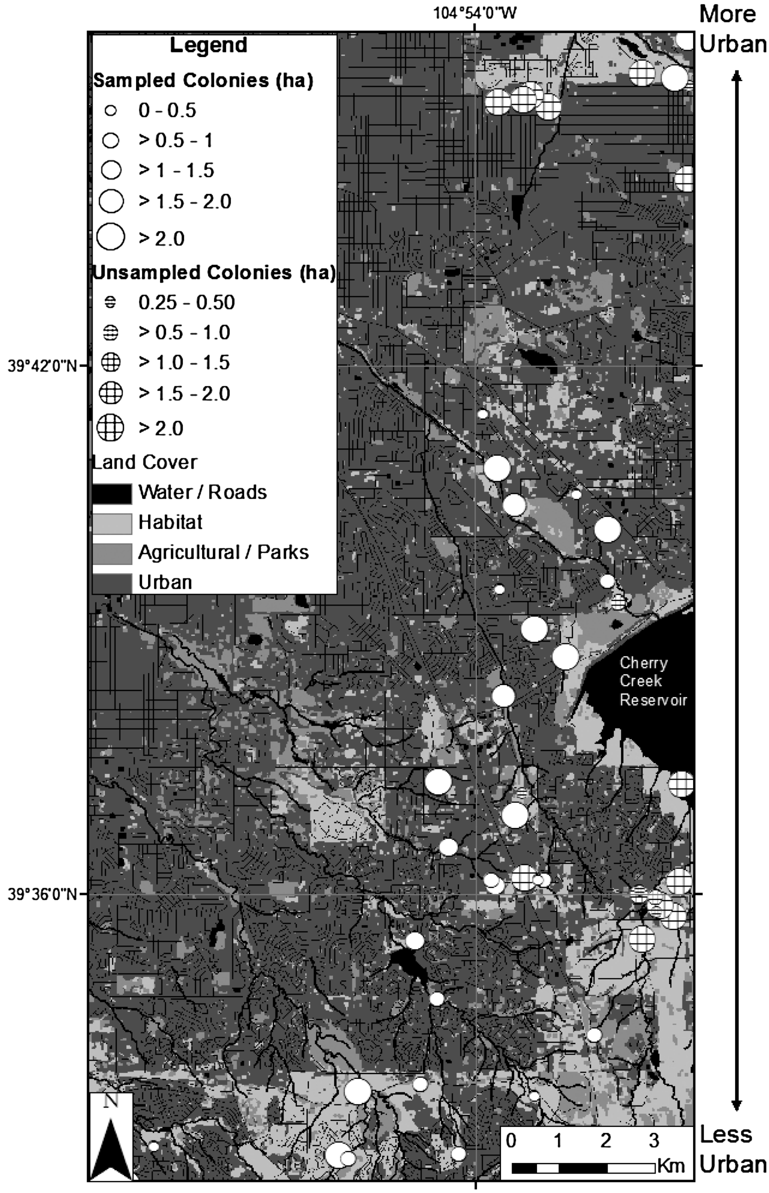

Figure 1. Map of the study area in Metropolitan Denver, CO, USA. Symbols do not represent actual fragment or colony dimensions, but rather location and relative size. Open circles are used to represent sites where behavioural sampling took place, while sites denoted with hashmarks could not be sampled.

& Ickes, 1999; Chipman et al., 2008). Colonies contain multiple coteries, each of which inhabit multiple burrows. In the Denver area, colonies are between 0.25 and 50 ha in area, and are always surrounded by roads and urban development. Behavioural sampling consisted of 2 min continuous focal sampling of individual prairie dogs, repeated 7 times per sampling occasion (once each on 7 different randomly selected individuals). We increased the likelihood that we were sampling different individuals by always selecting prairie dogs located at least 50 m from last known locations of other sampled prairie dogs. After reaching a colony, we waited a minimum of 5 min to begin sampling (Vosburgh & Irby, 1998), which was sufficient for animals to return to normal activity patterns, as animals were typically observed from across a road (Magle et al., 2005). Between each sample, at least 1 min elapsed, and a new focal animal was selected randomly (Valcarcel & Fernández-Juricic, 2009), from a portion of the colony not yet sampled during that session. Focal animals were always adults or yearlings, juveniles were never selected for focal animal sampling. During focal sampling, we recorded the length of time animals spent performing each behaviour. When a focal animal was lost from view or submerged into a burrow during a focal sample, that 2 min sample was terminated, and the next sample was initiated as normal. Behavioural categories included: foraging (prairie dog on all fours, chewing food), vigilance or alert behaviour (prairie dog had head raised, scanning for disturbances, which included both 'posting', or scanning on two legs, and quadrupedal scanning), resting, digging, amicable social behaviour (which included grooming, playing, 'kissing', and anal sniffing), and agonistic social behaviour (which included fighting, territorial disputes, fleeing from other prairie dogs, and interment in a burrow, categories modified from Hoogland, 1995; Vosburgh & Irby, 1998; Foster-McDonald et al., 2006; Manno, 2007; Pauli & Buskirk, 2007). Prairie dogs were typically observed from across roads, and always at a distance at which behaviours were unaffected by study personnel, which could be determined readily (Magle et al., 2005). Proportion of time spent in each behaviour was averaged across the seven scan samples for each sampling occasion. Because the proportion of time spent within each category sums to 1, we omitted both digging and resting behaviour from analyses to avoid a unit-sum constraint. We also omitted agonistic behaviours because they made up less than 1% of the total observation time.

Within the 54 prairie dog colonies present in the study area, we attempted to gather behavioural information from as many colonies as possible. However, because many sites were located on private land and could not be accessed, or were situated such that gathering behavioural observations without disturbing the animals was impossible, a total of 37 sites were sampled. All observations were taken during daylight hours, and during periods without inclement weather or predation attempts. We sampled some sites multiple times (mean $= 2.4$ sampling occasions, $\sigma = 2.0$, range 1–8), and recorded behaviour on a total of 92 sampling occasions across the 37 sites. The number of times a site was sampled was not significantly correlated with any average measures of proportion of time spent in each behaviour (all $p > 0.05$); thus, uneven sampling of sites was unlikely to affect behavioural results. However, there may have been a complex correlation structure among the sequential sampling periods for a given site; thus, to avoid pseudoreplication via repeatedly sampling the same site (Hurlbert, 1984), we calculated the average proportion of time spent in each behaviour for each colony in our primary statistical models, resulting in a sample size of 37 (corresponding to our 37 colonies; see Statistical Analyses below). As the study progressed, we began to record the time of day at the time of sampling, which was, thus, recorded for 66 out of 92 sampling occasions. We attempted to randomize the time of day that colonies were sampled, but some time periods were sampled unevenly, with 1.5% of observations taken between 0600 and 0800, 14% between 0801 and 1000, 34% between 1001 and 1200, 23% between 1201 and 1400, 8% between 1401 and 1600, and 19% between 1601 and 1800.

2.3. Measuring landscape variables

As part of an ongoing, long-term study of the effects of urbanization and habitat fragmentation on prairie dog ecology, we calculated landscape variables for each fragment in the study area as follows: All fragments and prairie dog colonies were digitized in ArcGIS 9.1 (ESRI), and the area of each prairie dog colony (ha) was determined. Prairie dog colony extent was defined by the extent of evident burrows (Hoogland, 1995), which could be readily determined due to very low vegetation on prairie dog colonies (Magle & Crooks, 2008, range 0.25–50 ha). The age of each fragment (time since fragment was completely isolated by urban development) was determined from review of parcel data from Denver, Adams, Arapahoe and Douglas county assessors that indicated the year developments were constructed (range 5–117 year). We determined the number of years since development for each parcel adjacent to a habitat fragment, and used the largest value as a surrogate for age; hence, fragment age may reflect an overestimate of the amount of time since isolation.

Because we were interested in whether behaviour may be impacted by the degree to which a colony is isolated, which has been shown to influence prairie dog dispersal and population dynamics (Magle & Crooks, 2009), we calculated measures of connectivity (or the inverse, isolation) for each colony (Crooks & Sanjayan, 2006). We used multiple measures of connectivity due to findings that no one measure is ideal for all situations (Goodwin, 2003). As a simple measure of isolation, of the type frequently used in ecological studies, we quantified the distance (edge-to-edge) between each colony and the nearest prairie dog colony (Nearest Colony, range 7.1–1627.8 m, with the minimum distance corresponding to colonies across a single road). From the perspective of a dispersing prairie dog, demographic metrics such as distance to the nearest colony may be a more meaningful measure of connectivity than fragment-based metrics such as distance to nearest habitat because prairie dogs are more likely to join existing colonies than to found a new colony (Hoogland, 1995; Magle et al., 2009). We were also interested in measures of connectivity that incorporated the entire nearby landscape, rather than simply quantifying the straight-line distance to a nearest neighbour. To that end, we created a 2-km buffer around each site and quantified the proportion of that buffer comprised of prairie dog colonies (Buffer Colonies, range 0–0.12). These buffer measures at a 2-km scale have performed well in studies of the effects of landscape elements on prairie dog populations (Johnson & Collinge, 2004; Magle & Crooks, 2009).

We were also interested in measures that explicitly acknowledge that different elements of the urban environment such as roads and streams may be particularly difficult for prairie dogs to traverse (Knaapen et al., 1992; Murphy & Lovett-Doust, 2004). To differentiate the landscape elements that may impact movement of animals (e.g., Roach et al., 2001), we created a cost surface raster for the study area (details in Magle et al., 2009). A cost surface is a spatial data layer where each cell is parameterized with a cost value representing how difficult it may be for an organism to move across. Thus, the 'cost' for an organism to move from one fragment to another is the least cost of possible pathways, represented as the sum of the costs of each cell that must be traversed. Cost surfaces are typically constructed based on known movement or habitat selection data (e.g., Ferreras, 2001; Adriaensen et al., 2003). Our cost surface was generated using parameters that exhibited high explanatory power for prairie dog distribution in previous studies (Magle et al., 2009), including water features, stream banks, land use types, and roads and highways. High cost values were applied to road crossings, especially highways and high volume roads, and low costs to cross habitat and travel along streambanks (as in Roach et al., 2001; Magle et al., 2009). We used the cost surface layer to calculate, for each site, isolation as the minimum cost distance to a nearest neighbour (Cost Distance, range 0.71–683.16 cost units).

To summarize, predictive variables in this study were colony area, fragment age, and three measures of connectivity: Nearest Colony, Buffer Colonies and Cost Distance. All variables were transformed by dividing by the highest observed value of that variable; thus, the range for each was 0 to 1, ensuring comparability.

2.4. Statistical analysis

Because colonies were sampled at different times of day, and previous studies had found a strong negative relationship between vigilance behaviour and time of day (with vigilance behaviour peaking at dawn and declining gradually thereafter; Loughry, 1993; Foster-McDonald et al., 2006), we used a simple linear regression to assess the impact of time of day on prairie dog behaviour. Restricting our dataset to the 66 data points that contained information on time, we used the number of minutes since dawn as a continuous, linear variable to predict the proportion of time spent in vigilance behaviour. This analysis used mixed effects models where vigilance behaviour was the dependent variable, minutes since dawn was a fixed effect, and colony was used as a random effect to account for multiple sampling of some colonies. We also used a mixed-effects ANOVA (with Tukey's Honest Significant Difference) to compare vigilance behaviour at different times of the year to investigate a seasonal effect in prairie dog behaviour. Previous work found that prairie dogs greatly increased vigilance in June, and throughout the summer months, presumably because juveniles emerge at that time and are extremely vulnerable (Loughry, 1993; Hoogland, 1995). We compared vigilance data taken in June through August ($N = 50$), when juveniles are emerging and extremely vulnerable, to the months September through December ($N = 29$), when juveniles are maturing and parental alertness may

Table 1. Correlation matrix showing Pearson correlation coefficients between predictive variables for prairie dog behavioural patterns in Denver, CO, USA.

Variable	Colony area	Fragment age	Buffer colonies	Cost distance
Colony area	1.00			
Fragment age	0.16	1.00		
Buffer colonies	0.04	0.06	1.00	
Cost distance	0.26	0.19	0.02	1.00
Nearest colony	−0.08	−0.29	−0.55	0.28

For details of variable determination, see text.

be gradually decreasing, and to January through May ($N = 13$), when juveniles are visually similar to adults and alertness would be expected to be relaxed. Season was modelled as a fixed effect, and colony was included as a random effect to account for multiple sampling of some colonies.

Finally, we constructed regression models to relate the proportion of time prairie dogs spent in vigilance, foraging, and amicable social behaviours to our set of predictor variables. For each of these 3 response variables, we calculated models comprised of every combination of the 5 predictor variables (32 models in each set). Although there were some correlations among predictor variables (Table 1), none were strong enough to warrant exclusion of independent variables from the same model (all $r < 0.6$; Tabachnick & Fidell, 1996). We used a version of Akaike's Information Criteria adjusted for small sample sizes (AIC_c; Akaike, 1973; Burnham & Anderson, 2002) to choose the best performing regression model predicting each of our response variables. Throughout this process, our unit of analysis was the colony, not an individual prairie dog. To determine the relative importance of each predictor variable, we also calculated variable importance weights, which are the summation of the weights for each model that contains a given variable. Variable importance weights can range from 0 to 1, and variables with an importance weight higher than approx. 0.35 have important explanatory power (Burnham & Anderson, 2002). Additionally, we calculated parameter estimates by using model averaging across all models for a given dependent variable, with estimates of variance derived using the Delta method (Burnham & Anderson, 2002).

Because vigilance behaviour differed in the September–December season (see Results), we assessed whether seasonal bias impacted our model selection process by performing a separate AIC analysis in which season was included as a categorical variable, with colonies sampled in September–December differentiated from those that were not. The variable for season was not present in the top 5 models, season had a relatively low (0.36) variable importance weight, and the rankings of the top 5 models and of the importance of other independent variables were not affected. Thus, we concluded that seasonal bias was unlikely to impact our model selection and results reported are from the analysis without season included.

3. Results

Prairie dogs spent 70% (SE = 18%) of their time foraging, 18% (SE = 19%) in alert or vigilance behaviour and 1.1% (SE = 0.2%) performing social behaviours. The proportion of time spent in vigilance behaviour did not depend on the time of day ($t = 1.11$, $p = 0.27$, $N = 66$). There was no significant difference in vigilance level before (January–May, mean vigilance = 0.20, SE = 0.06) and after juvenile emergence (June–August) (mean vigilance = 0.25, SE = 0.03, $F = 0.05$, $p = 0.52$, $N = 13, 50$). However, vigilance was somewhat lower in September–December (mean vigilance = 0.07, SE = 0.02, $N = 29$) than in spring before juvenile emergence ($F = 0.11$, $p = 0.12$), and was significantly lower in the fall and winter months than in the summer after juvenile emergence ($F = 0.16$, $p < 0.01$).

Although some model selection uncertainty was present, vigilance behaviour was best predicted by a model that included the variables for fragment age and the distance to the nearest colony (Table 2, a). These variables also held much more variable importance than the other tested predictors based on variable importance weights (Table 3). Fragment age was negatively related to the time spent in vigilance behaviour, with colonies in older fragments exhibiting lower levels of vigilance (Table 4). More isolated colonies, those with a larger distance to another colony, were characterized by higher levels of vigilance.

Several models of foraging behaviour had some support, but distance to the nearest colony was the only variable present in the top model (Table 2, b), and the most reliable predictor based on variable importance weights (Table 3). The direction of the relationship was negative, with prairie dogs on

Table 2. Results of AIC model selection procedure to determine the best models predicting prairie dog behavioural patterns in Denver, CO, USA.

	ΔAIC	Weight	Sum of weight
(a) Predictors of vigilance behaviour			
Age (−), nearest colony (+)	0.00	0.18	0.18
Age (−), cost distance (+), nearest colony (+)	0.97	0.11	0.29
Cost distance (+), nearest colony (+)	1.43	0.09	0.38
Age (−), buffer colonies (−), nearest colony (+)	1.65	0.08	0.46
Area (−), age (−), nearest colony (+)	1.90	0.07	0.53
Nearest colony	2.02	0.07	0.60
Area, age, cost distance, nearest colony	2.92	0.04	0.64
Buffer colonies, nearest colony	3.16	0.04	0.68
Area, cost distance, nearest colony	3.30	0.03	0.71
Age, buffer colonies	3.51	0.03	0.75
Area, age, buffer colonies, nearest colony	3.53	0.03	0.78
Area, nearest colony	3.64	0.03	0.81
Age	3.75	0.03	0.84
(b) Predictors of foraging behaviour			
Nearest colony (−)	0.00	0.10	0.10
Cost distance (+), nearest colony (−)	0.54	0.08	0.18
Age (+)	0.82	0.07	0.25
Age (+), nearest colony (−)	0.87	0.07	0.32
Area (−), nearest colony (−)	1.23	0.06	0.37
Area, cost distance, nearest colony	1.26	0.06	0.43
Area, age, nearest colony	1.68	0.04	0.47
Area, age	1.90	0.04	0.51
Buffer colonies, nearest colony	1.94	0.04	0.55
Cost distance	2.28	0.03	0.59
Buffer colonies, cost distance, nearest colony	2.34	0.03	0.62
Area, age, cost distance, nearest colony	2.55	0.03	0.65
Age, cost distance	2.56	0.03	0.67
Age, cost distance, nearest colony	2.65	0.03	0.70
Age, buffer colonies, nearest colony	2.66	0.03	0.73
Area	2.70	0.03	0.76
Buffer colonies	2.71	0.03	0.78
Age, buffer colonies	2.78	0.03	0.81
Area, buffer colonies, cost distance, nearest colony	3.03	0.02	0.83
Area, buffer colonies, nearest colony	3.17	0.02	0.85
Area, age, buffer colonies, nearest colony	3.43	0.02	0.87
Area, age, cost distance	3.53	0.02	0.89
Area, cost distance	3.68	0.02	0.91
Age, buffer colonies, cost distance, nearest colony	3.75	0.02	0.92

Table 2. (Continued.)

	ΔAIC	Weight	Sum of weight
Area, age, buffer colonies	3.87	0.01	0.94
Buffer colonies, cost distance	3.97	0.01	0.95
(c) Predictors of amicable behaviour			
Area (+), age (+), buffer colonies (−), cost distance (+)	0.00	0.37	0.37
Area (+), age (+), buffer colonies (−), cost distance (+), nearest colony (+)	1.32	0.19	0.56
Area (+), age (+), buffer colonies (−)	1.43	0.18	0.74
Area (+), age (+), buffer colonies (−), nearest colony (+)	3.37	0.07	0.81

Included are the models with <4.0 ΔAIC, which have considerably greater support (Burnham & Anderson, 2002). Top five models include directionality, where (+) indicates a positive relationship between the predictor and the behaviour type, and (−) depicts a negative relationship. Shown are relations of predictors to vigilance behaviour, foraging behaviour and social behaviour (see text).

Table 3. Variable importance weights, obtained by adding the model weights of each model containing a given variable, calculated separately for each response variable.

Behaviour	Area	Age	Buffer colonies	Cost distance	Nearest colony
Vigilance	0.30	0.67	0.31	0.39	0.86
Foraging	0.40	0.45	0.31	0.41	0.65
Amicable	0.93	0.99	0.87	0.69	0.32

more isolated colonies spending less time in foraging behaviour (Table 4), as might be expected from the inverse result on vigilance.

Colony area, fragment age and measures of connectivity all played a role in predicting amicable social behaviours in urban prairie dogs (Tables 2, c and 3). Prairie dogs in larger, more isolated colonies that were on older fragments exhibited higher rates of amicable interactions such as grooming and playing (Table 4). In the parameter estimates derived via model averaging (Table 4), the signs provided under the estimate column show the direction of the relationship between the dependent and independent variables, and the relative impacts and variability of each can be compared.

Table 4. Parameter estimates for variables used to predict each of the three behavioural variables in this study.

Behaviour	Variable	Estimate	SE	Upper 95% CI	Lower 95% CI
Vigilance	Intercept	0.24	0.06	0.35	0.13
	Age	−0.27	0.15	0.02	−0.56
	Nearest colony	0.21	0.13	0.48	−0.05
Foraging	Intercept	0.77	0.12	1.01	0.52
	Nearest colony	−0.16	0.09	0.01	−0.34
Amicable	Intercept	0.00	0.00	0.00	0.00
	Area	0.02	0.01	0.03	0.01
	Age	0.03	0.01	0.05	0.02
	Buffer colonies	−0.01	0.01	0.00	−0.03
	Cost distance	0.02	0.01	0.02	0.01

Included are the variables from the top predictive model, as derived from AIC methodology, for each response variable. Model averaging (based on AIC weights from model selection) was used to derive estimates. SE, standard error; CI, confidence intervals.

4. Discussion

Our findings demonstrate that behavioural patterns of prairie dogs vary along an urban gradient and are affected by the degree of urbanization, as measured by the size of colonies, the length of time they have been isolated, and their degree of isolation. In particular, the proportion of time prairie dogs invested in vigilance behaviour increased with distance to the nearest colony and decreased with fragment age. Vigilance behaviours are frequently the focus of prairie dog behavioural studies (e.g., Hoogland, 1979; Loughry, 1993; Kildaw, 1995; Vosburgh & Irby, 1998; Bekoff & Ickes, 1999; Magle et al., 2005; Pauli & Buskirk, 2007), because vigilance and alarm call behaviour are key to avoidance of predation (Hoogland, 1995), and may be altered upon disturbance (Vosburgh & Irby, 1998; Pauli & Buskirk, 2007), or in different environments (Magle et al., 2005). More isolated colonies (those with a larger distance to a neighbour and, therefore, embedded in the most urban landscapes) exhibited higher levels of vigilance, perhaps because they are more likely to be surrounded by urban stimuli like pedestrians, bicyclists, and loud traffic, as well as human commensals that may prey on prairie dogs, such as domestic dogs (*Canis lupus familiaris*, Bekoff & Ickes, 1999) and housecats (*Felis catus*, which were observed hunting prairie dogs in this study). These results are consistent with the risk-disturbance hypothesis (Frid & Dill, 2002; Fernández-Juricic et al., 2003; Pauli & Buskirk, 2007), which proposes that in response to human disturbance, novel stimuli, or hunting, animals perceive risk (Valcarcel & Fernández-Juricic, 2009) and increase their vigilance behaviour, alter their foraging, or otherwise modify their behaviour, ultimately at the cost of inefficient resource gathering and sometimes a loss of fitness (Mainguy et al., 2002; Pauli & Buskirk, 2007). Indeed, prairie dogs are capable of increasing vigilance in response to risk — colonies that are subjected to hunting by humans increase their level of vigilance eightfold (Vosburgh & Irby, 1998; Pauli & Buskirk, 2007).

Colonies in older fragments exhibited lower rates of vigilance, perhaps because animals habituate or behaviourally adapt to urban settings over a period of years. There may be reduced benefit of maintaining intensive vigilance patterns, which limits the time spent foraging, because of a lack of realized threat from human stimuli and/or reduced predation, assuming that any reduction in predation by native carnivores in urban areas was not counteracted by increased predation by human commensals. We observed a few instances of predation attempts by both native carnivores (coyotes, red-tailed hawks, Swainson's hawks) and exotic carnivores (domestic cats), but we do not have information on relative abundance of predators or their rates of predation on prairie dogs to fully evaluate this hypothesis.

On average, prairie dogs in this system spent 18% of their time exhibiting vigilance behaviour. We counted all instances in which an animal's head was raised and scanning for disturbances as vigilance behaviour (as in Vosburgh & Irby, 1998; Manno, 2007; Pauli & Buskirk, 2007), and as such may have overestimated the amount of vigilance compared to some previous researchers, who excluded scanning when prairie dogs were also masticating (e.g., Hoogland, 1979, 1995; Loughry, 1993; Kildaw, 1995). Nonetheless, the rate of vigilance we recorded is fairly low compared to previous values from the literature. Hoogland (1979, 1995) reported black-tailed prairie dogs in prairie habitat in South Dakota spent approx. 32–42% of their time scanning for predators, depending on social group size. Loughry (1993), also working in a protected natural area in South Dakota, recorded average vigilance rates varying between 20.6 and 27.5%, depending on sex and parental status. In rural Nebraska (Foster-McDonald et al., 2006), female prairie dogs spent 30–45% of their time in alert postures, depending on whether visual barriers were present. Although average vigilance was lower in our urban fragments than in rural settings, it varied tremendously (range 7–72%) such that for many colonies, vigilance was on par with levels in rural areas. For example, while the vigilance rate averaged only 16% in the least isolated colonies ($N = 27$, <1 km from the nearest colony), it was 38% in the most isolated colonies ($N = 10$, >1 km from the nearest colony), a value which falls within other reported measures. Similarly, the vigilance rate was only 7% in the oldest fragments ($N = 14$, >50 year), but was closer to other reported measures (30%) in the youngest fragments ($N = 7$, <10 year). The high degree of variation in vigilance associated colony isolation and fragment age suggests that any risk disturbance effects caused by humans and pets in this urban system are not consistent and can decrease over time. Thus, while prairie dogs in the most isolated urban colonies may exhibit high levels of vigilance on par with rural areas, this may be an acute effect of urban stimuli, not a chronic one.

Although some previous research has found that prairie dog vigilance was strongly affected by time of day (Loughry, 1993; Foster-McDonald et al., 2006, but see Pauli & Buskirk, 2007), we found no evidence of this relationship in this study, though low sample size may have limited our ability to detect temporal patterns. Prairie dogs in grassland systems typically display maximal vigilance at dawn, when low light levels increase the risk of predation (Loughry, 1993), with alertness levels gradually dropping throughout the day (Loughry, 1993; Hoogland, 1995). However, not only was the relationship between minutes since dawn and vigilance not significant in this study, the weak relationship present was actually reversed, with vigilance levels increasing slightly throughout the day. It is possible that this trend in vigilance correlates with human activity, which increases throughout the day. In a related fashion, it is conceivable that artificial lights in urban areas increase visibility and render additional vigilance at dawn unnecessary. However, additional data would be needed for verification of these hypotheses. Similarly, prairie dogs typically increase vigilance in the months following juvenile emergence because newly emergent animals are particularly vulnerable to predation (Loughry, 1993; Hoogland, 1995). However, in our study, we observed no significant difference in vigilance levels before and after juvenile emergence, though we did observe a large decline in vigilance in the late fall months (September through December). It is conceivable that juvenile emergence in May and June does not serve to greatly shift vigilance behaviour due to reduced rates of predation on juveniles by native predators, which are typically less prevalent in urban areas (Crooks, 2002; Faeth et al., 2005). The reason for the large decline in vigilance late in the year is unclear. It is possible that, because the vast majority of animals remain inactive belowground during these months (Hoogland, 1995), any animals that emerge from their burrows at this time do so solely to build body fat for the winter, and are unable to maintain anti-predator behaviours.

We found that prairie dogs on more isolated fragments (as measured by multiple metrics) spent less time in foraging behaviour, likely because increased vigilance on isolated fragments allowed for less foraging to take place, as prairie dogs spend the vast majority of their time (88% in this study) exhibiting one of these two behaviours. While isolated urban colonies have high proportions of bare ground (Magle & Crooks, 2008), depletion of vegetative forage on urban prairie dog colonies evidently does not lead to reduced body weight (Magle, 2008). The term for fragment age was also present among the top models, with colonies on older sites, which demonstrate lower vigilance, exhibiting higher rates of foraging. In addition to time constraints, it is possible that forage is being gradually depleted on prairie dog colonies isolated for long periods and, thus, elevated levels of foraging are eventually required to maintain body weight. Vegetation monitoring on colonies over a period of many years may be needed to verify this hypothesis. Larger colonies in this area exhibited a greater proportion of amicable social interactions among prairie dogs, perhaps because larger colonies are likely to support larger populations. These colonies may, thus, have larger coteries and more opportunity for cooperative rearing of juveniles (Hoogland, 1995). However, colonies in more isolated and older fragments also displayed higher rates of amicable behaviour, suggesting that cooperative behaviours are maintained even in urban habitat islands that experience density inflation and perhaps scarce resources (Magle & Crooks, 2007; Magle et al., 2007). Social behaviours are essential to the persistence of prairie dogs (Hoogland, 1995, 2006), and shifts in these behaviours in urban areas could be critical to their long-term persistence.

Our results suggest that prairie dogs exhibit behavioural plasticity in urban areas, reducing overall levels of vigilance and modifying behavioural patterns based on the degree of isolation of their habitat. Because the age of a habitat fragment plays an important role in determining the degree of behavioural shift, it is conceivable that these urban prairie dogs are exhibiting adaptation to the novel environment of an urban landscape, through habituation, cultural transmission, evolution, or a combination of the three. However, colonies in this area have only been verified to be isolated by urban development for approx. 50 years, or roughly 25 generations of prairie dogs, and further study is required to determine if indeed these shifts represent evolutionary changes. If present, these adaptations may help explain why this keystone species appears able to persist in highly urban areas (Magle & Crooks, 2009; Magle et al., 2010b), and even maintain some portion of its ecological role therein (Magle & Crooks, 2008; Salamack, 2008).

Urban environments will only continue to increase in prevalence, and acquisition of wildlife reserves is beginning to decline (Blair & Johnson, 2008). Thus, understanding the behaviour and adaptations of species that enable them to persist in fragmented systems should be a major focus for conservation in the 21st century (Buchholz, 2007; Marzluff et al., 2008). This study provides an evaluation of the behavioural habits of a keystone species greatly reduced in prevalence residing in an urban area. Because prairie dogs influence the distribution and abundance of other organisms (Agnew et al., 1986; Whicker & Detling, 1988; Miller et al., 1990, 1994; Lomolino & Smith, 2003; Forrest, 2005; Salamack, 2008), our findings may have implications for the entire urban ecological community in this region. For example, the increased foraging rate exhibited by urban prairie dogs given their reduced vigilance may influence the vegetative community and other species that rely on it. Additional research will be needed to clarify if the ecological relationships between prairie dogs and other plants and animals are maintained in fragmented urban systems (Lomolino & Smith, 2003; Magle & Crooks, 2008), and to what degree behavioural changes in urban prairie dogs impact these relationships. The black-tailed prairie dog has modified its behaviour to persist in highly urban areas, and in the absence of human intervention appears capable of persistence in these systems (Magle, 2008; Magle et al., 2010a,b). This species may provide a rare opportunity for research — an urban-adapted keystone species around which an ecologically functional urban ecosystem might be maintained.

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