



Long-term declines of a highly interactive urban species

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Abstract

Urbanization generates shifts in wildlife communities, with some species increasing their distribution and abundance, while others decline. We used a dataset spanning 15 years to assess trends in distribution and habitat dynamics of the black-tailed prairie dog, a highly interactive species, in urban habitat remnants in Denver, CO, USA. Both available habitat and number of prairie dog colonies declined steeply over the course of the study. However, we did observe new colonization events that correlated with habitat connectivity. Destruction of habitat may be slowing, but the rate of decline of prairie dogs apparently remained unaffected. By using our estimated rates of loss of colonies throughout the study, we projected a 40% probability that prairie dogs will be extirpated from this area by 2067, though that probability could range as high as 50% or as low as 20% depending on the rate of urban development (i.e. habitat loss). Prairie dogs may fulfill important ecological roles in urban landscapes, and could persist in the Denver area with appropriate management and habitat protections.

Keywords Connectivity · Prairie dog · Urban habitat · Interactive species · Habitat fragmentation · Landscape ecology

Introduction

The majority of the world's human population lives in urban areas, which represent the earth's fastest growing ecotype (Grimm et al. 2008). Urban regions also harbor biodiversity, albeit typically in less diverse communities than are observed in natural landscapes (McKinney 2002, 2006). While natural areas are maintained in a relatively constant state over the short term, land use within urban areas is dynamic and continuously changing. As such, urban areas are fundamentally different from other terrestrial systems, and yet have not been studied extensively, even as they continue to grow and expand (Miller and Hobbs 2002; Pickett et al. 2008). Wildlife represent critical components of these ecosystems,

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and despite their ubiquity and frequent interactions with humans (Soulsbury and White 2016), they are still relatively poorly understood in urban regions (Magle et al. 2012a). An advanced understanding of urban ecosystems is also necessary to predict and mitigate human-wildlife conflict in these regions, while maximizing the potential for long-term human-wildlife coexistence (Magle et al. 2012a; Fidino and Magle 2016).

Urbanization fragments habitat, which both directly and indirectly impacts natural communities. Reduction of habitat area means fewer populations can be supported, while roads and their associated traffic cause mortality for terrestrial species (Crooks and Sanjayan 2006; Forman 2003). In addition, fragmented sites are often characterized by higher prevalence of invasive species and/or disease, which can decimate native species (Adams and Lindsay 2010). However, indirect effects including genetic (Magle et al. 2010a), or demographic (Hanski and Ovaskainen 2002) instability can also cause slow declines in wildlife in isolated urban fragments. This phenomenon is termed “extinction debt” (Tilman et al. 1994) to illustrate that isolated habitats may exhibit relatively high levels of biodiversity for some period of time before these slow processes cause local extirpations. As such the observed wildlife communities in urban areas may not be stable, and declines may continue on the order of decades or longer. As so few long-term studies of animals in urban areas have been conducted (Magle et al. 2012a; Fidino and Magle 2016), it is presently unclear over what timescales these processes may play out, and the root cause of the declines.

Concepts from island biogeography (MacArthur and Wilson 1967) and metapopulation theory (Hanski 1998; Hanski and Gaggiotti 2004) have been frequently applied to urban habitat patches, largely because, like true islands, they have relatively discrete boundaries (Hanski 1998; Hanski and Gaggiotti 2004). As such, they lend themselves well to empirical tests of phenomena such as species extirpations and new colonizations as functions of distance between patches. As wildlife in urban areas are often ephemeral, moving between sites and often persisting for only brief periods of time, the application of this theory initially seemed quite useful. However, beyond certain broad predictions, such as higher diversity in larger patches, the application of island biogeography to urban areas has been problematic (Laurance 2008). For example, animals are often able to reside in the urban “matrix” between habitats, which is highly heterogeneous and may influence the embedded patches. Moreover, urban systems are also characterized by high levels of human activity and management, which can significantly influence the dynamics in wildlife populations (Werner 2011). After taking into account the general difficulty in detecting most terrestrial mammals (MacKenzie et al. 2002), and the potential time lags in local extinctions as outlined above (Tilman et al. 1994), assessing long-term changes in wildlife communities in urban landscapes can be challenging.

Black-tailed prairie dogs (*Cynomys ludovicianus*, hereafter prairie dogs) may represent a useful study organism to assess the long-term metapopulation dynamics of urban mammals. Prairie dogs are social, burrowing rodents characterized by complex communication behavior (Hoogland 1995). They are capable of persisting in urban areas, and are easily detected on the landscape due to the presence of their highly visible burrows (Magle et al. 2007, 2009, 2010a, b). In prairie landscapes, prairie dogs may function as keystone (Forest 2005; Kotliar et al. 1999; Miller et al. 1990, 1994, 2000, 2007), or highly interactive species (Soulé et al. 2003, 2005), though in urban landscapes there is little evidence these interactions are retained (Magle et al. 2012b; Beals et al. 2014). Urban prairie dogs may, however, provide important ecosystem services, including serving as prey for coyotes and thus reducing coyote attacks on pets (Magle et al. 2014). Despite their small size, prairie dogs are capable of colonizing new sites in urban landscapes, even across large spans of inhospitable terrain (Magle et al. 2010b). Although they have high potential ecological

importance, prairie dogs are also typically legislated as vermin and are often exterminated to make way for urban development (Hoogland 2006; Magle et al. 2010a). As such, prairie dogs occupy an unusual place among urban wildlife species—a readily detectable, potentially ecologically pivotal species capable of persisting in the heart of human development, yet uniquely vulnerable to the dynamic nature of urbanization.

We used a historical spatiotemporal dataset of prairie dog colony distributions in the Denver, CO metropolitan area spanning 5 years (2002–2007), which we then compared to additional data collected in 2017, to investigate metapopulation dynamics and the long-term persistence of this species in urban landscapes. We also characterized the rate of loss of habitat, both for prairie dogs and other species, to inform urban wildlife management and conservation in this region. Our previous study (Magle et al. 2010b) evaluated the short-term dynamics of this species in this area. By returning to the same study sites after 10 years, we were able to assess longer-term trends in urbanization, and evaluate whether the patterns observed over a 5 year timespan could predict the distribution of colonies a decade later. While urban prairie dog colonies are apparently genetically and nutritionally stable over short time periods, exhibiting neither inbreeding depression (Magle 2008) nor reduced body mass (Magle et al. 2010a), this study will for the first time provide insight into whether these colonies can persist in the long term given ongoing habitat development and the gradual loss of habitat connectivity.

Methods

We used a variety of techniques to characterize the presence of habitat patches, and of prairie dog colonies within those habitat patches, from 2002 to 2007, and again in 2017. Our intention was to measure rates of habitat destruction, prairie dog colonization, and prairie dog extirpation, and to relate these phenomena to potential covariates such as fragment area, age, and connectivity. We also used observed rates of habitat loss and prairie dog colony change from 2002 to 2007 to estimate the status of habitat and prairie dog colonies in the study area in 2017, and then compared those estimates to observed data. Finally, we use our projections to predict the potential distribution of prairie dogs 50 years in the future.

Study area/prairie dog monitoring

Our study area (13×29 km, ~ 374 km²) spanned from downtown Denver south through Denver's outer suburbs, and represented a gradient of decreasing urbanization north to south (Magle et al. 2010b). At the time of initial surveying (2002), the southern boundary represented the outer edge of urban development. In 2002, an exhaustive census revealed 384 habitat fragments within this study area, where a habitat fragment was defined as any plot of undeveloped land with an area of at least 0.25 ha that was not regularly landscaped or manicured by humans, and that was embedded in a dissimilar, less-hospitable, human-modified matrix, using paved roads to delineate the boundaries of fragments (Magle et al. 2010b).

From 2002 to 2007, all fragments were visited once per year and characterized as colonized or not colonized by prairie dogs, with occupancy defined by the presence of at least 1 live prairie dog (Magle et al. 2010b). Sites were visited between April and August, and only during daylight hours and in good weather. At the beginning of the study, 54 of the 384 fragments contained colonies, and as of 2007, 242 habitat fragments remained,

housing a total of 44 prairie dog colonies (Magle 2010b). For this study we revisited all 242 of those sites in 2017, 10 years after the last assessment, and used the same methods to investigate the long-term dynamics and viability of these populations into the future.

Measuring landscape variables

We calculated landscape variables for each fragment in the study area as predictors of the persistence of habitat fragments as well as the potential colonization-extinction dynamics of prairie dogs. Fragments were digitized in ArcGIS 9.1 (ESRI, Inc. 2011), and area of each fragment (ha) was determined as of 2002. Fragment age (time since complete isolation by urban development) was calculated from review of parcel data from Denver, Adams, Arapahoe and Douglas county assessors that indicated the year adjacent developments were completed (Magle et al. 2010b).

Connectivity is also a critical predictor of prairie dog distributions in urban landscapes (Magle et al. 2009; Magle and Crooks 2009). As fragments became developed through the course of the study we calculated numerous connectivity measures specific to each year. For each year we calculated a number of metrics previously found to perform well in predicting the distribution of prairie dogs in the system (Magle et al. 2009; Magle and Crooks 2009). These metrics included: the inverse of the distance between each habitat fragment and the nearest prairie dog colony (nearest_pd), the inverse of the distance between each fragment and its nearest neighboring habitat fragment (nearest_frag), the area-weighted distance from a fragment to the nearest prairie dog colony (aw_pd; Magle et al. 2009), and the area-weighted distance from a fragment to its nearest neighboring habitat fragment (aw_frag). Following Theobald (2006), area weighted distances were calculated as $(a_i a_j)^{0.7} / d_{ij}^{1.7}$ where a is the area of patches i and j and d is the Euclidean distance between them. Finally, following Saura and Rubio (2010), we calculated a graph-based habitat availability metric termed the probability of connectivity (PC) for the study region in each year. This metric is calculated as:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i \times a_j \times p_{ij}^*}{A_L^2}$$

where a_i and a_j represent the areas of fragments i and j , A_L^2 is the total area of the study region squared, and p_{ij}^* is the maximum probability of dispersal between patches i and j (i.e., the probability of the most likely path between i and j , including through other fragments). We assumed that fragments were not connected (i.e., $p_{i,j}=0$) if they were greater than 2000 meters apart. This distance was selected based on existing data on the dispersal events of prairie dogs (Hoogland 1995; Magle et al. 2010a). The probability of dispersal between fragments within 2000 meters was calculated as: $p_{ij} = \exp(\theta \times d_{ij})$, where θ is a distance decay coefficient and d_{ij} is the Euclidean distance between fragments (Urban and Keitt 2001). Following Urban and Keitt (2001), we calculated the tail distance corresponding to the distance decay coefficient as $\theta = \ln(0.05)/\omega$, where ω is the distance at which the probability of dispersal between fragments is estimated to be 0.05%. For this study we set ω to 5000 meters, again based on existing data on prairie dog movements (Hoogland 1995; Magle et al. 2010a). If fragments are not directly connected, dispersal may still occur between i and j through intermediate fragments that i and j are connected to. In such cases, p_{ij} was calculated as the product of the dispersal probabilities through intermediate patches. As there is the potential for many dispersal paths between fragments, PC uses

the maximum dispersal probability between i and j : p_{ij}^* . Finally, the relative importance of fragment k can be calculated as:

$$dPC_k = 100 \times \frac{PC - PC_{-k}}{PC}$$

where PC_{-k} is the probability of connectivity for the study region without fragment k . Large values of dPC_k reflect fragments that are more important to habitat connectivity.

Statistical analysis

After observing the initial occupancy state of each habitat fragment in 2002, each fragment could be in one of three states the following year: (1) a fragment containing prairie dogs, (2) a fragment without prairie dogs, or (3) a developed area that was no longer considered a habitat fragment. To represent this process, we developed a Bayesian multi-state model similar to a multi-state multi-season occupancy model (MacKenzie et al. 2009), but without a detection component because the status of a fragment is known (i.e., the probability of detecting the true status of a fragment is 1). This model formulation allowed us to estimate the probability that prairie dogs initially occupied one of the 384 fragments in 2002 (ψ), the probability a habitat fragment remains undeveloped from one time step to the next (ϕ), the probability of local extinction of prairie dogs within a fragment not caused by development (ϵ), and the probability of local colonization of unoccupied and undeveloped fragments by prairie dogs (γ). As we simultaneously modeled probabilities associated with habitat fragments (ϕ) and prairie dogs (ψ , ϵ , and γ), transitions from one state to the next are composed from the products of these varying probabilities (Fig. 1). Furthermore, all four of these probabilities were made a function of covariates via the logit link so that a variety of hypotheses regarding the local colonization-extinction dynamics of prairie dogs, as well as development rates (i.e., $1 - \phi$), could be tested.

This model makes 3 important assumptions. (1) The state of the fragment in the previous time step influences the transition to other states. For example, a fragment with prairie dogs present in 2002 may either remain at that state the following year at $P(\phi(1 - \epsilon))$, may have prairie dogs go extinct but remain a habitat fragment at $P(\phi\epsilon)$, or may be developed at $P(1 - \phi)$ (Fig. 1). (2) During the study period we never observed an event in which sites transformed from urban development to a more natural state. Therefore, our model also assumes that once a site is developed it may never return to habitat and remains a developed site with probability 1, precluding prairie dogs from colonizing the site again. (3) We assume that the data follow a Categorical likelihood. The Categorical distribution is a generalization of the Bernoulli distribution for more than two states and requires that all transition probabilities away from a given state sum to 1.

We fit 140 different models to the 2002–2007 dataset that were formulated by developing 14 parameterizations for ϵ (extinction) and γ (colonization), and 5 different parameterizations for ϕ (fragment persistence). We kept the same parameterization for the initial occupancy of prairie dogs in 2002 (ψ) across all models, which included fragment age, easting, northing, and fragment area. We did not test alternate parameterizations for this portion of the model because the initial distribution of prairie dogs in 2002 solely represents a glimpse of the dynamics of the system, rather than the processes that determine it (i.e., γ , ϵ , and ϕ) which were our primary interest. For γ and ϵ , we generated models based on a priori hypothesis regarding the study system. Our models (other than the intercept only model), included either fragment age, one of the connectivity metrics (nearest_pd,

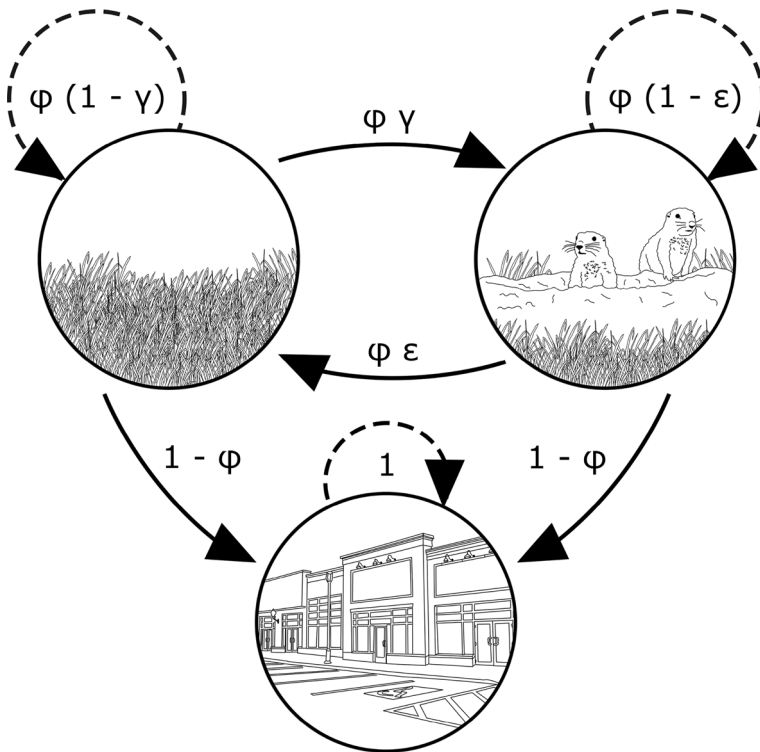


Fig. 1 Transition probabilities between the three possible states a habitat fragment could transition between from 1 year to the next. Solid lines indicate transitions from one state to another while dotted lines represent the state remaining the same from 1 year to the next. Probabilities used to generate these transitions include prairie dog colonization (γ), prairie dog extinction not due to development (ϵ), and patch persistence (ϕ). After a fragment is developed at $P(1-\phi)$ it remains in that state with $P(1)$

nearest_frag, aw_pd, aw_frag, dPC_k), easting and northing (to assess spatial trends), or easting and northing along with one connectivity metric, or fragment age (number of model parameterizations for γ and $\epsilon=14$). For ϕ , models included a single covariate which was either fragment age, fragment area, dPC_k , an indicator variable that denoted whether a habitat fragment ever contained prairie dogs between 2002 and 2007 (had_pd), or an intercept only model (number of model parameterizations for $\phi=5$). We did not include other factors that may influence the development of habitat fragments (e.g., unsuitable terrain or potential future land use) because those variables were not available to us. As such, we assume that each habitat fragment has at least some probability of being developed.

Colonization and extinction probabilities were always given the same parameterization within each model, and all combinations of ϵ , γ , and ϕ were generated which resulted in 70 models. Following this step, the same models were fit, with the addition of a temporally varying random effect on the intercept term for ϵ , γ , and ϕ , which resulted in the final 70 models. This second suite of models reflect the hypothesis that ϵ , γ , and ϕ are not fixed, but vary through time.

We compared these candidate models with Watanabe-Akaike Information Criterion (WAIC). WAIC is a fully Bayesian model selection criterion that is similar to Akaike

Information Criterion (AIC; Gelman et al. 2014). We assumed Logistic(0, 1) priors for all covariate parameters, which induces a uniform(0, 1) prior on the logit scale. Furthermore, temporal random effects were drawn from $N(0, \sigma)$ priors where each σ was given an Inverse-gamma(1, 1) prior. All models were fit in ver 4.3.0 of JAGS (Plummer 2003), in ver 3.3.3 of R (R Core Team 2016). Following a 2000 step adaptation and 5000 step burn-in, parameters were sampled 10,000 times across 6 chains. MCMC chains were thinned by 2. To verify that models converged we verified that Gelman-Rubin diagnostics for each parameter were < 1.10 for each model (Gelman et al. 2014). All continuous covariates were scaled to have a mean of zero and standard deviation of 1 before analysis.

Simulations

Using the best fit model from our analysis we: (1) used the dynamics of the system from 2002 to 2007 to simulate and predict the observed outcome in 2017 in order to determine whether short-term trends could be extrapolated to a longer scale, and (2) simulated the dynamics of the system from 2017 to 2067 under varying development scenarios to determine the probability that prairie dogs could be locally extirpated from the region within 50 years. For the latter, different development rates ($1 - \phi$) were simulated by adding to or subtracting from the posterior distribution of the ϕ intercept of the best fit model to represent scenarios where development rates were either higher or lower than we estimated. To propagate uncertainty in parameter estimation from our top model, one simulation was conducted for each sample of the posterior distribution ($n = 10,000$) per scenario. Furthermore, as the distribution of prairie dogs and fragments vary across simulations, connectivity metrics within the top model were recalculated each year per simulation. A simulation was considered finished if it ran the total number of years required, if the total number of fragments became zero, or if the number of prairie dog colonies became zero. We summarized prairie dog persistence rates as the number of simulations in which prairie dogs did not go extinct throughout the system, divided by the total number of simulations, calculated for each year.

Results

Prairie dogs occupied the greatest number of fragments at the beginning of the study (2002): 53 of the 384 fragments. Between 2002 and 2007, 142 of the fragments were developed, and by 2007 prairie dogs occupied only 42 of the remaining 242 fragments. An additional 71 fragments were developed between 2007 and 2017, and by the end of the study prairie dogs only occupied 23 of 171 fragments. The median distance of a habitat fragment not occupied by prairie dogs to a fragment that was occupied was 1311 m at the start of the study and increased to 1593 m by 2017. The median distance between neighboring fragments (of any type) similarly increased during this study from 326 m in 2002 to 443 m in 2017.

The top model fit to predict prairie dog colonization and local extinction (extirpation) rates included terms for easting and northing, nearest prairie dog colony, and temporal random effects (Table 1). Fragment persistence was best predicted by the graph-based habitat availability metric, dPC_k , and a temporal random effect (Table 1). The probability of initial occupancy in 2002 was greater on the eastern side of the study region ($\beta_{\text{easting}}^w = 0.83$, 95% CI 0.41–1.31) and higher in fragments of larger size ($\beta_{\text{frag_area}}^w = 0.77$, 95% CI 0.50–1.08). Average

Table 1 WAIC results from the top 4 models for prairie dog colonization (γ), prairie dog extinction (ϵ), and fragment persistence (ϕ), fit to data from 2002 to 2007 on prairie dog colonies in Denver, CO

γ	ϵ	ϕ	WAIC
Easting + northing + nearest_pd + u_t	Easting + northing + nearest_pd + u_t	$dPC_k + u_t$	1493.03
Easting + northing + u_t	Easting + northing + u_t	$dPC_k + u_t$	1496.00
Easting + northing + nearest_frag + u_t	Easting + northing + nearest_frag + u_t	$dPC_k + u_t$	1496.34
Easting + northing + frag_age + u_t	Easting + northing + frag_age + u_t	$dPC_k + u_t$	1496.94

u_t indicates that the model contains a temporal random effect within the linear predictor

yearly colonization rates were estimated to be low, at 0.99% (95% CI 0.24%–7.88%), but varied temporally. The estimated standard deviation in prairie dog colonization rates was 1.26 (95% CI 0.39–3.57). Thus, our top model predicted that yearly colonization rates should vary between 0.08 and 10.59% with 95% certainty. Colonization rates were higher on the eastern side of the study area ($\beta_{\text{easting}}^{\gamma} = 0.72$, 95% CI 0.14–1.46) and for habitat fragments that were closer to existing prairie dog colonies ($\beta_{\text{nearest_pd}}^{\gamma} = 0.44$, 95% CI 0.06–0.77).

While average local extinction rates exceeded average colonization rates at 7.67% (96% CI 3.71–15.25), they varied less temporally ($\sigma^{\epsilon} = 0.34$, 95% CI 0.02–1.43), resulting in a 95% predictive interval of yearly extinction rates between 4.06 and 14.01%. There was no clear relationship between local prairie dog extinction rates and easting ($\beta_{\text{easting}}^{\epsilon} = -0.06$, 95% CI -0.72–0.18) and northing ($\beta_{\text{northing}}^{\epsilon} = -0.23$, 95% CI -0.72–0.18) of a habitat fragment or its proximity to the nearest prairie dog colony ($\beta_{\text{nearest_pd}}^{\epsilon} = 0.06$, 95% CI -0.34–0.39). Fragments that were more important to the overall connectivity of the study area had higher persistence rates ($\beta_{dPC_k}^{\phi} = 1.13$, 95% CI 0.53–1.92). Moreover, average fragment persistence rates were high at 92.26% (95% CI 90.02–94.03%) and had the smallest temporal variance of all component rates ($\sigma^{\phi} = 0.11$, 95% CI 0.01–0.54).

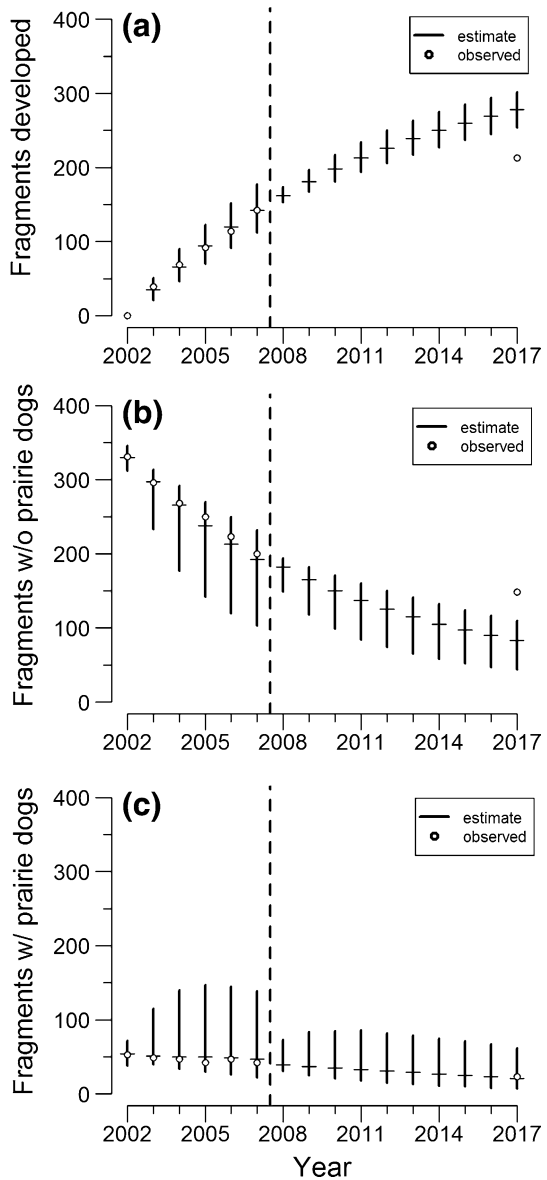
Overall, our top model closely reflected the observed data between 2002 and 2007 (Fig. 2). However, when we used this top model for forward simulations from 2007 to 2017, the model overpredicted the number of developed fragments (Fig. 2a), and thus underpredicted the number of fragments apparently available for prairie dogs (Fig. 2b, Fig. 2c). However, the predicted number of fragments with prairie dogs decreased through time, and the observed value of prairie dog colonies from 2017 closely reflected our prediction (Fig. 2c).

Using the top model we also simulated the dynamics of prairie dogs for 50 years under varying development rates to determine the probability that prairie dogs may become locally extirpated under different scenarios. We selected three different scenarios: the actual development rate estimated by our model ($1 - \phi = 7.74\%$), a 5% development rate and 10% development rate. Under the 7.74% scenario prairie dogs had a 40.21% chance to become extirpated throughout the study area within 50 years. This increased to 51.20% under a 10% development rate and decreased to 19.93% under a 5% development rate (Fig. 3).

Discussion

The ability to assess the dynamics of a highly interactive species in an urban landscape over a 15-year period is unusual, and provides insight into local persistence, colonization, and extinction rates that would not otherwise be possible. Prairie dogs provide an almost ideal species for studies of this type as they are visually apparent on the landscape and

Fig. 2 The estimated and observed state of habitat fragments from 2002 to 2017. Horizontal lines represent the median estimate from the best-fit model while vertical lines indicate 95% credible intervals around the estimate. Estimates from 2002 to 2007 were conditional on the observed state in 2002 while estimates from 2008 to 2017 were conditional on the observed state in 2007. The best-fit model over-predicted the number of developed sites in 2017 but precisely reflected the observed data between 2002 and 2007 (a). Likewise, this model correctly estimated the number of fragments without prairie dogs between 2002 and 2007 but under-predicted the number of habitat fragments without prairie dogs in 2017 (b). The number of fragments with prairie dogs decreased through time and was accurately estimated by the best-fit model between 2002 and 2007 and in 2017 (c)



heavily impacted by habitat fragmentation and roads (Magle et al. 2009, 2010b). In addition, their observed dynamics are a complex combination of biological and social factors, with extinctions potentially driven by a mix of plague (*Yersinia pestis*, Stapp et al. 2004), demographic or genetic instability (Hoogland 2006), and direct removal by humans (Magle et al. 2010b).

In general, the trends observed in this study were a reduction in overall available habitat, as well as the number of prairie dog colonies remaining. This is not altogether surprising, given the overall trend for urbanization across the world (Pickett et al. 2008), and the

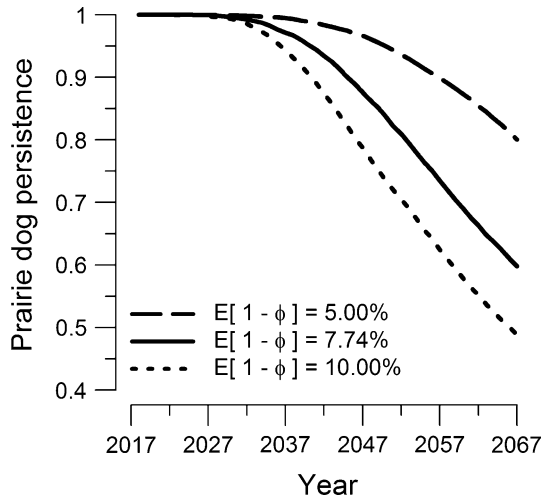


Fig. 3 The probability prairie dogs could persist within the study system in Denver, Colorado over 50 years under varying development rates ($1 - \phi$). The y-axis indicates the cumulative probability that prairie dogs are not locally extirpated by the associated year on the x-axis. Persistence rates decrease through time across all simulations, but decline most in the highest development rate scenario. Higher numbers on the y-axis indicate a higher probability that prairie dogs occupy at least 1 fragment in the study area. The solid line represents the average yearly development rate estimated by the best fit model (7.74%), while the two dashed lines are scenarios in which the average yearly development rate is either reduced to 5% or increased to 10%

similar observed trends from 2002 to 2007 (Magle et al. 2010b). We did not specifically seek out new habitat that may have become available in the interim, but in the portion of the study area we revisited in examining existing fragments, we never detected new nearby potential habitat, and we are unaware of any greening initiatives in the Denver, CO area that would have involved transformation of existing developed land. Rather, most such efforts involve the formation of new greenways and corridors in ongoing development in distant suburbs (Johnson and Klemens 2005). While the effects of this decline of prairie dogs on other urban species is relatively unknown, they are known prey for raptor species (Magle et al. 2012b), and apparently influence coyote behavior nearby their colonies (Magle et al. 2014). While prairie dogs may not retain their full keystone role in these urban regions (Magle and Crooks 2009; Magle et al. 2012b), they are an integral part of them, and their decline is bound to have cascading ecological effects, whether positive or negative, some of which will be difficult to anticipate.

When evaluating factors related to the persistence of prairie dogs in this landscape (the inverse of local extinction), we found few correlates. There were no spatial trends and the connectivity of habitat fragments had little impact on the probability of persistence. This points to human intervention via poisoning as the most likely cause of colony disappearances (Magle et al. 2010b), as plague or demographic instability would more likely covary with connectivity. Starvation is possible but unlikely, given that urban prairie dogs show no signs of decreased body mass (Magle 2008). Predation is an unlikely cause of the declines observed, because although coyotes and hawks both predate prairie dogs in this system, their densities in urban areas are almost certainly insufficient to eliminate entire colonies (Hoogland 1995; Magle et al. 2014). Colonization events, conversely, were higher among more connected colonies, which stands to reason given the difficulty these fossorial

mammals likely have in traversing urban terrain and roads (Magle et al. 2010a). Colonization events were also more common on the east side of the study area, which we suspect is for a similar reason—there are many prairie dog colonies just outside the study area to the east, in rapidly urbanizing suburbs, and initial occupancy was also higher in that direction. It is somewhat encouraging that the habitat fragments that were more critical to the connectivity of the overall system were less likely to be developed. It is presently unclear if this is the result of urban planning designed to maintain landscape connectivity, or a random artifact of the current patterns of development. Either way, if prairie dogs (and other wildlife) are to be conserved in the Denver area, it is critical that these highly connected patches be a focus for conservation (Crooks and Sanjayan 2006).

Our simulations of this system 50 years into the future revealed a relatively high probability of extinction for prairie dogs by 2067, between approximately 20 and 51%. However, care must be taken with the interpretation and validity of these simulations given our general uncertainty in parameter estimates and inability to estimate development rates over shorter time spans (Fig. 2a). Nevertheless, between 2002 and 2017 the number of prairie dog colonies throughout the study area precipitously declined from 53 colonies to 23 (Fig. 2c), which provides a strong indication that prairie dogs in this system have been in decline over the last 15 years. As prairie dog colonization rates were generally below extinction rates, we expect that more colonies will be lost in the future, especially from the western side of the city of Denver where colonization rates were at their lowest.

The potential loss of prairie dogs, a seemingly common urban species, from this system would have ecological implications, as explored above, as well as eliminate an important opportunity to connect urban residents to local wildlife species (Miller and Hobbs 2002; Miller 2005). Prairie dogs are a highly visible and distinctive component of nature in the Denver area and their loss undoubtedly would have social and educational consequences. However, there may be reason for hope. While habitat continues to be lost from this system, the rate of loss appears to be slowing, which may be why we underpredicted the number of habitat patches that would persist in 2017. It is extremely unlikely that the available habitat would ever drop to nothing, since some fragments represent natural areas owned by public, governmental entities. However, whether prairie dogs could persist in only this subset of sites—and indeed whether the managers of those sites would allow them to—remains unknown. Unfortunately, while we underpredicted the amount of available habitat, we predicted the number of remaining colonies quite well, indicating that at present, the rate of colony loss has remained constant. Colonization events remain rare, and in many cases prairie dogs are either not locating the available habitat, or are being removed by humans once they do so. It should be noted that several potentially important factors that no doubt influence prairie dog distributions in this system—soil type, vegetation, plague, and land use legacies, for example—could not be measured in this study, and as such these results should be interpreted somewhat cautiously. While more research is needed to clarify their role in urban landscapes, and certainly not all habitat is suitable for prairie dog colonies, we suggest that prairie dogs in this area are generally in need of conservation and management intervention, in the form of habitat protections. Given their relative lack of popularity (Milley 2008), this will likely also necessitate public outreach efforts. We also believe public participation in scientific efforts to map and monitor their colonies may help increase awareness and empathy for these important urban mammals (Dickenson et al. 2012).

Although our study provides a rare glimpse into dynamics of an urban mammal over a 15-year period, we are limited by the lack of observations between 2007 and 2017. Continuous monitoring may have helped determine whether local extirpations were caused by

development (Magle et al. 2010b) and provided a clearer picture of the threats to these populations. However, we still find it likely that most local extinctions observed were the result of human intervention, given the lack of spatial trend in those events, and previous findings that urban prairie dogs are unlikely to disappear based on genetic (Magle et al. 2010a), or nutritional (Magle 2008) instability. Adding more temporal data points would also have enabled us to better fit non-linear models to the declines in both habitat availability and prairie dog colonies to assess whether either are truly levelling off.

Prairie dogs are an iconic species throughout the Great Plains (Hoogland 1995), and are somewhat unique among highly interactive species in their ability to persist in urban habitat. While our long-term dataset shows decline in these colonies across a highly urban landscape, there is reason for hope that they could still be conserved in perpetuity. Prairie dogs are capable of colonizing new habitats, even across major roads and highways (Magle et al. 2010a), and appear capable of persistence in the absence of human development. The decline that we describe shows some signs of slowing, indicating that these colonies could remain indefinitely if adequate habitats are protected or created. Prairie dogs represent an enormous opportunity to connect people to local species, and also provide critical ecosystem services (Hoogland 1995, 2006), including providing habitat to other species (Miller et al. 1994, 2000) and reducing conflicts between humans and coyotes (Magle et al. 2014). In the long-term, achieving conservation goals on an urbanizing planet will require finding ways to protect species in the heart of human development (Rosenzweig 2003). This system provides a unique opportunity to use long-term data and the ideals of reconciliation ecology to discover how to protect an important prairie species in a major metropolis.

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