Food limitation at species range limits: Impacts of food availability on the density and colony expansion of prairie dog populations at their northern periphery

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ABSTRACT

Understanding limiting factors affecting population growth for imperilled species is crucial for conservation and management. This research investigates whether black–tailed prairie dog (Cynomys ludovicianus) populations are food limited on their northernmost range extent. We measured background vegetation rates and used food supplementation in a ‘before–after–control–impact’ (BACI) design to test whether increased food positively impacted prairie dog population density and colony expansion. Experimental results did not support food limitation. Overall, density increased from 2008 to 2009 but remained relatively similar between control and treatment plots. Correlations between natural, non-supplemented vegetation biomass and prairie dog density suggest that natural food availability in 2008 may have driven population growth into 2009. Natural food availability was highly variable among years and prairie dog densities may be impacted by food scarcity in some years but not others. Colony spatial expansion was greater in the absence of food supplementation, suggesting food scarcity may drive colony expansion. This research has important implications for the conservation and management of prairie dogs and species that depend on them such as reintroduced black–footed ferrets (Mustela nigripes) in Canada and other populations across their range.

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1. Introduction

Understanding the processes which drive population growth and dynamics are crucial for conservation managers to make sound ecological decisions for species conservation (Sinclair and Krebs, 2002; Bowden et al., 2003). Black-tailed prairie dogs (Cynomys ludovicianus) (hereafter ‘prairie dogs’) are a keystone species (Miller et al., 1994) and an integral part of the North American prairie ecosystem. As such, they are an important target species for prairie conservation because protecting them may help protect the ecosystem. Furthermore, with the reintroduction of black-footed ferrets (Mustela nigripes), a specialist predator of prairie dogs (Miller et al., 1996), to Canada since 2009, the need for conservation and management of prairie dogs within these northern colonies has increased. Populations of prairie dogs in Canada are at the northernmost extent for the species (Ceballos et al., 1993; Hoogland, 1995).

Northern prairie dog populations are quite vulnerable to stochastic events, such as extreme weather or disease outbreaks (Gummer, 1999), which similar to prairie dog populations at the southernmost range (Avila-Flores et al., 2012), may be impacted (either negatively or positively) by climate change. Canadian prairie dogs are listed as ‘threatened’ due to potential cumulative risks, their low population size and isolation from southern populations (COSEWIC, 2011).

Populations residing on the peripheral ranges of species distributions are often assumed to occupy sub-optimal habitat and exhibit higher population fluctuations compared to populations located in more central regions of a species range (Caughley et al., 1988; Hampe and Petit, 2005). However, some populations residing at the range limits have been known to persist during range collapses and may fulfill an important rescue function for species persistence (Chanell and Lomolino, 2000). Classic bottom-up effects of resource limitation affect populations through differences in food resources which can vary with environmental gradients (McNaughton et al., 1989; Polis, 1999). Climate, especially in northern areas, may limit populations directly, by affecting individual physiology for example, and indirectly by affecting primary productivity of forage (Barton and Zalewski, 2007). Prairie dog populations at their
northernmost extent may be limited by food resource availability due to the harsh winter climate and shorter growing season. Food scarcity has been suggested as limiting prairie dog populations (Avila-Flores et al., 2010) and indeed, at the southern range extent, low availability of food resources due to drought conditions appeared to limit prairie dog population growth (Facka et al., 2010). Furthermore, reduced vegetation biomass had negative effects on behaviour and growth rates of Utah prairie dogs (Cheng and Ritchie, 2006).

The highly colonial nature of prairie dogs (Hoogland, 1995; King, 1955) may result in costs to the individual through increased competition for resources, i.e. per capita decline in the availability of food, mates and territories (Coulsou, 1968; Lack, 1954; Naug and Wenzel, 2006; Shields and Crook, 1987; Tenaza, 1971). At high densities, intra-specific competition for food may limit further growth of prairie dog populations. Food availability (through its influence on carrying capacity) may influence population size, dispersal and expansion of prairie dog colonies (Garrett and Franklin, 1988). Coteries may, over time, become depleted of food sources resulting in high intra-specific competition and subsequent dispersal. Increased colony expansion into suitable habitat adjacent to the colony edge has previously been correlated with high burrow density within colonies of prairie dogs (Cincotta et al., 1987). The possible mechanism behind this may be a per capita decline in food availability with increasing density forcing the expansion of edge coteries (Garrett and Franklin, 1988). While other studies have suggested that prairie dogs are food-limited, none have tested population dynamics experimentally with food addition. This study will expand on previous prairie dog research, contributing to fundamental knowledge on the biology of imperilled rodents, and highlight important management for prairie ecosystems and species at range limits.

Our objective was to determine if prairie dog population density and expansion at the northern extent may be limited by food availability. We hypothesized that food resources may be limited, and, if in short supply, density-dependent factors could limit population growth or lead to a population decline. This hypothesis was tested using a “before–after–control–impact” (BACI) (Green, 1979) experiment that manipulated food availability through food supplementation. We predicted that if food is limiting, then prairie dogs in food-supplemented sites should experience higher survival and/or recruitment that would subsequently increase density, compared to control plots. We also hypothesized that conditions that increase intra-specific competition, such as limited food availability and/or high prairie dog density, could trigger dispersal that might lead to colony expansion.

2. Materials and methods

2.1. Study area

This study took place in the Frenchman River valley within Grasslands National Park, located in southwestern Saskatchewan, Canada (49°07′N 107°45′W) from June 2008 to September 2009. In Canada, prairie dogs only occur in Grasslands National Park and adjacent lands (Gummer, 1999). There are 22 prairie dog colonies in Canada, ranging in size from 4.7 ha to 198.5 ha with a maximum distance between colonies of less than 10 km, half of these colonies are currently located within the boundary of the West Block of Grasslands National Park. Grasslands National Park is a mixed grass prairie ecosystem (Fargey and Marshall, 1997; Gummer, 1999; Spreadbury, 2002). Mixed grass prairies are generally dominated by wheatgrass (Pascopyrum spp.), spear grass (Austrostipa spp.) and blue grama grass (Bouteloua gracilis) species (Desmond et al., 2000). The range in elevation of the colonies is approximately 762–816 m above mean sea level. Mean monthly precipitation during the growing season (April–September) for 2008 was 50.07 mm and for 2009 was 25.38 mm (Environment Canada). Three of the largest colonies within the park were selected for this study: Snake-Pit, Larson and Monument (approximately 199 ha, 168 ha, and 134 ha, respectively).

2.2. Experimental design

We used 18 trapping grids, six in each of the three colonies. Each grid was randomly positioned within the outer edge of each colony in order to assess food supplementation effects on density and colony expansion. Perimeters of colonies were easily identified by reduced vegetation height within colonies, marking the extent of foraging and clipping of vegetation, i.e. the clip-line (Hoogland, 1995; Koford, 1958). Plots were placed at least 400 m apart to decrease the chance of sampling the same individual within different plots. This distance was based on the average area for a coterie territory (55 m² or 0.3 ha) (Hoogland, 1995). All plots were randomly chosen to ensure independence and verified on ground that they were within the colony perimeter and had evidence of burrows and prairie dogs within the grid. Three of the six plots within each colony were randomly chosen for supplemental feeding (treatment plots), and the three remaining plots were control sites. Each plot consisted of 48 traps (40.6 cm × 22.9 cm × 22.9 cm; Integrated Pest Supplies Ltd., New Westminster, BC) spaced 10 m apart in a 10 × 10 and 4 × 4 nested hollow-grid design (Wilson et al., 2007).

2.3. Food supplementation

Nutrena commercial rabbit pellets (NatureWise® Performance Rabbit Formula; Cargill, Minneapolis, MN) were used as supplemental food. Each supplemented plot received an estimated excess of the daily energy requirements (11.79 kg per plot/week). This amount was based on average daily energy requirements (approximately 50–70 g/prairie dog) (D. Whiteside, pers. comm.; Koford, 1958), for average densities of prairie dogs per hectare (17/ha) from a mark-recapture study in 2007 (Stephens, 2012). Using the experimental BACI design, food supplementation was initiated after the first trapping session (i.e. before treatment phase) in mid-July 2008 and was provisioned once per week until mid-October 2008. Supplemental feeding did not occur during winter months while prairie dogs were hibernating, but began again in mid-March 2009 as prairie dogs emerged from hibernation, continuing until the end of May 2009. In 2008, the supplemental food pellets were dyed with a mixture of non-toxic ultraviolet-fluorescent powder (Radiant Color, Inc., Richmond, CA) and peanut-oil to confirm consumption of supplemental food by prairie dogs.

2.4. Mark-recapture

Trapping was conducted from June until September in 2008 and 2009. Within each field season, there were two trapping sessions: a spring session from June to mid-July and a summer session from August to mid-September. Each trapping session lasted for 5 consecutive days per plot (weather permitting) where we assumed population closure for each plot. Each trap was staked into the ground and initially wired open for 5 days, to allow prairie dogs to habituate to the traps. Traps were pre-baited with a mixture of peanut butter and oats once a day in the morning for 2 days prior to trapping (Severson and Plumb, 1998). During active trapping sessions, traps were opened and set, observed for 2 h, and then traps were closed and any captured prairie dogs were processed. Trapping was conducted during peak activity times in the early morning (Hoogland, 1995).
Captured prairie dogs were placed in a canvas bag and weighed, sexed, aged, checked for reproductive status and individually marked with a subcutaneous implanted microchip (12 mm Fecava, Avid Canada, Calgary, AB) above their right hip, then released at the trap location where they were caught. Recaptured prairie dogs were scanned with an Avid external receiver (Avid Mini Tracker II) to identify the unique microchip code. Mass was recorded with Pesola spring scales (1000 g and 2500 g) to the nearest 10 g. Sex was determined by the distance between the genitalia and the anus, 2–3 cm for adult males and immediately adjacent for adult females (Hoogland, 1995). Age was determined by size and mass of the individual; in the spring juveniles were easily recognized and generally weighed less than 700 g compared to adults which generally weighed between 700 and 1600 g (Hoogland, 1995; personal observation). Categories of reproductive status (i.e. active versus non-active) were determined for females based on the visible condition of the nipples: lactating if nipples were descended, full and round with little hair surrounding them, post-lactating if the nipples were flat, dry and with little hair surrounding the area, and non-reproductive if nipples were small and covered by hair. All animal capture and handling followed procedures specified in the University of Calgary Animal Care Protocol (#BI 2008-47) and the Calgary Zoo’s Biological Research Review Committee Protocol (#2008-04).

2.5. Vegetation surveys

Vegetation transects were sampled to estimate the percent cover, height and biomass of the major vegetation types using Robel and Daubenmire techniques (Daubenmire, 1959; Robel et al., 1970). Vegetation was sampled in June and July in 2008 and 2009 during the peak-growing season. Transects were 70 m in length with 18 sample quadrats (20 cm × 50 cm) every 4 m. We collected vegetation data from three transects within each study plot and three transects outside of the colony immediately adjacent to each study plot in a potential expansion zone (50 m × 140 m) outside the colony perimeter after), and colony. In addition, the interaction between treatment and food supplementation phase was modelled. We counted burrows both within study plots and in immediately adjacent zones (50 m × 140 m) outside the colony perimeter (delimited by the clip line, i.e. the height of the vegetation (Hoogland, 1995; Koford, 1958)) each year during our summer session to capture late-spring colony expansion. Burrows were classified as active, inactive or plugged. Active burrows had evidence of digging and prairie dog faeces around the entrance, or a prairie dog was visually seen or heard within the burrow. Inactive burrows had no evidence of the factors associated with active burrows and typically had cobwebs visible around the entrance of the burrow.

3. Data analysis

3.1. Mark-recapture

Prairie dog density was estimated using spatially explicit capture-recapture (SECR) analysis in program DENSITY (version 4.4.5) (Efford et al., 2009, 2004). For this analysis, we used the null estimator ($M_0$). Home range centres were assumed to have a Poisson distribution (Efford, 2004; Griffith and Haining, 2006). A buffer zone of 100 m from the outer trap grid was incorporated into the density estimation. This buffer was approximately four times the root-pooled-square-variance (RPSV) (Wilson et al., 2007). Because two or three prairie dogs were sometimes caught simultaneously in a single trap, we used the multi-live type of detector function which allows for this scenario in the density estimation process. For all estimates, the coefficient of variation CV = SE/D was calculated as a measure of precision. A CV < 30% was taken as an interpretable estimate of density (Wilson et al., 2007). To determine whether there was a supplemental treatment effect explaining the variation in prairie dog density, we used generalized linear mixed models (GLMMs) in R (version 2.11; R Development Core Team, 2007). We fitted GLMMs which used Laplace methods for estimation and assumed a Poisson error distribution with a log link function (Bolker et al., 2009). The following variables were included as fixed effects: (1) treatment designation, i.e. control or supplemental food, (2) colony, (3) phase, i.e. before or after food supplementation and (4) vegetation biomass as a covariate.

3.2. Vegetation

We combined grass and forbaceous plants together as a ‘preferred edible vegetation’ category (Uresk, 1984). We combined all other types of vegetation into a ‘non-preferred’ category and abiotic categories into a ‘non-edible’ category. The percent cover of each of these categories, was calculated for all transects and plots. Robel pole measurements of vegetation height were also averaged per transect, for each plot (Robel et al., 1970). Robel pole measurements can be used to estimate biomass (Robel et al., 1970). Using ordinary least squares regression, the vegetation height was re-sgressed on the total vegetation weight using the 2008 data for all transects per plot combined. To increase linearity, we used the logarithm to base 10 for vegetation height and weight. Because biomass was not collected in 2009, the relationship between vegetation height and biomass in 2008 was used to estimate biomass in 2009.

We used GLMMs assuming a Gaussian error distribution with an identity link function (Zuur et al., 2009) to determine variables explaining variation in the vegetation data from the outside potential expansion zones immediately adjacent to each study plot. The response variables for the outside colony vegetation GLMMs were: (1) percent preferred edible vegetation, (2) vegetation biomass. Fixed effects included additive effects of treatment (i.e. supplemented or control), food supplementation phase (i.e. before or after), and colony. In addition, the interaction between treatment and food supplementation phase was modelled.

3.3. Burrows

To analyze burrow use we used GLMM analyses that assumed a Poisson error distribution with a log link function (Bolker et al., 2009; Zuur et al., 2009). Density of active burrows was the response variable. Fixed variables included prairie dog density inside the study plots, treatment, food supplementation phase, vegetation biomass inside and outside the plot, and vegetation height outside the plot. In addition, interactions between treatment and food supplementation phase as well as treatment with inside plot biomass were modelled as fixed variables.

3.4. Model interpretation

For all GLMM analyses, the interaction between colony and plot was modelled as a random variable to overcome autocorrelation in the sampling design due to the nested structure of plot within
colony. For model selection purposes, a null model was run using the intercept only. Models were ranked using Akaike’s Information Criterion (Akaike, 1973; Burnham and Anderson, 2002) and Akaike weights were calculated. The Akaike weight of a given model is the weight of evidence for that model within the model set (Burnham and Anderson, 2002). A treatment effect may be evident with strong support for a positive food supplementation phase-treatment interaction. Any additive effects of colony, session or treatment would help describe background spatial and temporal differences in density between control and treatment plots. Additionally, models that include these variables and the food supplementation phase-treatment interaction will control for their covariance when considering treatment effects. Model support was compared graphically due to the different patterns that may arise from interaction and additive effects. In the graphs, we would expect treatment plots to show greater densities compared to control plots after food supplementation. A significant interaction between treatment and food supplementation phase would indicate that treatment and control plots responded differently during the different food supplementation phases of this experiment. A significant interaction effect, coupled with associated graphs that show response variables to increase at treatment sites following food supplementation, would provide support for the hypothesis given the BACI design.

4. Results

4.1. Mark-recapture

During this study, 1019 individual prairie dogs were trapped with 5072 captures. Although trapping plots were randomly chosen to standardize and minimize potential differences in ecological and demographic attributes, variation was observed both within and between colonies, treatments and years (Lloyd, 2011). Average prairie dog densities with standard errors (treatment and control plots combined) were: 5.69 ± 2.85/ha, 7.46 ± 2.07/ha, 12.43 ± 2.67/ha, 12.35 ± 2.33/ha, for spring/summer sessions 2008 and 2009, respectively. Prairie dog density increased for the majority of plots in 2009, with 5072 captures. Although trapping plots were randomly chosen, weights were calculated. The Akaike weight of a given model is the weight of evidence for that model within the model set (Burnham and Anderson, 2002). A treatment effect may be evident with strong support for a positive food supplementation phase-treatment interaction. Any additive effects of colony, session or treatment would help describe background spatial and temporal differences in density between control and treatment plots. Additionally, models that include these variables and the food supplementation phase-treatment interaction will control for their covariance when considering treatment effects. Model support was compared graphically due to the different patterns that may arise from interaction and additive effects. In the graphs, we would expect treatment plots to show greater densities compared to control plots after food supplementation. A significant interaction between treatment and food supplementation phase would indicate that treatment and control plots responded differently during the different food supplementation phases of this experiment. A significant interaction effect, coupled with associated graphs that show response variables to increase at treatment sites following food supplementation, would provide support for the hypothesis given the BACI design.

4.2. Vegetation

The average percent (±1 standard error) of preferred edible vegetation in outside-colony potential expansion zones during 2008 was 24 ± 2% for controls and was 26 ± 3% for treatment plots. In 2009, the percentage of preferred edible vegetation in the outside zones for treatment plots was 19 ± 3% and for control plots was 13 ± 2%. With all plots combined, the preferred edible vegetation in the outside zone declined in 2009 (16 ± 2%) from (25 ± 3%) in 2008. Overall, greater percentages of non-preferred vegetation compared to preferred edible vegetation were observed in the expansion zones possibly showing low food availability outside colonies. The top model for vegetation included food supplementation phase with an Akaike weight of 0.32 and an evidence ratio of 5.13 compared to the null model, suggesting that the percent of preferred edible vegetation was indeed greater in 2008 before food supplementation than in 2009 after supplementation.

Table 1. Generalized linear mixed-effect models of prairie dog density (Pdensity). Fixed effects include: food supplementation phase (before and after food addition), treatment (i.e. control or food supplemented plots), colony, and vegetation biomass. The random effect is a colony-plot interaction because plots are nested within colonies.

<table>
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<th>Parameters</th>
<th>AIC</th>
<th>Delta AIC</th>
<th>Model Weight</th>
<th>Log likelihood</th>
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The logarithm of vegetation height and total biomass in 2008 had a linear relationship ($p < 0.001$, $F = 143.30$, $df = 82$, adjusted $R^2 = 0.63$). Using this relationship, we estimated the total biomass for 2009. The average total biomass for the outside zones adjacent to control plots in 2008 was 8.21 ± 2.21 g and in 2009 was estimated to be 6.67 ± 1.85 g. For treatment plots the average total biomass in 2008 was 7.85 ± 1.45 g and was estimated to be similar in 2009 at 7.28 ± 2.20 g. The top model for explaining vegetation biomass in the potential expansion zones included food supplementation phase effects with an Akaike weight of 0.29. However, the null model was also a high-ranking model with Akaike weight of 0.21 and a delta AIC less than two from the top model, therefore, none of the tested variables were considered important in explaining vegetation biomass in the potential expansion zones.

### 4.3. Burrow density

In 2008 control plots had on average 19.05 /ha active burrows in the expansion zone, compared to 24.13 /ha active burrows for treatment plots. In 2009, control plots had 68.73 /ha active burrow density in the expansion zone and treatment plots had 44.29 /ha active burrow density. The percent increase in active burrow density between 2008 and 2009 was 260% for plots in the expansion zone next to controls and 84% next to food-supplementation plots. The top model from the set of GLMMs of active burrow density in colony peripheries. Only models with at least 1% support are included in the table, together they account for 95% of the Akaike weights. The coefficient of the interaction between treatment and food supplementation phase was positively related to active burrows outside the plot; however, control plots had a greater increase in active burrow density compared to supplemented plots after food addition (Fig. 2). Prairie dog density inside the study plot was positively related to active burrow density outside. Vegetation biomass inside the plots was negatively related to active burrows outside and vegetation biomass outside the plots was positively related to active burrows outside. Therefore, plots with greater vegetation biomass inside had lower numbers of active burrows in expansion zones.

### 5. Discussion

Our BACI experiment using food supplementation did not show the expected positive effect of food addition on prairie dog density, and therefore, did not support the hypothesis that food availability always limits prairie dog population growth. However, a correlation of natural vegetation availability in 1 year with density in the following year, suggests that vegetation biomass may affect prairie dog density with a time lag effect. Moreover, food supplementation effects suggest that food scarcity is apparently linked to expansion attempts along colony edges, likely because of per capita competition over limited resources.

Overall, control plots had slightly greater, however non-significant, prairie dog densities when compared to supplemented plots after food supplementation. The lack of a discernible food supplementation effect was most likely due to the high per capita food conditions for prairie dogs in 2008, i.e. any potential effects of food supplementation were masked by treatment and control sites having sufficient food in our year of study. Precipitation levels during the spring of 2008 were likely responsible for the greater amount of preferred edible vegetation on plots compared to 2009. Larger vegetation biomass and low prairie dog densities most likely led to an abundance of food per capita in 2008 and prairie dogs on control plots could likely find sufficient food as easily as prairie dogs on supplemented plots. Consequently, we suggest that food was not limiting prairie dogs during 2008. In contrast, in 2009 less vegetation coupled with higher prairie dog densities may have caused lower per capita food availability; the contrast in conditions among years may suggest that food may be limiting for prairie dogs in some years but not others. Because northern prairie dogs hibernate over the winter and reproduce in the spring, the ability of the population to grow each year may be dependent not only on food availability in the spring of a given year but also on food availability in the previous year. Consequently, the relationship between prairie dog density and food resources may involve a time-lag between years. In 2008 preferred edible vegetation was more abundant than in 2009, during which vegetation was scarce.
enough to fall below the critical required threshold for continuous prairie dog occupancy (Clippinger, 1989). Vegetation differences were almost certainly due to the two-fold difference in precipitation among years. Given that prairie dog density and reproduction (numbers of juveniles and reproductively active females), fluctuated dramatically between years, while sightings of predators and overall prairie dog survival did not drastically change between years (Lloyd, 2011), and we did not observe high mortality or population collapses (>85%; Cully et al., 2010) which could be attributed to sylvatic plague during this study, we believe that the most parsimonious explanation for the observed density fluctuations is the per capita availability of food resources. We hypothesize that precipitation-driven fluctuations in primary productivity of vegetation may be driving, with a time-lag, the fluctuations of prairie dog productivity and density between years within northern prairie dog colonies. Further research is needed within this system to discern whether these patterns hold true, and what factors influence and limit population growth of prairie dogs in northern climates over time.

Attempted settlement into areas beyond colony edges may be driven by food scarcity. Vegetation, outside of prairie dog colonies can influence expansion (Franklin and Garrett, 1989; Garrett and Franklin, 1988); in our study the percentage of preferred edible vegetation in potential expansion zones was similar adjacent to food supplemented and control plots, but non-preferred edible vegetation was more abundant outside the colony than within the colony edges. Lower food availability outside the colony could potentially limit colony expansion or make prairie dog settlement of such areas risky for dispersers. Nevertheless in 2009 active burrow densities increased significantly in expansion zones next to control plots, and these increases were greater than for sites adjacent to supplemented sites. Since 2009 had relatively little preferred food available and food-supplemented sites had lower rates of burrow increases in expansion zones, dispersal into expansion zones next to non-supplemented control sites was likely driven by food scarcity. Increased food availability in supplemental plots likely decreased the need for dispersal and expansion. Similarly, Avila-Flores et al. (2012) found, at least for one time period, that areas of prairie dog colonies with low vegetation biomass were more likely to go extinct in subsequent years. Overall, the change in active burrows between 2008 and 2009 in expansion zones suggests food supplementation did not increase expansion: indeed, expansion appeared to be more linked to food scarcity.

Prairie dog density for supplemented and control sites combined was important in explaining active burrow density within the expansion zones. The relationship between prairie dog density and active burrow density outside the plots was positive, suggesting that intra-specific competition, most likely for coterie food resources, may be a mechanism promoting intra-colony dispersal and expansion in prairie dogs. This relationship between prairie dog density and expansion is consistent with observations in previous studies of prairie dogs (Garrett and Franklin, 1988; Knowles, 1985). In addition to established methods of burning or mowing vegetation to facilitate expansion of prairie dog colony edges (Franklin and Garrett, 1989), the addition of supplemental food to sites to reduce expansion (i.e. near park boundaries which border private lands) or to control direction and expansion of prairie dog colonies into more suitable areas, may be beneficial in some instances.

Expansion of burrow sites can only occur when suitable habitat is available near the perimeter of the colony (Garrett et al., 1982); otherwise available habitat becomes a limiting resource. The Canadian prairie dog colonies are relatively old (>15 years (Garrett et al., 1982)) and consequently may be nearing carrying capacity, due to the changes in dominant vegetation composition and cover as a colony ages (Garrett et al., 1982). We hypothesize that prairie dog populations at the northern extent of their range may have reached a point where they are functioning near the carrying capacity of the environment. If this is true it may have implications for the management of prairie dogs and other imperilled prairie species, meaning conservation strategies such as habitat improvements, possibly coupled with translocations, may be required to increase prairie dog populations at their northern range extent.

6. Conclusions

Vegetation availability may affect black-tailed prairie dog densities with a 1 year time-lag, but per capita food availability appears to be linked to colony expansion attempts within years. These bottom-up processes, in turn, are most likely influenced by climatic variations in precipitation and winter severity, which, coupled with social behaviours, may modify population growth, density-dependent dispersal and colony expansion of black-tailed prairie dogs.

We hypothesize that the most likely mechanism driving fluctuations of population growth is density-dependent intra-specific competition that is linked to fluctuating food resources. Due to our finding that prairie dog densities were correlated to natural vegetation the previous year, we suggest that per capita food availability in a given year may have lag effects for the subsequent year. This interaction between prairie dog density and food resources, in particular, likely affects the subsequent overwinter survival and spring reproduction in the following year, producing annual fluctuations in density.

The implication of a time-lag relationship between density and food between years with two-fold differences in precipitation, suggests the importance of precipitation to northern prairie dog population dynamics. Similarly, population changes in southern prairie dog populations have been suggested to follow precipitation regimes (Davidson et al., 2010). The Intergovernmental Panel on Climate Change (IPCC) predicts an increase in temperature and a decrease in the amount and frequency of precipitation for
the Canadian prairie region with climate change (Flanagan and Adkison, 2011). Therefore, climate change may lead to more drought-like conditions for this region over multiple years, which could negatively affect the population growth of northern prairie dog colonies. If prolonged drought conditions are predicted, then management strategies that mitigate this need to be developed for northern prairie dog populations.

Expansion of current colonies and overall population growth through the formation of new colonies, through reintroductions, are long-term goals for the conservation of prairie dogs in North America (Facka et al., 2010). Mechanisms that limit populations at range edges must be considered in order for reintroductions to be successful (Facka et al., 2010). The apparent ‘time–lag’ population dynamics of this species and the variability of precipitation, particularly under climate change trends, need to be considered as part of the conservation of this species at the northern extent and elsewhere in their range. Given the limited distribution and abundance of prairie dogs at the northern extent of their range, their ‘threatened’ status and the dependence of recently reintroduced black-footed ferrets in Canada on them, ongoing habitat management that facilitates suitable vegetation growth within and outside colonies, may be necessary to sustain northern prairie dogs and co-dependent species in the long term.

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