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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.

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 similarly 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 (Channell 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

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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 (Coulson, 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 m^2 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® Perfomance 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 them. 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).