Grazing Intensity influences Ground Squirrel and American Badger Habitat Use in Mixed-Grass Prairies

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Abstract

Ground squirrel (*Spermophilus* spp.) and American badger (*Taxidea taxus*) burrowing activities are ecologically important disturbances that contribute to the heterogeneity of prairie environments. These activities also have a strong impact on habitat suitability for many other grassland species. However, effects of cattle grazing intensity on ground squirrel and American badger burrows are not well understood. From 2006-2012, we evaluated effects of grazing intensity and vegetation type on American badger burrow occurrence and ground squirrel burrow abundance using a manipulative grazing experiment in Grasslands National Park of Canada, Saskatchewan. The study area consisted of nine 300-ha pastures at a range of stocking rates, from very low to very high for the region. Each pasture had ten plots (six upland and four lowland) where vegetation and burrow surveys were completed. Burrow abundance and occurrence, and vegetation structure, were assessed for 2 years prior to the introduction of cattle to this landscape in 2008, which followed at least 15 years without livestock, and from 2009-2012, following introduction of livestock. Data were analyzed using generalized linear mixed models. In upland habitats, ground squirrel burrow counts increased with increasing grazing intensity and decreasing vegetation biomass; conversely, badger burrow occurrence increased with decreased stocking rates and increasing average litter cover and vegetation biomass. Abundance and occurrence of both ground squirrel and badger burrows in lowland habitats was relatively independent of grazing intensity or vegetation. Vegetation composition had little impact on ground squirrel or badger burrows. A range of grazing intensities may contribute to maintaining diversity of burrowing mammals in prairie environments.

Key Words

Burrowing animals; livestock; prairie conservation; vegetation composition; vegetation structure

INTRODUCTION

Ground squirrels (*Spermophilus* spp.) and American badgers (*Taxidea taxus*) play an ecologically important role in prairie environments (Umbanhowar Jr.1995, Eldridge 2004), primarily due to their creation and expansion of burrows. Excavation activities bring soil to the ground surface, aerate the soil, redistribute nutrients, and can positively or negatively alter soil moisture (Eldridge 2004, Eldridge et al. 2009) and local plant community composition (Borchard and Eldridge 2012), while badger burrows may provide shelter for other species including ground squirrels and burrowing owls (*Athene cunicularia*) (Messick and Hornocker 1981, Lindzey 2003). Thus, ecological effects of badger and ground squirrel burrows have both short and long-term effects.

Few studies have determined the effects of cattle grazing on badger activities or badger habitat use possibly because prey availability, not vegetation structure or composition, has been assumed to be the driving force behind habitat selection by badgers (Lindzey 2003, Eldridge 2004). Habitat selection by ground squirrels is better understood, although the effects of cattle grazing on ground squirrels are not. Cattle grazing might positively or negatively influence ground squirrel habitat use since large herbivores like cattle may compete with ground squirrels for food, yet promote the relatively short vegetation structure that they prefer (Kruger 1986, Fehmi et al. 2005, Cheng and Ritchie 2006).

The abundance of badger and ground squirrel burrows might have a dynamic relationship under natural conditions due to trophic interactions and predator-prey dynamics. Abundance of grassland herbivores may be controlled by the abundance and quality of the vegetation available for consumption (Báez et al. 2006), and if cattle indirectly affect the abundance of ground squirrels, this may in turn influence the abundance of this food source for badgers, and therefore, habitat use by badgers (Eldridge 2004). Understanding these trophic interactions between herbivores, between herbivores and the plant community, and between herbivores and carnivores, could help us further understand the ecological roles and management of badgers and ground squirrels in North American prairies.

We evaluated the effects of grazing intensity and habitat structure and composition on abundance of ground squirrel burrows and occurrence of American badger burrows in a northern mixed-grass prairie. Our objectives were to: (1) examine the relationship between cattle grazing intensity and duration, and ground squirrel burrow abundance and badger burrow occurrence, (2) evaluate relationships between ground squirrel burrow abundance and badger burrow occurrence and vegetation composition and structure, and (3) determine if there is evidence that ground squirrel burrow abundance and badger burrow occurrence are correlated, which might suggest that badgers select sites with greater ground squirrel activity. Because very few previous studies have evaluated effects of cattle grazing on either of our focal species, we made only tentative hypotheses and predictions prior to our study. We hypothesized that if ground squirrels select habitat with improved visibility of predators, they would have more burrows in sites with higher grazing intensities, while if they select habitat to avoid competition for food with cattle, ground squirrels would select habitats with lower grazing intensities. We hypothesized that if American badgers selected sites with better visibility of prey, they would select more heavily grazed sites, whereas if they selected habitats with better cover to allow them to hide from prey, they would select more lightly grazed sites.

METHODS

A grazing experiment was initiated in the East Block of Grasslands National Park of Canada (GNPC) in southern Saskatchewan (approximately lat 49°01'00" N, long 106°49'00" W) in 2006 (Koper et al. 2008), located in the Biodiversity and Grazing Management Area (BAGMA). This portion of the park is characterized by a sub-humid climate, a mean annual precipitation of approximately 350 mm, and annual evapotranspiration of approximately 347 mm (Kottek et al. 2006). Plant species commonly found in upland habitats were typical of mixed-grass prairies, and include *Sphaeralcea coccinea, Pediomelum argophyllum, Phlox hoodii, Tragopogon dubius, Elymus lanceolatus, Bouteloua gracilis, Geum triflorum,* and *Ratibida columnifera*. The plant community found in lowland habitats was dominated by grasses but also included a more abundant shrub component (primarily *Artemisia cana*). Lowland plant communities included species such as *Rumex occidentalis, Sarcobatus vermiculatus, Agrostis scabra, Hordeum jubatum,* and *Potentilla gracilis*.

The ground squirrels commonly found in GNPC included Richardson's ground squirrels (*Spermophilus richardsonii*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*). *S. richardsonii* was observed much more frequently than *S. tridecemlineatus*. From here on, the term ground squirrels will be used to collectively refer to both species, as we were not able to conclusively distinguish between their burrows. The only badger species present in the park was the American badger *(Taxidea taxus*). We used burrow counts as indices of activity of both taxa. We recognize that burrow counts are not a precise index of animal abundance; however, the activity levels of these species, specifically burrow abundance, may be more important ecologically than the abundance of the animals themselves, because of their effects on both soil and vegetation communities, and thus many other species that inhabit these communities (Messick and Hornocker 1981, Lindzey 2003, Yensen and Sherman 2003). In most cases, "badger burrows" were probably originally ground squirrel burrows that had been further excavated by badgers while foraging for their prey. No black-tailed prairie dogs *(Cynomys ludovicianus*) or other burrowing species that could be confused with ground squirrels occurred in our study area. Coyote (*Canis latrans*) burrows could be distinguished from badger burrows as they were larger. Red fox (*Vulpes vulpes*) burrows might be confused with badger burrows, but this species was relatively rare in our study area and thus most badger burrows were probably correctly identified as such.

The BAGMA study site has never been cultivated or heavily grazed by livestock. Livestock were removed from the BAGMA grasslands upon purchase of the lands by Parks Canada in 1992, and were absent until the reintroduction of cattle for the present experiment. In 2008, BAGMA was divided into nine pastures (average size 296 ha, range 280-331 ha), and each pasture was assigned a grazing intensity that was estimated to result in biomass removal of 0 % - 70 % annually, including three pastures that were unfenced and ungrazed controls (Koper et al. 2008). The control pastures were dispersed across the study area, both to represent a range of geographical locations and to minimize fencing requirements. Stocking rates were assigned randomly to the remaining pastures, with the condition that higher stocking rates were located downstream of lower stocking rates (not including control pastures) on two separate creeks to accommodate a different research project about effects of stocking rates on water quality. The six grazed pastures had stocking rates that ranged from 0.25 to 0.83 animal unit months (AUM) per hectare ($4.0\ ha \cdot AUM^{-1}$ to $1.2\ ha \cdot AUM^{-1}$), with season-long grazing by yearling steers between late May and early September each year. The entire study area is very lightly grazed by free-ranging ungulates including pronghorns (*Antilocapra americana*) and mule deer

(*Odocoileus hemionus*), and thus our research specifically addressed effects of additive grazing by livestock. Baseline ecological data were collected from May to August in 2006 and 2007 prior to the reintroduction of livestock, and data were also collected May to August from 2008 to 2011 during livestock grazing. During the summer of 2012, data were collected from May to August, but no cattle were present. As there is presumably some time lag between changes in cattle density and ecological responses, and because vegetation and burrow surveys were initiated each year in mid-June, generally only 2-3 weeks after the initiation of season-long livestock grazing for that year, we assumed that most effects of grazing were driven by the stocking rates in the previous calendar year rather than the current calendar year. As a result, we did not analyze data from 2008, as we considered it a transition year between grazed and ungrazed conditions.

In each pasture, four plots were surveyed in the valley lowlands and six plots were surveyed in the upland grasslands. Vegetation and burrow plots were located 25 m south of the center of a 3.2-ha circular point-count plot used for bird surveys in another study. Point-count plots were located randomly in each pasture, with the conditions that they were more than 50 m from fences to minimize edge effects, and were more than 100 m apart to maximize independence. In each plot, a 50-m by 20-m modified Whittaker plot was established using measuring tapes, and a smaller 20-m by 5-m plot was placed in the middle of the bigger plot. One meter by ½ m quadrats (frames) were set at 10 fixed locations along the measuring tapes of the two larger plots within which several vegetation characteristics were assessed: vegetation biomass; canopy height (not measured prior to 2008); cover of structurally important components such as bare ground; plant species occurrence; and estimated cover of each plant species. Four researchers per year measured vegetation. To minimize effects of observer bias, all researchers were trained concurrently and extensively prior to surveys, there were always one or more observers consistent among sequential years, and observers worked concurrently within the same plots to ensure their methods were consistent. To assess vegetation biomass, Robel poles were placed in the middle of the quadrats and 50% and 100% obscurity readings at 5-cm increments were taken at a height of 1 m from the ground and 4 m from the pole for each of the four directions around the pole (modified from Robel et al. 1970). The readings were then averaged across the four directions to get a single obscurity measure per quadrat. To measure canopy height, we placed a piece of Styrofoam with a slit in the centre around a meter stick, let it fall to its natural height on the vegetation, and then measured the height at which it rested. Cover is an estimate of how much space each measured variable occupied in the quadrat; for plant species, cover indicated how much ground that species would have shaded. Nine cover classes were used (1 = > 0 to 0.1%, 2 = 0.1 to 1%, 3 = 1 to 3%, 4 = 3 to 10%, 5 = 10 to 25%, 6 = 25 to 50%, 7 = 50 to 75%, 8 = 75 to 95%, and 9 = 95 to 100%). For analyses, cover classes were replaced with the midpoint percentage of each class range. A single estimate of percent cover for litter, bare ground, and each plant species was determined for each plot by averaging these midpoints across the 10 quadrats in each plot, so that both vegetation and burrow analyses could be conducted at the same spatial scale (plot scale). Litter depth, defined as dead vegetation sloped at an angle of 45° or greater, was measured using a meter stick placed in the center of the quadrat.

Walkthrough surveys, which were used to visually detect all plant species, badger and ground squirrel burrows, and cattle droppings ("dung pats") within each Whittaker plot, involved researchers walking along parallel transects about 1 m apart throughout each plot, thus we are confident that detection probability of dung pats and burrows within Whittaker plots was close to 1.0. Burrows that had diameters of 15 cm or more were classified as badger burrows, whereas burrows smaller than 15 cm were classified as ground squirrel burrows. Generally, badger burrows were easily distinguished from ground squirrel burrows based on size (Poulin et al. 2005). Areas that may have been burrows in the past but have since filled in with soil or plant materials were not counted. Individual cattle defecation events were defined as single dung pats, and were identified as such using size, shape, and pattern or direction of the droppings (Henderson 2009, unpublished data). Cattle dung could be easily distinguished from dung of sympatric species. Because cattle dung pats may take years to decompose in semi-arid prairies, dung pat counts represent cumulative grazing intensity over recent years (Milchunas et al. 1989), and also represent variation in grazing intensity within pastures due to selective foraging by cattle (Manthey and Peper 2010).

In all analyses, the data were separated by habitat position (upland [UP], or lowland [LO]) because of the marked differences in the vegetation composition and structure between these habitat types. Year since grazing began (2006 and 2007 = 0; 2009 = 1; 2010 = 2; 2011 = 3, 2012 = 4) was included in all models except for the model assessing the relationship between badger burrow occurrence and ground squirrel burrow abundance. We used diagnostic plots and deviance $\cdot$ df^{-1} ratios to ensure outliers were not present, and to select an appropriate distribution of the residuals from among the following options: normal (Gaussian), negative binomial, Poisson, and binomial distributions. Badger burrow abundances were low, and thus were converted to presence/absence data and fit a binomial distribution (1 = present, 0 = absent), whereas ground squirrel burrow abundance followed a negative binomial distribution. Vegetation structure followed normal distributions in uplands, but negative binomial distributions in lowlands. We used $\alpha = 0.05$ for all analyses.

Generalized linear mixed models (GLMM) were used to determine whether the occurrence of badger burrows was correlated with ground squirrel burrow abundance, and to determine the extent to which burrow abundance or occurrence were related to vegetation structure or composition, and grazing intensity (see below). GLMMs are hierarchical models in which random variables are included to statistically control for the lack of independence among plots sampled repeatedly over several years, and among plots located in the same sites (Fitzmaurice et al. 2004). This hierarchical approach maximizes power and allows for a multi-scale analysis. Plot and pasture were used as random variables in our GLMMs to control for repeated sampling of plots over multiple years (“plot”), and among plots from within the same pastures (“pasture”). Occasionally, models did not converge with both random variables in the model, usually because of overparameterization and a very small (not significantly different from 0) parameter estimate for the “plot” random variable. In these cases, this suggested that only one random variable was required to account for overdispersion, and thus the random variable “plot” was not required in the model and was removed.

We conducted separate models to address three types of questions: what were effects of (1) grazing intensity, (2) vegetation structure, and (3) vegetation composition on abundance of ground squirrel burrows and occurrence of badger burrows. These three analyses were separated, rather than run as a global model, because grazing intensity was manipulated within an experimental framework, while vegetation structure and composition were indirectly influenced by grazing and spatial and temporal environmental variation. Therefore, we are confident that observed effects of grazing on burrow abundance were causal, whereas relationships between burrows and vegetation structure and composition must be considered correlative.

To model effects of grazing on burrow abundance or occurrence, we used two different indices of grazing intensity, at two different spatial scales. The first was cattle dung pat abundance (Julander 1955, Abensperg-Traun et al. 1996, Manthey and Peper 2010; hereafter, "grazing intensity"), which has the advantage of providing a plot-specific measure of grazing intensity (*n* = 36 lowland, *n* = 54 upland plots). This index is useful since burrow abundance and occurrence were also measured at the plot scale, and because cattle grazing intensity varies within pastures. However, some studies suggest that this index is not an accurate measure of grazing intensity (Milchunas et al. 1989, Tate et al. 2003, Dorji et al. 2013). Therefore, we also conducted our analyses using separate GLMM models with cattle stocking rate (in AUM $\cdot$ ha^{-1}; hereafter, "stocking rate"), which represents a known index of grazing intensity at the pasture scale (*n* = 9 pastures). An interaction term (dung pat counts * year since grazing began; stocking rate*year since grazing began) was initially included in each model, but none of the interaction terms were significant so they were removed from the final models to minimize collinearity.

To evaluate whether effects of stocking rate that we detected were caused by stocking rate, and were not spurious patterns that were correlated with stocking rate by chance, we used the pre-grazing data from 2006 and 2007 to evaluate whether burrow abundance was correlated with "future stocking rate" (the stocking rate imposed on pastures starting in 2008). A significant correlation would have indicated a spurious relationship with stocking rate.

Relationships between vegetation structure and ground squirrel burrow abundance, and badger burrow occurrence, were also assessed. Bare ground cover (%), average litter cover (%), average Robel pole 100% obscurity (cm), and year since grazing began were included in the vegetation structure models. Despite high correlations among some predictor variables ($r \sim 0.7$), bare ground cover, average litter cover, average Robel pole 100% obscurity, and year since grazing began were included in the final vegetation structure GLMM because they were believed to be ecologically important and because excluding influential variables from models, even if they are collinear with other variables, can result in incorrect conclusions about the influence of the variables that remain in the models (Smith et al. 2009).

We also assessed relationships between common or ecologically important plant species and abundance or occurrence of burrows. Plant species that occurred in the majority of the plots sampled, or were considered to be potentially important to badger or ground squirrel habitat selection as reported in the literature (e.g., MacCracken et al. 1985, Eldridge 2004, Mullican et al. 2005), were assessed within the model by comparing burrow counts to plant species cover classes. Independent variables included cover of blue grama grass (*Bouteloua gracilis*), northern wheatgrass (*Elymus lanceolatus*), sagebrush (*Artemisia cana*), plains prickly-pear cactus (*Opuntia polyacantha*), common dandelion (*Taraxacum officinale*), and silverleaf Psoralea (*Pediomelum argophyllum*). Year since grazing began was included in this model to account for yearly variation in the vegetation structure and composition as a result of differences in precipitation and other factors.

We used a similar approach to measure effects of stocking rate and duration (in years) on vegetation biomass and canopy height. We modelled effects of stocking rate, year, and an interaction between the two, using GLMMs. If the interaction term was not significant, it was removed and the model was conducted without it. To evaluate whether significant relationships with stocking rate were caused by stocking rate, and were not spurious, we used the pre-grazing data from 2006 and 2007 to evaluate whether biomass was correlated with “future stocking rate”, as above. These data were not available for canopy height.

RESULTS

Cattle Grazing and Burrows

Cattle grazing intensity, measured both at the plot scale using dung pats and at the pasture scale using stocking rate, had a significant positive effect on the relative abundance of ground squirrel burrows in upland habitats, but not lowland habitats (Table 1, Figure 1). On average there were 2.5 times more ground squirrel burrows in upland plots that had a high grazing intensity (dung pat count = 100 pats) compared to plots that had no cattle grazing (dung pat count = 0 pats). There were no pre-existing significant trends in the abundance of ground squirrel burrows for the upland habitats before grazing began ($p = 0.147$), suggesting that the effects of grazing intensity we detected were caused by grazing intensity. Lowland habitats could not be tested for pre-existing trends in ground squirrel burrow abundance because the model would not converge. Abundance of ground squirrel burrows declined over time but the interaction between grazing intensity and duration of grazing was not significant (Table 1).

American badger burrow abundance was independent of grazing intensity at both the plot and pasture scale in lowland habitats (Table 1, Figure 1). In upland habitats, when occurrence of American badger burrows was analyzed using dung pats as an index of grazing intensity at the plot scale, there was no apparent effect of grazing intensity (Table 1). However, badger burrow occurrence was negatively correlated with stocking rate in upland sites at the pasture scale (Table 1, Figure 1). There was no pre-existing trend in the occurrence of badger burrows in upland habitats before grazing began ($p = 0.925$) suggesting that the observed effect was caused by grazing intensity. Lowland habitats could not be tested for pre-existing trends in the occurrence of badger burrows because the model would not converge. Occurrence of American badger burrows increased over time (Table 1), but because the interaction between grazing intensity and duration of grazing was not significant, as with ground squirrel burrows, this highlights: (1) that the effect of grazing did not increase as number of years of grazing increased, and (2) that the increase in occurrence of badger burrows over time did not vary with grazing intensity or stocking rate, and thus was not caused by grazing.

Vegetation Composition and Structure, and Burrows

Ground squirrel burrow abundance was correlated with vegetation structure in similar ways in upland and lowland habitats (Table 2). Burrow abundance was higher in sites with lower vegetation biomass, but was relatively insensitive to local occurrence of plant species. Of the six plant species included in the vegetation composition model, only *Taraxacum officinale* was correlated with ground squirrel burrow counts, and only in lowland plots (β = -0.588, p = 0.028, 95% LCL = -1.112, 95% UCL = -0.063; all other vegetation composition variables $p > 0.062$).

Vegetation structure was not related to badger burrow occurrence in the lowland plots, but in upland habitats badger burrow occurrence was positively correlated with percent litter cover and vegetation biomass (Table 2). Few plant species were related to the occurrence of badger burrows, and results were not consistent between upland and lowland sites (uplands: *Pediomelum argophyllum*, β = 0.084, p = 0.051, 95% LCL = -0.000, 95% UCL = 0.169; lowlands: *Elymus lanceolatus*, β = 0.036, p = 0.049, 95% LCL = 0.000, 95% UCL = 0.072; all other vegetation composition variables $p > 0.123$).

Cattle Grazing and Vegetation Structure

There were no significant pre-existing trends for biomass in either upland or lowland pastures ($p > 0.4511$). Biomass decreased with stocking rate in both uplands and lowlands, and increased with year in lowlands between 2009 and 2012 (Figure 2). Effects of stocking rate on biomass increased over time in uplands ($p < 0.001$) but not lowlands ($p = 0.140$). In both uplands and lowlands, stocking rate had a significant negative effect on canopy height, and canopy height increased on average over time (Figure 2). However, effects of stocking rate on canopy height did not increase with number of years grazed ($p > 0.1433$).

Ground Squirrel Burrow Abundance and Occurrence of American Badger Burrows

In lowlands, there was a strong positive correlation between ground squirrel burrow abundance and badger burrow occurrence ($\beta = 0.160$, $p < 0.001$, 95% LCL = 0.078, 95% UCL = 0.242); by back-transforming parameter estimates using e^{β}, we calculated that the odds of badger burrow occurrence increased by 17% with each additional ground squirrel burrow. There was a non-significant positive trend between badger burrow occurrence and ground squirrel burrow abundance in the upland plots ($\beta = 0.110$, $p = 0.053$, 95% LCL = -0.001, 95% UCL = 0.200).

DISCUSSION

Cattle grazing intensity resulted in significant increases in abundance of ground squirrel burrows in upland plots, perhaps because grazing reduced vegetation height and biomass, consistent with our hypothesis that ground squirrels might construct burrows in sites with good visibility, allowing them to locate and identify predators. Cattle foraging behaviour also increases forage quality (Cheng and Ritchie 2006), tramples, exposes and disturbs soil, while also reducing vegetation height. In contrast to these results, a previous study found little or no effect of grazing on ground squirrel density (Fehmi et al. 2005). We also found no effect of grazing intensity on abundance of ground squirrel burrows in lowland sites, perhaps because the lowland sites we studied are structurally and compositionally more variable than upland sites. We caution that this experiment was conducted when the region was experiencing wetter climatic conditions than usual (Environment Canada 2013). Effects of grazing may increase (Gillen et al. 2000), or the relationship between livestock and ground squirrels could become competitive, in less productive years (see also Fehmi et al. 2005, Cheng and Ritchie 2006, Proulx 2010).

Occurrence of American badger burrows decreased as grazing intensity in uplands increased. To the best of our knowledge, this is the first study to assess the effects of grazing intensity on occurrence of American badger burrows. Higher stocking rates may negatively affect badger abundance for the same reason that they positively influence ground squirrel abundance: vegetation removal improves the ability of ground squirrels to detect and avoid predators, and thus lower stocking rates might provide more cover for foraging badgers (e.g., Cheng and Ritchie 2006); however, this explanation is speculative.

Although we detected trends in American badger burrow occurrence ground squirrel burrow abundance over time, these trends were not driven by grazing. Precipitation was above average during our study period (Environment Canada 2013), resulting in relatively tall and dense vegetation, and the cumulative effect of these relatively mesic conditions may have favoured species that prefer taller vegetation, such as American badgers, over species that prefer shorter vegetation, such as ground squirrels. The significant relationship between grazing intensity and burrow abundance and occurrence in uplands, in concert with the changes in abundance and occurrence of burrows detected over time, suggest that both livestock management and environmental variability can influence habitat suitability for ground squirrels and American badgers.

Ground squirrels are often found in grasslands with relatively short vegetation (Downey et al. 2006). While vegetation height and density can be reduced due to foraging by ground squirrels, our results suggest that ground squirrels also selected sites with higher cattle grazing intensities and stocking rates, contributing to this habitat association. We found few consistent correlations between ground squirrel burrow abundance, or badger burrow occurrence, and cover of plant species, suggesting that those few associations we detected may be spurious.

There are several reasons why ground squirrel and badger burrows may be correlated in some grasslands. Ground squirrels are important prey for American badgers, and thus badgers may select sites with an abundance of ground squirrels (Messick and Hornocker 1981, Vander Haegen et al. 2001, Lindzey 2003, Eldridge 2004). Alternatively, it has been hypothesized that occurrence of badgers and ground squirrels are correlated because both require similar habitats (Lindzey 2003, Eldridge 2004). Because ground squirrel burrows tended to be associated with shorter, grazed vegetation, while badger burrow occurrence tended to be associated with taller, less heavily grazed vegetation, our results suggest more support for the former than the latter hypothesis, although as we could not be sure which burrows were active, our analyses cannot be considered conclusive.

Our results suggest that ground squirrels can co-exist with and sometimes benefit from grazing by cattle. High stocking rates may remove too much above-ground vegetation in grasslands locally impacted by heavy grazing to remain suitable for American badger populations, although badgers may benefit from livestock grazing indirectly due to associated increases in prey availability, particularly at a regional scale. A range of stocking rates and large enough pastures to allow cattle to forage selectively would provide a heterogeneous mosaic with appropriate cover, habitat, and prey for American badger populations while also providing suitable habitat for ground squirrels. This type of heterogeneous landscape-scale grazing regime has previously been recommended for maintaining ecologically diverse prairie communities

(Fuhlendorf and Engle 2001), but contradicts typical management recommendations for livestock production (Teague and Dowhower 2003). Nonetheless, ground squirrel and badger burrowing activities are ecologically important disturbances (Umbanhowar Jr.1995, Eldridge 2004), and thus loss of ground squirrels or American badgers from prairie environments could significantly reduce ecological heterogeneity and, thus, ultimately the economic value of rangelands (Vander Haegen et al. 2001).

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Table 1. Effects of grazing intensity, measured at the 20-m x 50-m plot scale using dung pat counts, and at the 296-ha pasture scale using stocking rate (animal unit months (AUM) per hectare), and grazing duration on the abundance of ground squirrel burrows and occurrence of American badger burrows in upland and lowland mixed-grass prairie habitats in the grazing experiment located in the Biodiversity and Grazing Management Area in Grasslands National Park of Canada, Saskatchewan, 2006-2012 (excluding 2008). Parameter estimates (*β*) are followed by upper and lower 95% confidence limits in parentheses.

			American Badger		Ground Squirrel	
Scale	Position	Variable	*β*	*p*	*β*	*p*
Plot	Lowland	Grazing intensity (dung pats · plot^{-1})	0.007 (-0.007–0.021)	0.309	0.002 (-0.004–0.008)	0.494
		Duration (years)	0.329 (0.150–0.508)	<0.001	-0.279 (-0.390–-0.168)	<0.001
	Upland	Grazing intensity (dung pats · plot^{-1})	-0.004 (-0.012–0.004)	0.372	0.009 (0.003–0.015)	0.002
		Duration (years)	0.216 (0.083–0.350)	0.002	-0.416 (-0.509–-0.322)	<0.001
Pasture	Lowland	Stocking Rate (AUM · ha^{-1})	0.193 (-1.056–1.441)	0.761	0.179 (-0.374–0.732)	0.524
		Duration (years)	0.362 (0.163–0.560)	<0.001	-0.281 (-0.405–-0.158)	<0.001
	Upland	Stocking Rate (AUM · ha^{-1})	-0.886 (-1.618–-0.153)	0.018	0.822 (0.238–1.406)	0.006
		Duration (years)	0.279 (0.101–0.457)	0.002	-0.448 (-0.581–-0.315)	<0.001

Table 2. Correlations between vegetation structure and the abundance of ground squirrel burrows and occurrence of American badger burrows in upland and lowland mixed-grass prairie habitats in the East Block of Grasslands National Park of Canada, Saskatchewan, 2006-2012 (excluding 2008). Parameter estimates (*β*) are followed by upper and lower 95% confidence limits in parentheses.LCL LCL and UCL indicate lower and upper confidence limits, respectively.

	Position	Variable	*β*	*p*
Ground squirrel burrow abundance	Lowland	Bare cover (%)	-0.009 (-0.032–0.014)	0.441
		Average litter cover (%)	0.003 (-0.006–0.011)	0.527
		Year since grazing began	-0.218 (-0.355–-0.080)	0.002
		Average Robel 100% obscurity (cm)	-0.050 (-0.089–-0.010)	0.014
	Upland	Bare cover (%)	0.038 (-0.002–0.079)	0.064
		Average litter cover (%)	0.011 (-0.002–0.024)	0.103
		Year since grazing began	-0.257 (-0.391–-0.123)	<0.001
		Average Robel 100% obscurity (cm)	-0.080 (-0.134–-0.026)	0.004
American badger burrow occurrence	Lowland	Bare ground cover (%)	0.022 (-0.027–0.072)	0.370
		Average litter cover (%)	0.007 (-0.016–0.030)	0.564
		Year since grazing began	0.443 (0.111–0.776)	0.009
		Average Robel 100% obscurity (cm)	-0.006 (-0.067–0.056)	0.857
	Upland	Bare ground cover (%)	0.063 (-0.033–0.159)	0.198
		Average. litter cover (%)	0.024 (0.001–0.048)	0.043
		Year since grazing began	0.431 (0.202–0.660)	<0.001
		Average Robel 100% obscurity (cm)	0.115 (0.021–0.209)	0.017

Figure 1 Predicted effects of grazing intensity at the (a) pasture scale (animal unit months (AUM) · ha^{-1}) and (b) plot scale (dung pats · 0.1 ha^{-1}) on ground squirrel burrow abundance and American badger burrow occurrence in the Biodiversity and Grazing Management Area in Grasslands National Park of Canada, Saskatchewan, 2006-2012 (excluding 2008). * indicates significant slope at $\alpha = 0.05$.

Figure 2. Predicted effects of grazing intensity at the pasture scale (animal unit months (AUM) · ha^{-1}) and grazing duration on vegetation structure in the Biodiversity and Grazing Management Area in Grasslands National Park of Canada, Saskatchewan. GI indicates significant ($\alpha = 0.05$) effect of grazing intensity; Y indicates significant effect of year; SR*Y indicates significant change in effect of stocking rate with change in year. (A) Vegetation biomass in upland (SR*Y), (B) vegetation biomass in lowland (SR, Y), (C) canopy height in upland (SR, Y), and (D) canopy height in lowland (SR, Y) mixed-grass prairies. Data for biomass were collected 2006-2012 (excluding 2008), data for canopy height were collected 2009-2012.