

Impacts of cattle grazing on small-rodent communities : an experimental case study

C. Bueno, K.E. Ruckstuhl, N. Arrigo, A.N. Aivaz, and P. Neuhaus

Abstract: We used experimental cattle ungrazed and grazed sites to evaluate what impact different intensities of cattle grazing have on deer mice (*Peromyscus maniculatus* (Wagner, 1845)) and meadow voles (*Microtus pennsylvanicus* (Ord, 1815)). Live-trapping of these small rodents was conducted on paired treatment plots (grazed and ungrazed) at Sheep River Provincial Park in southwestern Alberta, Canada. Before grazing started, both rodent species were equally abundant in either grazed or ungrazed sites. Introduction of grazing resulted in strong but differing responses by both rodent species. Deer mice had higher population density (measured as individual animals trapped) in the grazed than in ungrazed plots, but their body mass was negatively correlated with increasing grazing pressure. Meadow voles were more heavily affected by grazing, as a strong avoidance of cattle-grazed plots was observed already at low grazing intensity. In addition, cattle grazing had noticeable effects, impacting the survival, sex and age ratios, and the ectoparasite prevalence of these two rodent populations. We conclude that there are diverse and different levels of impact of cattle grazing on those two rodents, leading to much more complex species interactions than previously thought. We suggest that the presence or absence, density, and body condition of small mammals could be used as a tool for ecosystem health assessment.

Résumé : Nous utilisons des sites expérimentaux broutés et non broutés par le bétail afin d'évaluer l'impact de différentes intensités de broutage par le bétail sur les souris du crépuscule (*Peromyscus maniculatus* (Wagner, 1845)) et les campagnols de Pennsylvanie (*Microtus pennsylvanicus* (Ord, 1815)). Nous avons procédé à du piégeage vivant de ces petits rongeurs sur des parcelles expérimentales appariées (broutées et non broutées) dans le parc provincial de Sheep River, sud-ouest de l'Alberta, Canada. Avant le début du broutage, les deux espèces de rongeurs étaient également abondantes dans les sites broutés et non broutés. L'introduction du broutage a causé des réactions fortes, mais distinctes, chez les deux espèces de rongeurs. Les souris du crépuscule ont une plus forte densité de population (nombre d'animaux piégés) dans les parcelles broutées que dans les non broutées, mais leur masse corporelle est en corrélation négative avec l'augmentation de la pression de broutage. Les campagnols de Pennsylvanie sont plus affectés par le broutage, puisqu'on observe un évitement des parcelles broutées, dès les faibles intensités de broutage. De plus, le broutage du bétail a des effets observables en modifiant la survie, les rapports des sexes et des âges et la prévalence des ectoparasites chez ces deux populations de rongeurs. Nous concluons qu'il existe des niveaux divers et différents d'impacts du broutage du bétail sur ces deux rongeurs, ce qui représente des interactions beaucoup plus complexes entre les espèces qu'on ne le croyait antérieurement. Nous suggérons d'utiliser la présence ou absence, la densité et la condition corporelle des petits mammifères comme outils d'évaluation de la santé des écosystèmes.

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Introduction

Cattle grazing has been practiced for hundreds of years with varying impacts on the environment. While some believe that cattle grazing is beneficial because it suppresses tree growth, others have suggested negative impacts because it introduces direct feeding competition with native herbivores. Cattle grazing for example impacts agro-pastoral ecosystems through the removal of both live and dead

vegetation (Altesor et al. 2006), soil compaction (Steffens et al. 2008), hillside erosions, riparian habitat deterioration, and soil nutrient content modification (Bakker et al. 2004; Steffens et al. 2008).

Grazing activity has direct and indirect impacts on native species exploiting the same areas by changing habitat suitability. Negative impacts of cattle grazing have been reported for mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) (Kie et al. 1991), bighorn sheep (*Ovis canadensis* Shaw,

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1804) (Brown et al. 2010), ground-nesting birds (Fondell and Ball 2004), odonates (Foote and Hornung 2005), and rodent species associated with habitats with substantial ground cover (hispid pocket mouse (*Chaetodipus hispidus* (Baird, 1858)), western harvest mouse (*Reithrodontomys megalotis* (Baird, 1858)), white-footed mouse (*Peromyscus leucopus* (Rafinesque, 1818)), and hispid cotton rat (*Sigmodon hispidus* Say and Ord, 1825); Bock et al. 1984). Conversely, some studies described positive effects of cattle grazing in small mammals preferring open habitats (e.g., Merriam's kangaroo rat (*Dipodomys merriami* Mearns, 1890), which are abundant on grazed sites; Bock et al. 1984), while one study (Bakker et al. 2009) showed different reactions to cattle grazing by different species: rather positive for European rabbits (*Oryctolagus cuniculus* (L., 1758)) and negative for common voles (*Microtus arvalis* (Pallas, 1778)). In addition, the sex ratio of rodent populations may also be influenced by habitat disturbance. For example, Pearson et al. (2001) found differences in sex ratio according to habitat; however, their results were site-dependent. Bowers and Smith (1979) found that there were more male than female deer mice in less suitable habitats (e.g., the most xeric habitats).

In our study, we focus on small rodents to evaluate the consequences of grazing pressure on two co-occurring wild species. Small rodents are excellent study organisms because their rapid reproductive cycles allow for observing rapid responses in population density to environmental perturbations. Most studies investigating the impacts of cattle grazing on small mammals obtained results that varied greatly according to the system and region that were being studied (Grant et al. 1982; Hayward et al. 1997; Matlack et al. 2001, 2001; Steen et al. 2005; Oksanen et al. 1999; Tabeni and Ojeda 2005; Damhoureyeh and Hartnett 1997; Smit et al. 2001; Evans et al. 2006). Owing to this variation, two main hypotheses in the ecological literature are commonly put forward to explain the effects of cattle grazing on the behaviour and ecology of small-rodent species: (1) a decrease of vegetation increases predation risk and thus population density (Kotler 1984; Kotler and Blaustein 1995) and (2) the quality and quantity of vegetation available is influenced by cattle grazing and thus strongly influences habitat use of small rodents (Arsenault and Owen-Smith 2002) and their performance and persistence on the landscape. Although our experimental setup was not aimed to look at predation risk, the primary aim of our study was to experimentally test the effect of cattle grazing on rodent habitat use (testing hypothesis 2), and in particular, its indirect effects on population age and sex ratios, and on body mass, parasite loads, and survival on the individual scale. We focused on one generalist species, the deer mouse (*Peromyscus maniculatus* (Wagner, 1845)), and one specialist rodent species, the meadow vole (*Microtus pennsylvanicus* (Ord, 1815)) (Desrosiers et al. 2002), to assess the following hypotheses: (i) cattle grazing influences habitat use and population age and sex ratios of both rodent species by negatively influencing fitness, body condition (as measured through mass changes and parasite loads), and survival; (ii) because of the divergent ecological niches of deer mice and meadow voles, the magnitude of the effects of cattle grazing differs. We thus predicted that the population density of rodents (measured as individuals trapped during a trapping session), body condition, and survival would be lower and

parasite loads higher in grazed plots than in animals occupying ungrazed plots. As deer mice are known to occur both in open and closed habitats, we predicted that they would be more plastic and thus less affected in their response to cattle grazing than meadow voles.

Materials and methods

Study site and experimental design

The study was conducted in the Sheep River Provincial Park (50°39'0"N, 114°35'4"W; Alberta, Canada) from the end of May to the end of September 2007. The area is part of a larger piece of public land and has a long history (~100 years) of cattle grazing through the summer and fall seasons. Twelve sites (hereafter referred to as "trapping sites"), a minimum of 40 m distance from each other, were selected for the experimental setup. In each trapping site, our treatment consisted of paired plots (35 m × 35 m each), separated by ≥40 m. In each trapping site, one of the two plots was fenced with barbed wire (hereafter referred to as "ungrazed"), while the other remained open (four short stakes demarcating the corners) and accessible to cattle (hereafter referred to as "grazed"). The fenced ungrazed plots and controls had already been in use for a study on vegetation biomass production for two consecutive years prior to our study (Brown et al. 2010, Chaikina and Ruckstuhl 2006), and therefore, we neither could change their size nor assume that the grazed and ungrazed plots were identical prior to cattle presence in the park during the summer of 2007. Grazing in the park starts in mid-June and ends in mid-October. During this time, cattle were moved within grazing allotments, providing a heterogeneous grazing pattern over all control areas throughout the season.

Trapping frequency and design

Rodent communities in each trapping site were sampled every 12–15 days in what we termed "trapping sessions". Each trapping session was performed during three consecutive nights. In total seven to nine trapping sessions were conducted per trapping site throughout the entire study season. During each trapping session, 13 traps (Longworth® small-mammal live traps composed of an 11 cm tunnel and a 14 cm × 6.5 cm × 8.5 cm nesting area) were placed in a grid-like fashion throughout each grazed and ungrazed plot. Traps were set up in the evening between 6 and 10 pm and checked the following morning between 6 and 10 am. Traps were baited using a mixture of crushed oats, sunflower seeds, peanut butter, and apple. Synthetic cotton was provided to keep trapped animals warm. Traps were cleaned and refilled at the beginning of every trapping session. All captured animals were individually marked using numbered fingerling fish tags (National Band & Tag Co. Monel#1) attached to both ears. For each trapped individual, the sex, age (if adult or juvenile), body mass (using Pesola® spring scale calibrated to the nearest gram), body length (measured from the point of the nose to the beginning of the tail and scaled to the nearest millimetre), and presence or absence and type of ectoparasites (fleas (order Siphonaptera), larvae of the botfly genus *Cuterebra* Clark, 1815, and mites (subclass Acari)) were recorded.

To quantify the level of grazing pressure, we noted evidence of trampling by cattle, presence of cattle faeces, and

vegetation height differences between grazed and ungrazed plots and estimated grazing pressure. Grazing pressure was estimated jointly for the grazed and ungrazed plot and categorized at the beginning of each trapping session. Consequently, ungrazed plots could get grazing values greater than zero (i.e., when the surrounding areas were under grazing pressure). Four levels of grazing pressure were noted: level 0—no trampling or faeces and no vegetation height differences between grazed and ungrazed plots; level 1—few signs of recent cow presence and little visual difference in vegetation height between grazed and ungrazed plots; level 2—presence of trampling, cow faeces, and visible vegetation height differences between grazed and ungrazed plots; level 3—large amounts of trampling and cow faeces and very obvious vegetation height differences between grazed and ungrazed plots. This qualitative estimation of grazing pressure was further validated by direct vegetation height measurements (one-way ANOVA, $F_{[3,70]} = 10.874$, $P < 0.001$, $MSE = 0.0459$; L. Hartog, C. Bueno, and P. Neuhaus, 2007 unpublished data, Vrije Universiteit Amsterdam, the Netherlands).

The sampling effort (i.e., the number of trapping sessions) was comparable for the four levels of grazing pressure investigated (level 0 = 20 trapping sessions; level 1 = 17 trapping sessions; level 2 = 32 trapping sessions; level 3 = 26 trapping sessions). Thus, no corrections for the analyses based on the intensity of grazing pressure were necessary.

Rodents included in the study

Although four different species of small rodents were caught (131 deer mice, 3 western jumping mice (*Zapus princeps* J.A. Allen, 1893), 82 meadow voles, and 2 southern red-backed voles (*Myodes gapperi* (Vigors, 1830)), deer mice and meadow voles were the only species with sufficient observations to be included in the present study. Both species are very common in prairies (Neuburger 1999; Bunker 2001). Deer mice preferably inhabit places with low ground cover and spend most of their time above ground (Pearson et al. 2001). Their diet is diverse, which makes them generalists: they can eat seeds of herbaceous plants, various fleshy fruits (genera *Fragaria* L., *Rubus* L., *Vaccinium* L., *Prunus* L., *Malus* P. Mill., and *Crataegus* L.), genus *Juglans* L., acorns, underground mushrooms (genus *Endogone* Link Ex Fries, 1823), and invertebrates (Desrosiers et al. 2002). In contrast, meadow voles are specialists both in terms of ecological niche and diet. Meadow voles are strongly associated with habitats with heavy ground cover (Peles and Barret 1996), where they build above- and below-ground tunnel systems (Neuburger 1999; Desrosiers et al. 2002). They mostly feed on grasses, including young shoots during spring; leaves and flowers during summer; and seeds, roots, or bulbs during winter. Their diet sometimes includes arthropods and mushrooms (Desrosiers et al. 2002). Both species have a promiscuous mating system (Birdsall and Nash 1973; Boonstra et al. 1993b) and have short gestation times (Innes and Millar 1994; Mihok and Boonstra 1992; Millar and McAdam 2001). Even if they can breed all year long, they show a seasonal pattern in temperate zones (i.e., highest reproductive rates occur between May and October). Reproductive maturity is reached at around 40 days old with four to seven young per litter. The longevity can reach several years, but mean

age is thought to be shorter than a year (Neuburger 1999; Innes and Millar 1994; Bunker 2001; Millar and McAdam 2001).

Statistical analyses

Observations of all data within a trapping session were pooled. Data of deer mice and meadow voles were analysed separately. We analysed the effects of grazing impacts (explanatory variable) on rodent communities considering the following response variables: population density (individuals trapped during a trapping session), survival, fitness, and body condition (body mass and ectoparasite load) of individuals.

Grazing impacts on rodent population density was investigated using a Wilcoxon signed-ranks test in SPSS version 16.0 (SPSS Inc., Chicago, Illinois, USA). To compare the number of trapped individuals (including recaptures from the last trapping sessions and new individuals) between the grazed and ungrazed plots, data from sites with grazing pressure levels 1–3 were pooled into one category, called grazed sites. Individuals that were recaptured during the same trapping session were recoded only once per trapping session for the analyses.

Impacts of grazing on rodent survival were tested using methods implemented in MARK version 5.1 (White and Burnham 1999). Survival was defined as the period of (detected) presence of an individual in one plot. This approach attempted to fit survival models to our capture–recapture observations by considering effects of trapping site (i.e., grazed and ungrazed plot) on the survival of individuals. Individuals trapped in both grazed and ungrazed plots were excluded from this analysis (13 deer mice and 1 meadow vole) because they could bias models owing to their nonspecific response to the treatment. Six models were evaluated— S_0 : basic survival estimation (no effect tested); $S_{\text{treatment}}$: effect of treatment only; S_{site} : effect of trapping site only; $S_{\text{site+treatment}}$: effect of trapping site with an additive and constant effect of treatment; $S_{\text{site} \times \text{treatment}}$: effect of trapping site with an additive but nonconstant effect of treatment; and S_{time} : effect of season only. Models explaining our data were selected according to their goodness of fit using Akaike's information criterion corrected for small sample size (AIC_c) and its associated AIC_{mass} value (i.e., the ranking of the goodness of fit for the six models expressed as a percentage). Best fit models were retained if their AIC_{mass} exceeded 90%. For deer mice, no model obtained at least 90% AIC_{mass} by itself. In that case, models were first ranked according to their AIC_{mass} and only models summing to 90% of cumulative AIC_{mass} were retained (i.e., the most explicative models). These selected models were then compared using a χ^2 test to assess whether they significantly differed from each other.

The effects of grazing impacts on demographic parameters were investigated using the age and sex ratios of the two rodent communities. Both ratios were calculated by pooling observations at the trapping-session scale for each site and for each treatment. We conducted a χ^2 test to compare age and sex ratios between grazed and ungrazed plots in the presence (grazing levels 1–3) or absence (level = 0) of grazing, respectively.

Furthermore, we investigated the effects of grazing levels (defined jointly for the grazed and ungrazed plots for each

trapping site, at each trapping session) on the body mass of trapped individuals using a linear mixed-effects model (in R version 2.7.1; R Development Core Team, Vienna, Austria; available from <http://www.r-project.org/>, accessed 23 June 2008). The mass of trapped individuals was fitted into a model considering the grazing pressure level, the treatment (i.e., grazed or ungrazed plot), the sex, parasite intensity, and the interaction between grazing pressure and treatment as explanatory variables. Sex was included to account for possible sexual dimorphism and sexual differences in habitat selection (Bowers and Smith 1979; Boonstra et al. 1993a). Trapping site, trapping-session number (to avoid an effect of season), the individual identity, and body size (to avoid effects of individual and (or) age) were entered into the model as random variables.

Finally, the prevalence of ectoparasites on trapped individuals was compared between grazed and ungrazed plots. We included data for three parasite groups (fleas, botflies, and mites) and compared the number of infected individuals in both grazed and ungrazed plots using a χ^2 test.

Results

A total of 131 deer mice and 82 meadow voles were tagged during the study, representing 1438 and 949 trapping events, respectively. For both rodent species, the number of trapped individuals varied between sites and throughout the season. Deer mice and meadow voles were trapped in 8 of the 12 sampling sites of the study. The number of trapped deer mice varied from 1 to 22 (8.36 ± 0.9 , mean \pm SE) per treatment and trapping session, and the number of trapped meadow voles from 1 to 16 (4.68 ± 0.63 , mean \pm SE). Individuals stayed in a confined home range, as no individuals were trapped on more than one site. This result was also mostly true at the local scale, as individuals were generally associated with either the grazed or the ungrazed plots except for 13 deer mice and 1 meadow vole that were trapped at least once in both plots.

For both rodent species, no significant differences in numbers of individuals trapped during a trapping session were observed between the grazed and the ungrazed plots before grazing started (Wilcoxon; deer mice: $N = 18$, ties = 5, $Z = -1.409$, $P = 0.159$; Fig. 1A; meadow voles: $N = 18$, ties = 11, $Z = -0.597$, $P = 0.551$; Fig. 1B). In contrast, little to high grazing pressure significantly affected the number of trapped individuals between the grazed and the ungrazed plots. Interestingly, both rodent species reacted differently to cattle grazing: deer mice became more abundant in the grazed plots (Wilcoxon; $N = 55$, ties = 29, $Z = -2.433$, $P = 0.015$; Fig. 1A), whereas meadow voles were most often trapped in the ungrazed plots (Wilcoxon; $N = 55$, ties = 25, $Z = -4.686$, $P < 0.001$; Fig. 1B).

Survival was strongly site-dependent and affected by the presence or absence of grazing pressure in both rodent species. In deer mice, three models estimating survival had to be considered before reaching 90% of the cumulative AIC_{mass} (Table 1). The three models were significantly different from the basic model (S_0) assuming a constant survival rate and explained, respectively, 58% (site effect only, S_{site}), 20% (site effect as an additive with constant treatment effect, $S_{\text{site+treatment}}$), and 14% (site effect as an additive with a site-

depending treatment effect, $S_{\text{site}\times\text{treatment}}$) of the overall variation. However, these three models did not significantly differ from each other (Table 2), suggesting that both site and treatment effects explained variations in the survival of deer mice. In meadow voles, only one model was needed to reach 90% of the cumulative AIC_{mass}. This model considered the site effect and the site-dependent treatment effect ($S_{\text{site}\times\text{treatment}}$; Table 1). As meadow voles were almost solely trapped in the ungrazed plots, there was only one site where we had enough data to directly compare survival in both treatments. Analysing only this particular site, it appeared that survival tended to be lower in the grazed than ungrazed plots. This model was significantly different from the model that accounted for only treatment effect ($S_{\text{treatment}}$) ($\chi^2_{[4]} = 13.666$, $P = 0.0084$).

Although females were the most commonly trapped sex in both deer mice and meadow voles (mean (SE) of females/males sex ratio: deer mice 1.64 ± 0.14 ; meadow voles 1.84 ± 0.21), grazing had no effect on the population sex ratio of either rodent species (Table 3); In contrast, grazing had an impact on the age ratio of rodent populations. In early summer before grazing started, no significant difference in age ratio between treatments was observed, whereas the proportion of adults in both rodent species was higher in ungrazed than in grazed plots. Overall, adults were more often trapped than juveniles in both species (mean (SE) adults/juveniles age ratio: deer mice 1.24 ± 0.20 ; meadow voles 3.77 ± 0.55). However, there were significant differences in adult juvenile ratios between grazed and ungrazed plots for both species (Table 3).

Although cattle grazing did affect individual body mass and parasite intensity, the effects were not the same for deer mice and meadow voles. Irrespective of treatment, the mean (SE) mass of deer mice was 19.90 ± 0.32 g for adults and 14.28 ± 0.20 g for juveniles, whereas the mean (SE) mass for meadow voles was 27.51 ± 0.52 g for adults and 14.57 ± 0.32 g for juveniles. The sample size for body mass was balanced for deer mice but very unbalanced for meadow voles (owing to their strong avoidance of grazed areas). Before grazing started, the body mass of deer mice was higher in the grazed than ungrazed plots for every trapping site (Fig. 2A; body mass displayed as residuals considering body size, individual identity, site, and trapping session as random variables). After grazing had begun, the mass of deer mice was lower in the grazed plots than in the ungrazed plots (Fig. 2A). When grazed and ungrazed data were pooled together, increasing grazing pressure appeared to have a negative impact on the mass of deer mice (Table 4; Fig. 2A). In contrast, the mass of meadow voles was not significantly influenced by grazing pressure or by treatment (Table 4; Fig. 2B); however, it was positively correlated with botfly parasitism (Table 4).

Individual parasite prevalence was not homogeneously influenced by grazing pressure. Botfly larvae (8 infected deer mice and 15 infected voles), mites (1 deer mouse and 3 meadow voles), and fleas (49 deer mice and 56 meadow voles) were observed in some individuals, whereas 79 deer mice and 34 meadow voles never showed any parasite infestation. There was no effect of cattle grazing on the number of botfly larvae and mites found on either rodent species (botfly larvae and deer mice: $\chi^2_{[1]} = 1.23$, $P > 0.1$; botfly larvae and meadow vole: $\chi^2_{[1]} = 0.45$, $P > 0.1$; mites and deer mice:

Fig. 1. Small-rodent abundance, as a function of presence or absence of cattle grazing on the trapping site. The mean number of individuals trapped per trapping session and per site is displayed for the grazed (○) or in the ungrazed (■) treatments, respectively. (A) Results for deer mice (*Peromyscus maniculatus*) and (B) meadow voles (*Microtus pennsylvanicus*). Grazing presence 0 indicates no grazing, whereas 1 indicates grazing levels 1, 2, or 3. The mean, standard errors, and significance levels are indicated (*, $P < 0.05$; ***, $P < 0.001$).

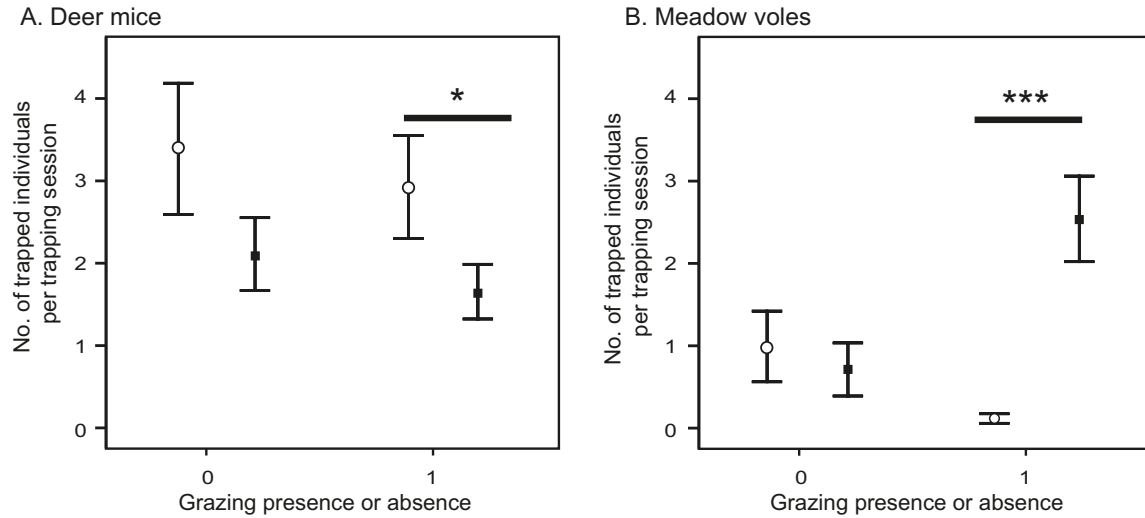


Table 1. Survival (S) models for deer mice (*Peromyscus maniculatus*) and meadow voles (*Microtus pennsylvanicus*).

Species	Model	$N_{\text{parameters}}$	Deviance	AIC_c	AIC_{mass}
Deer mice	S_{site}	6	163.73	287.71	0.58
	$S_{\text{site}+\text{treatment}}$	7	163.73	289.85	0.2
	$S_{\text{site}\times\text{treatment}}$	8	162.29	290.58	0.14
	S_0	2	176.78	292.4	0.06
	$S_{\text{treatment}}$	3	176.39	294.07	0.02
	S_{time}	9	169.9	300.36	0
Meadow voles	$S_{\text{site}\times\text{treatment}}$	7	78.92	179.17	0.91
	$S_{\text{treatment}}$	3	92.58	184.14	0.08
	$S_{\text{site}+\text{treatment}}$	9	83.24	188.05	0.01
	S_{site}	9	86.2	191.01	0
	S_{time}	9	88.44	193.26	0
	S_0	2	104.98	194.44	0

Note: The recapture rate was estimated as constant for all the models and was equal to 0.92 for deer mice and 0.96 for voles. AIC_c is the Akaike's information criterion corrected for small sample size. AIC_{mass} is the ranking of the goodness of fit for the six models expressed as a percentage. Models significantly explaining survival variations are in boldface type.

$\chi^2_{[1]} = 0.58$, $P > 0.1$; mites and meadow voles: $\chi^2_{[1]} = 0.51$, $P > 0.1$). Similarly, there was no effect of cattle grazing on fleas found on deer mice ($\chi^2_{[1]} = 0.12$, $P > 0.1$). Conversely, flea intensity on meadow voles was higher in ungrazed than in grazed plots ($\chi^2_{[1]} = 4.01$, $P < 0.05$).

Discussion

Our survey started in spring prior to the introduction of cattle into the study area. At that point there was no difference in abundance of meadow voles and deer mice in grazed and ungrazed plots. These results suggest that seasonally grazed areas were able to recover towards a natural state in these sites. At least two factors could explain the absence of measurable effects of grazing on small-rodent communities at the interseasonal scale. First, cattle were not introduced into the study site before mid-June. This delay allowed the vegetation to develop without strong pressure from large grazers

Table 2. Pairwise comparisons of survival models in deer mice (*Peromyscus maniculatus*).

Model comparison	df	χ^2	P
$S_{\text{site}} - S_0$	4	13.045	0.011
$S_{\text{site}} - S_{\text{site}+\text{treatment}}$	1	0.002	0.967
$S_{\text{site}} - S_{\text{site}\times\text{treatment}}$	2	1.438	0.487
$S_{\text{site}+\text{treatment}} - S_0$	5	13.047	0.023
$S_{\text{site}+\text{treatment}} - S_{\text{site}\times\text{treatment}}$	1	1.437	0.231
$S_{\text{site}\times\text{treatment}} - S_0$	6	14.484	0.025

Note: Models differing significantly from each other are in boldface type.

(except for native ungulates) during the early-growing stages. In addition, the removal of dead litter advances green up and enhances the nutritive quality of the early vegetation regrowth (Alpe et al. 1999; Short and Knight 2003), which may mitigate the negative effects on rodent communities associated with grazing. Consequently, we assumed that the

Table 3. Effect of treatment and grazing pressure on sex and age ratios of deer mice (*Peromyscus maniculatus*) and meadow voles (*Microtus pennsylvanicus*).

Species	Grazing presence (1) or absence (0)	Plot	Sex ratio (female/male)	df	χ^2	Age ratio (adult/juvenile)	df	χ^2
Deer mice	0	Grazed	35/26 = 1.35	1	0.04	36/25 = 1.44	1	0.88
	0	Ungrazed	21/17 = 1.23			26/12 = 2.17		
	1	Grazed	104/55 = 1.89	1	0.92	77/84 = 0.92	1	4.40*
	1	Ungrazed	54/37 = 1.46			56/35 = 1.60		
Meadow vole	0	Grazed	11/7 = 1.57	1	2.02	15/3 = 5.00	1	0.86
	0	Ungrazed	11/2 = 5.50			9/4 = 2.25		
	1	Grazed	5/2 = 2.50	1	0.00	3/4 = 0.75	1	7.86**
	1	Ungrazed	98/41 = 2.39			118/22 = 5.36		

Note: Grazing presence is based on a pool of grazing pressures 1, 2, and 3, whereas absence is based on grazing pressure of 0. Significant differences for each pair tested are in boldface type. *, $p < 0.05$; **, $p < 0.01$.

Fig. 2. Effect of grazing pressure on body mass of deer mice (*Peromyscus maniculatus*). Using a linear mixed-effects (lme) model, the effect of covariables (i.e., trapping site, seasonal and individual variations, and body size) were removed from the measured mass of trapped individuals. These “mass residuals” were then plotted against the grazing pressure and compared between (A) the grazed plots and (B) the ungrazed plots. The mass residuals were averaged at the trapping-session level and the results were displayed with standard errors.

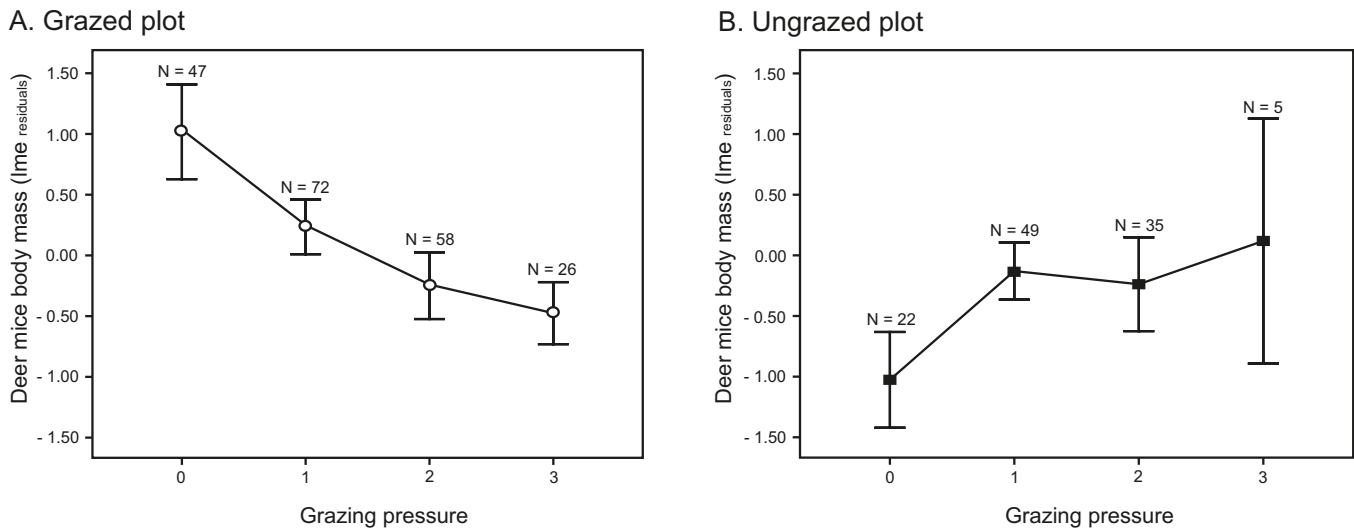


Table 4. Effects of grazing on rodent body mass, as investigated using linear mixed-effect models, for deer mice (*Peromyscus maniculatus*) and meadow voles (*Microtus pennsylvanicus*).

Species	Model variable	Value	SE	t	P
Deer mice	Intercept	20.107	0.581	34.598	0.000
	Grazing	-0.757	0.212	-3.564	0.001
	Treatment	-2.126	0.575	-3.700	0.000
	Sex	-0.465	0.334	-1.390	0.166
	Presence of botfly	2.031	1.087	1.868	0.063
	Grazing × treatment	1.125	0.393	2.863	0.005
Meadow vole	Intercept	26.857	1.648	16.296	0.000
	Grazing	0.491	1.151	0.427	0.671
	Treatment	-1.974	1.668	-1.183	0.240
	Sex	-1.367	0.969	-1.411	0.162
	Presence of botfly	4.159	1.419	2.932	0.004
	Grazing × treatment	0.318	1.280	0.249	0.804

Note: Model statistics for deer mice: $N = 314$ observations; Akaike's information criterion (AIC) = 1674.6; $df = 208$. Model statistics for meadow voles: $N = 161$ observations; AIC = 1044.2; $df = 80$. Significant model variables are in boldface type.

vegetation produced early during the growing season supplied adequate shelter and food for our two rodent species. Second, small mammals with their fast reproductive rate and quick reactions to environmental fluctuations might have uniformly used areas as soon as differences in vegetation cover between treatments were no longer apparent.

The onset of cattle grazing in June had rapid and significant effects on both small-rodent species. Interestingly, deer mice and meadow voles differed in the magnitude of their reaction, similar to what Bakker et al. (2009) found comparing the impact of cattle grazing on European rabbits and common voles. Overall, deer mice showed higher numbers of individuals caught per trapping session in grazed plots and did not show any sign of avoidance of grazed areas when cattle were introduced. Our results were consistent with two previous studies showing that grazing may even increase the number of deer mice (Philips 1936; Matlack et al. 2001). In contrast, other studies on the same species did not find such increase in density (Hayward et al. 1997; Jones et al. 2003). Although examination of our survival analysis revealed no significant difference between models, all models were significantly different from the null model of a constant survival rate. Thus, these models point to heterogeneity between sites as a major explanatory factor for survival rates. Because of these differences, the results of the survival analysis regarding the potential impact of cattle grazing still remain unclear, a conclusion commonly reached by other studies (Keesing 1998; Schmidt et al. 2005). These inconsistencies in the results of survival analyses across studies could be explained by the flexibility of deer mice in terms of niche choice (Bowers and Smith 1979; Geier and Best 1980; Galindo and Krebs 1985): deer mice are opportunistic feeders (Bunker 2001; Desrosiers et al. 2002) and can adapt well to open habitats (Pearson et al. 2001). Although it has been said that deer mice can adapt well to changes in their environment, our study showed that cattle grazing did have a significant negative effect on their body mass. Before grazing began, deer mice were significantly heavier in the grazed than ungrazed plots, most likely owing to earlier green up in previously grazed plots compared with the ungrazed plots. However, with an increasing grazing pressure, the initial difference in body mass vanished rapidly and was followed by a rapid decrease of mass in deer mice trapped in grazed plots. The observed effect of body mass decrease in the grazed plot may be a result of two interacting factors. First, grazing intensity has been shown to negatively affect the quality and quantity of forage especially when cattle are allowed to graze over the whole growing season and when the intensity of grazing is high (Plumb and Dodd 1993; Alpe et al. 1999; Chaikina and Ruckstuhl 2006). Second, small rodents need high-quality food rather than high quantities of food, which makes them more sensitive to variations in food quality (Arsenault and Owen-Smith 2002). Similar to our results, other studies also observed heavier individuals in ungrazed than grazed plots for two small-mammal species (male Mearns's pouched mice (*Saccostomus mearnsi* Heller, 1910): Keesing 1998; female red rock rats (*Aethomys chrysophilus* (de Winton, 1897): Saetnan and Skarpe 2006).

Meadow voles showed a clear avoidance of cattle-grazed plots, as very few individuals were trapped in grazed plots and most individuals were trapped in the ungrazed plots.

These results are consistent with those of Giuliano and Homyak (2004) who also studied meadow voles, and with Smit et al. (2001) and Evans et al. (2006) who observed field voles (*Microtus agrestis* (L., 1761)), an European species, that occupies an ecological niche similar to that of the meadow vole in North America. This avoidance of grazed sites may be due to the decrease in vegetation cover associated with cattle grazing. Indeed, it has been shown that density of meadow voles is positively correlated with vegetation cover (Peles and Barrett 1996). In addition, low migration rates of meadow voles have been reported in habitats with high vegetation cover (Lin and Batzli 2004). We were unable to perform a similar analysis on our voles, as we only had enough data to estimate and compare survival in both the grazed and the ungrazed plots for one of the sites. The data gathered from this site indeed showed a decreased survival rate in the grazed plot similar to Peles and Barrett's (1996) study.

Because Peles and Barrett (1996) reported a lower body mass in meadow voles when vegetation cover was reduced, we expected similar mass changes in our study. The absence of a significant effect of grazing on body mass of meadow voles in our study could simply be due to the fact that only very few meadow voles were actually trapped outside the ungrazed plots, indicating that our study lacked the power to detect differences even if it was there.

Surprisingly, meadow voles that were infested with botfly larvae were significantly heavier than noninfested individuals. We propose four hypotheses to explain this result: (1) the mass of the parasite larvae themselves on each rodent could explain the higher body masses of infested meadow voles; (2) only heavier individuals survive infection of botfly parasites and thus these heavier individuals are more likely to be trapped during the trapping season; (3) heavier individuals move less and are thus more susceptible to botfly infection; and (4) botflies preferentially parasitize heavy individuals.

Flea prevalence on communities of meadow voles was higher in the ungrazed than grazed plots. High flea prevalence may have been observed because of high population densities of meadow voles, which may lead to an increase in flea transmission, as has been reported in brown rats (*Rattus norvegicus* (Berkenhout, 1769)) (Abu-Madi et al. 2005). This effect was most likely reinforced by the sedentary behaviour of meadow voles in the ungrazed plots (only once was the same individual trapped in both grazed and ungrazed plots).

Further evidence that cattle grazing affects these rodents was obtained through examination of shifts in age ratios in our study populations. In the presence of grazing, a higher proportion of adults compared with juveniles were trapped in ungrazed than grazed plots. Collins and Barrett (1997) suggested that ungrazed plots might present a more suitable habitat than grazed areas. Territorial adults might prevent juveniles from settling on their territories, forcing them to disperse into unoccupied, lower quality habitat. We could not directly observe transfer of individuals between ungrazed and grazed plots—only 14 out of a total of 213 different individuals were trapped in both grazed and ungrazed plots.

Our study did not find a significant difference in the sex ratio of either populations of deer mice or meadow vole between sites. Our results are in line with other studies that suggest cattle grazing does not have an impact on the sex ratio of populations (Peles and Barrett 1996; Schmidt et al. 2005).

Seasonal disturbance owing to cattle activities were clearly revealed in our two rodent species, but the degree and direction of the impact varied. For instance, the generalist deer mice seemed to occupy open spaces created by cattle, but they paid fitness costs through decreased body mass. On the other hand, the specialist meadow voles showed a direct and strong avoidance of cattle-grazed areas.

To conclude, this study demonstrates how cattle grazing can have diverse impacts on different levels leading to shifts in species densities, biodiversity, and individual condition or quality. These results underline the importance of careful selection of grazing regimes and ranges to avoid a potential loss and shifts in biodiversity. Additionally, it is important to keep in mind that such changes most likely have strong trickle-down effects on predatory species such as raptors, coyotes, etc. We suggest that monitoring small-mammal populations, their body condition, and their densities could be used as important management tools to assess the stability and health of grassland ecosystems.

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