

THE EFFECTS OF TIMING OF GRAZING ON PLANT AND
ARTHROPOD COMMUNITIES IN GRASSLANDS
OF SOUTHWEST MONTANA

by

Stacy Christine Davis

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Dr. Laura Burkle (Co-Chair)

Dr. Wyatt Cross (Co-Chair)

Approved for the Department of Ecology

Dr. David Roberts

Approved for The Graduate School

Dr. Ronald W. Larsen

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ABSTRACT

Grassland plants have co-evolved with native ungulate grazers for millions of years, but over the last 100 years there has been a shift towards grazing by domestic livestock in North America. Many of the grazing-induced changes in plant and arthropod communities depend on how the grazing regime is implemented. Timing of grazing is one component of the grazing regime that is less well understood than grazing intensity and type of grazer, but is predicted to have important implications for plant and higher trophic level responses. The purpose of this study was to experimentally assess how timing of grazing affected plant and arthropod communities in high-elevation grasslands of southwest Montana. We designed a 2-year field experiment that manipulated cattle grazing by implementing two grazing initiation dates, one beginning in mid-June and the other in mid-July. We compared plant (biomass and height) and arthropod characteristics (density and biomass of orders) across two years that differed in cumulative precipitation. Grazing reduced total plant biomass, forb biomass, and plant height with little to no recovery regardless of timing of grazing. The density of the most dominant arthropod order, Hemiptera, was reduced in both grazing treatments. By comparing end of season plant responses to grazing, we found that total plant biomass was unaffected in the drier year while forb biomass was unaffected in the wetter year. Many end of season arthropod responses were reduced by grazing in both study years. Although both grazing treatments reduced many plant and arthropod characteristics, grazing earlier in the growing season may impact higher trophic levels that are reliant on the presence of forbs and Hemiptera earlier in the growing season. These results have important implications for meeting conservation grazing objectives and for how timing of grazing may influence food availability for grassland-associated avian species of concern, in particular, smaller passerines.

THE EFFECTS OF TIMING OF GRAZING ON PLANT AND ARTHROPOD
COMMUNITIES IN GRASSLANDS OF SOUTHWEST MONTANA

Introduction

Grazing is a key process that shapes the ecology of grasslands in North America (Glenn et al. 1992). Grassland plants have co-evolved with native ungulate grazers for millions of years (McNaughton 1986), but over the last 100 years there has been a shift towards grazing by domestic livestock in the western United States (McNaughton 1993). Functional differences between domestic and native grazers, such as freedom of movement and long-distance mobility, can affect their impact on plant communities (McNaughton 1986). In general, domestic livestock grazing tends to have stronger effects on plant diversity (Bakker et al. 2006, Collins et al. 1998), vegetation structure (Davidson et al. 2010), and ecosystem functioning (Bai et al. 2012) than native ungulate grazing. Grazing-induced changes to plant communities can also lead to changes in arthropod communities, including density, biomass, and diversity (Gibson et al. 1992a, Dennis et al. 1998, Joern and Laws 2012). The responses of the arthropod community to grazing are contingent upon the arthropod group in consideration; some groups respond strongly to changes in vegetation structure (Bell et al. 2001, Gibson et al. 1992b), while others respond to shifts in vegetation composition (Schaffers et al. 2008).

Many grazing-induced changes to plant and arthropod communities depend on how the grazing regime is implemented. Some components of the grazing regime,

such as intensity and grazer identity, have relatively well-known effects on vegetation height (Sjödin et al. 2008), plant diversity (Olf and Ritchie 1998), and arthropod species richness and abundance (Dennis et al. 1998, Cagnolo et al. 2002). Previous research manipulating grazers at coarse temporal scales have found that the season in which grazing takes place (e.g., spring versus fall) can affect plant and arthropod communities (Perez-Camacho et al. 2012, Anderson and Frank 2003, Morris 1973, Lenoir and Lennartsson 2010). In certain areas of the United States, the length of the growing season is severely reduced, making it very important to plan when and where to graze during the short growing season of summer. Very little research has focused on how fine-scale temporal differences in grazing (hereafter, timing of grazing) will affect vegetation structure and arthropod availability. Timing of grazing decisions, such as when to initiate grazing, can be especially pertinent in high-elevation grasslands, where grazing only occurs during the short growing season.

Several factors are predicted to influence how plants respond to timing of grazing, including plant phenology and resource availability, such as moisture. Plants are most susceptible to grazing during phenological stages of active growth, but the timing of this growth phase varies among species (Mueggler 1967, Maschinski and Whitham 1989). In addition, many plants exhibit life history strategies that influence their susceptibility to grazing throughout the growing season. For example, grasses are more likely to regrow if grazing occurs before flowering because the location of apical and axillary buds near the base of the plant

at this time means they are able to regrow following a grazing event (Briske 1991). Resource availability (i.e., water, nutrients) is also predicted to influence how plants respond to timing of grazing. One of the most important resources in grasslands is water availability and many studies have shown that community structure and productivity of grassland plants are strongly influenced by precipitation and soil moisture (Milchunas et al. 1989, Sims and Singh 1978). Several authors have suggested that the negative effects of grazing may be mitigated by favorable soil water conditions (Milchunas et al. 1989, Chase et al. 2000). To date, few studies have addressed how timing of grazing may interact with precipitation and soil moisture availability to influence plant and arthropod communities. This area of research is important for planning future grazing regimes because climate change is predicted to alter patterns of precipitation, timing of snowmelt, and length of growing season in the western United States (Romme and Turner 1991, Cayan et al. 2001).

Deciding when to graze can have important implications for higher trophic levels. Recently, there has been a lot of focus on using grazing to increase biodiversity and to provide habitats suitable for species of conservation concern, such as grassland bird species (WallisDeVries et al. 1998). In particular, livestock grazing can be used to modify vegetation structure to benefit the foraging and nesting habitat requirements for birds (Derner et al. 2009). Timing of grazing has the potential to temporally alter the availability of plants and arthropods. Such temporal shifts have important implications for grassland birds, especially if these

shifts occur during periods of high energy demand, such as during chick development and adult molting (Sveum et al. 1998, Peterson 1970, Drut et al. 1994). Previous research has shown that increased availability of food resources may be associated with increased chick survival (Drut et al. 1994, Gregg 2006). Therefore, timing of grazing treatments that influence temporal patterns of food availability can be utilized to benefit avian species of concern.

In an effort to quantify the effects of timing of grazing on plants and arthropods in western grasslands, we experimentally manipulated cattle grazing over the course of two growing seasons that differed in cumulative precipitation. We asked: (1) how does timing of grazing affect plant and arthropod communities, (2) how do these effects vary throughout the growing season and (3) how might precipitation and soil moisture affect how grazers influence plant and arthropod communities at the end of the growing season? While we expected grazing at any point during the growing season to temporarily reduce plant biomass and height, we hypothesized that plots grazed earlier in the growing season would have greater plant biomass and height than late-grazed plots at the end of the growing season due to the increased time available for regrowth (Oesterheld and McNaughton 1991). Additionally, we hypothesized those arthropod orders (i.e., Hemiptera [true bugs] and Araneae [spiders]) strongly affected by vegetation characteristics (Gibson et al. 1992a, Gibson et al. 1992b, Korosi et al. 2012) to mirror the response of the plant community to timing of grazing. Finally, we hypothesized that increased precipitation and soil moisture would mediate responses to grazing, with dampened

effects of grazing in a wet year versus a dry year due to increased water availability and plant growth potential (Milchunas et al. 1989, Anderson and Frank 2003). Our results provide a more comprehensive understanding of the effects of timing of grazing on plant and arthropod communities, as well as how these effects may differ in wet vs. dry years. This knowledge is crucial for informing habitat management decisions, particularly in high-elevation grasslands that have an extremely short growing season relative to lower elevations.

Methods

Study Area

We conducted grazing experiments in 2011 and 2012 at Red Rock Lakes National Wildlife Refuge (RRL), located in the Centennial Valley of southwest Montana (44°40' N, 111°47' W, 2030m elevation). The climate at RRL is characterized by long, cold winters and short, mild summers with highly variable annual precipitation (U.S. Fish and Wildlife Service 2009). Mean annual air temperature and precipitation at Lakeview, Montana (c. 11 km from study sites) are 1.56° C and 500 mm, respectively, with May and June being the wettest months (U.S. Fish and Wildlife Service 2009). The length of the growing season, defined as the period of time between the last frost of spring and the first frost of fall, was similar in both years in that frost-free months were from June to September (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>).

Grasslands occupy more than 800 hectares at RRL and are important habitats for long-billed curlew, sandhill cranes, savannah sparrows, and other migratory birds (U.S. Fish and Wildlife Service 2009). The majority of these grasslands are dominated by graminoids, such as Idaho fescue (*Festuca idahoensis*), basin wildrye (*Leymus cinereus*), Nuttall's alkaligrass (*Puccinellia nuttalliana*), and Sandberg bluegrass (*Poa secunda*) (U.S. Fish and Wildlife Service 2009). Forb coverage and diversity varies, depending on soil moisture and type, but silvery lupine (*Lupinus argenteus*), rosy pussytoes (*Antennaria rosea*), and common yarrow (*Achillea millefolium*) are the most common forbs (U.S. Fish and Wildlife Service 2009). Current management allows grazing to occur on many of the grasslands at RRL, with grazing intensities ranging from 0.31 to 0.85 AUM/acre between 1994 and 2006 (U.S. Fish and Wildlife Service *unpubl. data*). Additionally, since the 1950s, 90% of grazing has been initiated after July 10th due to concern over nest trampling of protected avian species (e.g. long-billed curlew and sandhill cranes). Although the long-term grazing history of our specific sites used in this study was unavailable because it was privately owned until 2007, most grazing units at RRL are grazed by cattle on a 3-year grazing unit rest-rotation (U.S. Fish and Wildlife Service 2009).

Experimental Design

We conducted our research over two years that differed in precipitation and timing of snowmelt. Accumulated annual precipitation averaged 460 mm in 2011 and 400 mm in 2012 (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>), with snowmelt occurring approximately 1 month

earlier in 2012 (Natural Resources Conservation Science SNOTEL site at Tepee Creek; c. 24 km from study sites). Accumulated annual precipitation was similar in both years until May, but over 250% more precipitation (53 mm difference) fell between May and June in 2011 compared to 2012 (Figure 1). By conducting a similar grazing experiment in both years, we were able to examine how precipitation may have mediated the responses of plant and arthropod communities to timing of grazing.

In both years, we established two cattle grazing treatments: early graze (starting mid-June) and traditional late graze (starting mid-July). We also established control plots, which were ungrazed for the season. Early and late treatment plots were grazed by cattle for equal durations (grazed for 2 weeks) and at equal intensities (0.9 AUM/acre, where 1 AUM=1 cow-calf pair). Three experimental blocks were established in 2011 and four experimental blocks in 2012, with each block containing three plots. Within each block, plots were randomly selected for one of the three treatments. Due to trespass grazing in early July of 2012, two plots were removed from analyses (one control and one early-grazed), thus reducing the number of replicates for control and early-grazed treatments from four to three.

In 2011, our grazing experiment was conducted at a large spatial scale, with c. 34 hectare plots. We initially designed the experiment wanting to have larger plots, which is more realistic for management and the scale that grazing happens at. However, the location of these large grazing plots was in heterogeneous, sub-

irrigated wet meadows, which resulted in a high degree of patchiness in grazing. Within each plot on each sampling event, at least five sampling points were randomly selected out of 25 sampling points randomly established. In order to reduce the variability we observed in local conditions and in patchiness of grazing, we modified the design slightly for 2012 by conducting our grazing experiment in more homogeneous, non-irrigated grasslands at a much smaller spatial scale, with c. 2 hectare plots. Although these were much smaller plots than a typical grazing unit, we were able to examine the effects of timing of grazing on plants and arthropods, without additional confounding factors. Within each plot on each sampling event, ten sampling points were randomly established east or west of a centrally located north-south transect. Since cattle severely trampled the area near water tanks, we created a 30 m buffer zone near the water tanks where no sampling occurred. On each sampling event, we sampled in different ordinal directions from sampling points to avoid clipping the same vegetation. Quadrats were located at least 1 m away from previously sampled quadrats. In both years, we avoided potential “edge effects” between treatments by not sampling in 10 m buffer zones between neighboring plots. Vegetation and arthropods were collected concurrently from each quadrat at each sampling point, six times between mid-June and early September in 2011 and four times between early June and late August in 2012.

Vegetation Sampling

Above-ground plant biomass was quantified by clipping vegetation to ground level in a 0.03m² quadrat in 2011 and to 5 cm in a 0.25m² quadrat in 2012.

Vegetation samples were sorted as graminoids or forbs. Total plant biomass included live and dead vegetation that represented the previous and current year of growth. Prior to clipping vegetation in 2012, we measured vegetation height by estimating the height of 80% of vegetation at four equally-spaced points within the 0.25m² quadrat (Stewart et al. 2001).

Arthropod Sampling

Prior to sampling vegetation at each sampling point, we collected arthropods with an enclosed 0.25m² plastic barrel that was quickly placed over the collection area, minimizing arthropod escape and restricting the sampling to a known area. We then used an inverted leaf blower/vacuum sampler (suction cylinder area of 0.013 m²; Craftsman XRZ 2000; 30s/sample) to extract arthropods by moving the sampler evenly across the vegetation in the enclosed area (Kruess and Tschardt 2002). In 2012, we also used sweep netting in an effort to sample a larger area of the plot and potentially collect different groups of arthropods. Sweep netting took place during hours of peak arthropod activity (1100-1500) on calm sunny days. We collected a total of 36 sweep net samples on sampling events 2-4 by walking swiftly in the center of each plot in a north-south transect for 50m (40 sweeps per sample). All arthropods from each sample were frozen until processed. Density and biomass were determined for five sampling points per plot in 2011 and for all 10 sampling points per plot in 2012. In both years, density was determined by separating arthropods greater than 1mm from vegetation debris, counting, and then identifying individuals to order and size class. Size classes varied depending on the arthropod

order in 2011, but in 2012 all arthropod orders were measured to the nearest mm. Biomass was determined for the six arthropod orders that collectively made up over 95% of total composition in terms of abundance (Hemiptera [true bugs], Araneae [spiders], Hymenoptera [mainly ants], Diptera [flies], Coleoptera [beetles], and Orthoptera [grasshoppers]). In 2011, we dried and weighed arthropods in each size class to obtain dry mass. In 2012, since more specific size classes were utilized (to the nearest mm), we converted the length of each arthropod to dry mass by using Rogers et al.'s (1977) taxon-specific length/mass regression equations. Total biomass for each arthropod order was calculated as the sum of all size classes in each sample and individual biomass was calculated as total biomass/number of individuals for each sample.

Soil Sampling

Due to visible variability in soil moisture within the sub-irrigated plots in 2011, we measured soil moisture at each of the 25 sampling points in each plot three times throughout the summer. In 2012, we measured soil moisture at each of the 10 sampling points in each plot on all four sampling events. Three soil moisture readings were taken within 30 cm of each other using an Aquaterr 300-T soil probe at a depth of 15 cm. All readings were within 60 cm of the sampling point.

Statistical Analyses

In 2011, we were unable to detect strong grazing effects because of large variability in soil moisture and plant biomass resulting from sub-irrigation and

visible heterogeneity in cattle grazing. Additionally, the discrepancy between the large plot sizes in 2011 relative to the small quadrats for plant sampling may have biased our results by randomly sampling in ungrazed areas (i.e., no treatment). We therefore restricted our in-depth analysis of the effect of timing of grazing throughout the entire growing season to the 2012 study year. We only used 2011 data to compare to 2012 data in order to determine how the cumulative effect of grazing on plant and arthropod responses at the end of growing season may have differed with variations in precipitation between the study years.

Effects of Timing of Grazing on Plants and Arthropods Across the Growing Season. To determine the effects of timing of grazing on plant and arthropod characteristics in 2012, we used a repeated-measures analysis of variance (rmANOVA) approach. Treatment and sampling event (sampling event as the repeated measure) were included as independent variables, as well as the interaction term between them. When significance in main effects or interactions were detected ($p < 0.05$), *post-hoc* one-way ANOVAs and Tukey's Honestly Significant Difference (HSD) multiple comparisons were used to determine treatment differences within each sampling event, as well as sampling event differences within each grazing treatment. We did not adjust alpha levels with a Bonferroni correction because doing so may lead to a higher probability of a type II error and a lack of a standard alpha across studies (Gotelli and Ellison 2004). All plant and arthropod variables, except plant height, were square-root transformed

+0.5 to meet assumptions of normality and homogeneity of variances (Gotelli and Ellison 2004).

Because graminoids made up over 90% of the total plant biomass in all plots, we reported total plant biomass in place of graminoid biomass. In addition, we did not report average individual biomass (i.e., body size) of arthropod orders, due to their similarity to the total arthropod order biomass results. Finally, we did not report sweep net sample results because they were qualitatively similar to vacuum sample results. All data were analyzed using R version 2.15.2 (R Core Team 2012) and JMP 10.

Effects of Precipitation and Soil Moisture on End of Growing Season Responses to Timing of Grazing. In order to compare the magnitude and direction of grazing effects on plants and arthropods over our two study years (2011 and 2012) that varied greatly in precipitation, we conducted an effect size analysis which allows a standardized (i.e., responses relative to the control) comparison of responses across multiple studies (Rosenberg et al. 2000). For this analysis, we only examined end of the growing season characteristics, here defined as late August when sampling events lined up in both years and when plants began to die back. This time of year also represented the greatest cumulative differences in precipitation between the two study years. Additionally, the effects of herbivory on plants at the end of one growing season are most likely to influence patterns of growth during the following season (Sullivan and Howe 2009). For each timing of grazing treatment, we calculated the standardized mean difference

between a given plant or arthropod variable in treatment versus control plots using mean log response ratios (Hedges et al. 1999). We conducted this analysis on total plant biomass, forb biomass, and density and biomass of arthropod orders that collectively made up over 95% of total abundance in each study year (Hemiptera, Araneae, Hymenoptera, Diptera, Coleoptera, and Orthoptera). For both years, we used Rogers et al.'s (1977) taxon-specific length/mass regression equations using mean lengths based on the larger size class ranges that we established in 2011 in order to standardize methodology in biomass calculations in the two study years. A negative value of the log response ratio indicated lower values for the response variable in the treatment plots compared to the control plots. Effect sizes for each response variable were summarized with a random-effects model using 95% confidence intervals with bias-corrected bootstrapping (Rosenberg et al. 2000). The effect size was considered statistically significant if the bootstrapped confidence interval, calculated with 1000 iterations, did not bracket zero. All effect size calculations were conducted using MetaWin version 2.1 (Rosenberg et al. 2000).

After conducting the effect size analysis, we wanted to further examine soil moisture and its role in influencing plant and arthropod responses to the grazing treatments. We compared mean total plant biomass, forb biomass, total arthropod density, total arthropod biomass, and soil moisture at the end of the growing season across all treatments for each study year using t-tests. In addition, we used Pearson correlation coefficients to examine finer-scale relationships between soil moisture and (1) total plant biomass, (2) forb biomass, (3) total arthropod density, and (4)

total arthropod biomass at the end of the growing season across all treatments for each study year.

Results

Effects of Timing of Grazing on Plants and Arthropods Across the Growing Season

Average total plant and forb biomass differed significantly across grazing treatments, but these effects depended upon the sampling event (Table 1). Total plant biomass was similar in all treatments prior to any grazing (Table 2) and remained constant in control plots throughout the growing season (Table 3). Early- and late-grazing significantly reduced total plant biomass by 53% (84.73 g/m²) and 49% (109.76 g/m²), respectively (Table 3). Mean plant biomass in both grazed treatments remained 40% lower than control plots throughout the rest of the growing season, although neither treatment was significantly different from control plots (Figure 2a; Table 2). The only significant difference among treatments was immediately after the early graze in late June, when grazed plots had less than half the total plant biomass of other treatments (Figure 2a; Table 2).

Forb biomass showed nearly identical responses to grazing as total plant biomass, but with a significant difference between both early- and late-grazed plots when compared to control plots in July and August (Figure 2b; Table 2). Forb biomass in early- and late-grazed plots was significantly lower (<50%) than control plots at the end of the growing season (Figure 2b; Table 2).

Since total plant biomass was similar in all treatments prior to any grazing (Table 1) and post-treatment plant height was strongly correlated with total plant biomass ($r=0.74$, $p<0.0001$, Pearson's correlation), we assumed there were no pre-treatment differences in plant height. Plant height responses to grazing were similar to total plant and forb biomass responses, but there were significant treatment differences in plant height between early- and late-grazed plots at the end of the growing season (Figure 2c; Table 2). Although early- and late-grazed plots had equal total plant biomass at the end of the growing season (Figure 2a; Table 2), early-grazed plots had 17% taller vegetation compared to late-grazed plots in late August (Figure 2c; Table 2).

Arthropod density in control plots was largely composed of Hemiptera (57%), Hymenoptera (23%), and Araneae (10%) across all sampling events. The remaining 10% was composed of Coleoptera, Diptera, Orthoptera and six additional low density orders. Patterns of dominance with respect to total arthropod biomass and density were similar, and the majority of arthropod biomass was made up of Hemiptera (40%), Hymenoptera (19 %), Araneae (16%), and Orthoptera (14%). Early-grazing resulted in a 50% reduction in Hemiptera density when compared to control and late-grazed plots in late June (Figure 3a; Table 2). Similarly, late-grazing significantly reduced Hemiptera density by 54% (~ 82 individuals/m²; Figure 3a; Table 3). At the end of the growing season, Hemiptera density in grazed plots did not differ from control plots (Figure 3a; Table 2). Although Hemiptera density was affected by grazing treatments, there was no effect of grazing on Hemiptera biomass

(Table 1). Grazing did not significantly affect the density or biomass of any other arthropod order (Table 1).

Density or biomass of some arthropod orders (Diptera, Coleoptera, Araneae, and Orthoptera) varied significantly among sampling events (Table 1), irrespective of grazing treatments. Coleoptera density significantly decreased by 62% (~ 11 individuals/m²; Figure 3b; Table 3) and Orthoptera biomass increased by 20-fold (~ 57.6 mg/m²; Figure 3c; Table 3) across the growing season, revealing phenological differences for certain arthropod orders.

Effects of Precipitation and Soil Moisture on End of Growing Season Responses to Timing of Grazing

The effect sizes of grazing treatments on end of growing season plant biomass and forb biomass varied depending on the study year. Regardless of timing, grazing only had a negative effect on end of season total plant biomass in the wet year (2011) and forb biomass in the dry year (2012; Figure 4a, b). Grazing had largely negative effects on end of season arthropod density and biomass (Figure 4c, d), and Hemiptera appeared to be the main arthropod order driving this pattern (Figure 4e, f). In both study years, grazing treatments reduced total arthropod and Hemiptera density and biomass (Figure 4c, e). Other arthropod variables, such as total arthropod biomass and Araneae density, were reduced by grazing, but these effects varied with grazing treatment and/or year (Figure 4d, g). The effects of timing of grazing on density of Hymenoptera and Coleoptera were more complex

and idiosyncratic, with few negative effects in 2011 and variable effects in 2012 (Figure 4h, i).

Plant and arthropod communities exhibited inter-annual variation in end of growing season characteristics, regardless of grazing. In 2011, there was greater cumulative precipitation (Figure 1), greater variability of soil moisture values (Figure 5a), and greater mean soil moisture (Figure 6e) than in 2012. In addition, mean total plant biomass, forb biomass, and arthropod density across all treatments were significantly greater in 2011 than in 2012 (Figure 6a, b, c). Total arthropod biomass did not differ among study years (Figure 6d). Correlations between soil moisture and plant and arthropod variables across all treatments at each sampling point were all relatively weak ($r < 0.4$). The only significant correlations were for soil moisture and plant biomass, which was positively correlated in 2011 ($r = 0.37$, $p < 0.001$) and negatively correlated in 2012 ($r = -0.25$, $p = 0.01$).

Discussion

Our grazing experiments in western grasslands demonstrated that grazing reduced plant and arthropod characteristics within one growing season, regardless of timing of grazing. The density of a dominant arthropod order (Hemiptera) was reduced with grazing in the beginning of the growing season. Early grazing impacts on this dominant arthropod order may have potentially important ramifications for higher trophic levels, such as avian species of concern, that rely on Hemiptera density in the beginning of the growing season. Inter-annual differences in plant and

arthropod responses to grazing at the end of the season may have been a result of differences in accumulated precipitation between study years. Understanding temporal variation in plant and arthropod responses to timing of grazing and how these may differ across years varying in precipitation are crucial for furthering rangeland management.

Effects of Timing of Grazing on Plants and Arthropods Across the Growing Season

Grazing is known to have significant effects on plant diversity (Bakker et al. 2006, Collins et al. 1998), vegetation structure (Davidson et al. 2010), and ecosystem functioning (Bai et al. 2012), yet few studies have quantified how timing of grazing impacts the plant community. We expected both treatments to temporarily reduce plant biomass and height, but also for early grazing to result in greater plant biomass and height than late grazing at the end of the growing season due to increased time available for regrowth (Oosterheld and McNaughton 1991). Both grazing treatments temporarily reduced plant biomass and height, and plant height was greater with early grazing when compared to late grazing at the end of the season. If differences in plant height persist into the next growing season, this information could be used to inform management of grassland birds that require specific vegetation heights for nesting (Derner et al. 2009). In contrast, total plant and forb biomass were similar in both grazed treatments at the end of the season.

Several explanations may help explain why plant biomass did not fully recover from early grazing more so than late grazing in our study, despite the

increased time available for regrowth. First, a plant's ability to regrow after grazing can vary with local conditions, such as the availability of nutrients and moisture (Maschinski and Whitham 1989). Plant regrowth after grazing may have been limited in 2012 because precipitation was minimal between June and August, a key time period in which grazed plants may have benefited from additional precipitation and soil moisture. This hypothesis is further supported by the lack of plant growth in control plots across the entire growing season, suggesting water-limited conditions. Furthermore, plant biomass recovery may depend on the phenological stage of plants during grazing. Clipping studies indicate that grasses and forbs are harmed most during the transition from flower stalk formation to seed ripening, which is a time when plants are storing carbohydrates for the dormant period (Mueggler 1967). In our study, it is likely that the majority of grasses and forbs were in this developmental stage during grazing; however, we did not closely track phenological stages of plant species. Finally, there may have been belowground recovery from early grazing that we did not measure. Frank et al. (2002) showed that grazers in Yellowstone National Park stimulated root production seven times more than shoot production.

In addition to there being no differences in end of season plant biomass between early and late grazed plots, there were also no significant differences in end of season total plant biomass between grazed and control plots. The 40% reduction in mean biomass in both early- and late-grazed plots (Figure 2a) suggests that total plant biomass never fully recovered from either grazing treatment, a pattern we

may have detected with increased replication. A power analysis using total plant biomass results from late August indicated that six plots per treatment (instead of four) would be necessary to detect a treatment difference (i.e., at $\alpha=0.05$; power=0.32).

In addition to having large effects on plant communities, grazers can impact arthropod density, biomass, and diversity (Gibson et al. 1992a, Dennis et al. 1998, Joern and Laws 2012). However, generalizations about effects of grazers on arthropods are elusive (Bell et al. 2001) due to the large variation in how different arthropod groups respond to grazing (Sjödin et al. 2008, Gibson et al. 1992a). Cagnolo et al. (2002) suggested that the response of arthropods to grazing may vary with the availability of food, refuges, or oviposition sites, all of which may be altered with grazing-induced plant community changes. We had hypothesized arthropod orders (i.e., Hemiptera [true bugs] and Araneae [spiders]) that are strongly affected by vegetation characteristics (Gibson et al. 1992a, Gibson et al. 1992b, Korosi et al. 2012) to mirror the response of the plant community to timing of grazing. This was the case for Hemiptera, the dominant arthropod order. Hemiptera density followed a very similar pattern to timing of grazing as the plant community. Previous studies also showed that Hemiptera are highly sensitive to grazing-induced structural vegetation changes (Gibson et al. 1992a, Korosi et al. 2012).

The effect of timing of grazing on Hemiptera density was temporary, since Hemiptera recovered from both grazed treatments by the end of the growing season. Morris and Lakhani (1979) likewise found a time-specific response of

Hemiptera to changes in the vegetation community; cutting the vegetation earlier in the growing season (May) versus later in the growing season (July) reduced the abundance of Hemiptera, but the effects were also short-lived. Even though the effects of timing of grazing on Hemiptera density were temporary, Hemiptera are an important part of our grassland community, comprising over 50% of arthropod density and over 30% of arthropod biomass. A reduction in Hemiptera density with no effect on Hemiptera biomass suggests a shift towards larger-sized Hemiptera with grazing. However, we did not find a significant effect of grazing on Hemiptera individual biomass, perhaps due to low statistical power.

Previous studies have found that spiders (Araneae) are positively associated with certain vegetation features, such as plant height (Gibson et al. 1992b); thus, we expected spiders to exhibit the same responses as the plant community to grazing treatments. We found no effect of timing of grazing on spider density, even though plant height was reduced by grazing. One possible explanation is that an appropriate level of plant architectural diversity remained to maintain sufficient spider habitat, irrespective of grazing (Gibson et al. 1992b). Additionally, there may be species-specific responses to timing of grazing, potentially driven by varying foraging strategies (Lenoir and Lennartsson 2010), that could be explored in future studies by identifying spiders and other arthropod groups to a more specific level than order.

With the exception of Hemiptera, our results showed that arthropod orders were unaffected by timing of grazing. While some studies that manipulated grazing

intensity concur with our results (e.g., Mysterud et al. 2005), many others have found a negative effect of grazing on arthropods (Dennis et al. 1998, Rambo and Faeth 1999, Cagnolo et al. 2002). It is likely these conflicting results are due to differing habitat types, grazing intensity, grazer identity, and length of experiment. We may have observed greater responses from the arthropod community if our grazing treatments ran for longer than two weeks, although the duration of grazing is limited due to the shortened growing season of our high-elevation study site.

Effects of Precipitation and Soil Moisture on End of Growing Season Responses to Timing of Grazing

We found that end of season plant biomass was reduced by grazing, regardless of timing of grazing, but the effect depended on the study year and functional group. We had hypothesized that increased precipitation and soil moisture would mediate responses to grazing, with dampened effects of grazing in a wet year versus a dry year due to increased water availability and plant growth potential (Milchunas et al. 1989, Anderson and Frank 2003). This was the case for forb biomass; end of season forb biomass was unaffected by grazing in the wet year. However, we observed the opposite result with total plant biomass; end of season total plant (grass) biomass was reduced with grazing in the wet year, but unaffected in the dry year. A possible reason for differences in plant responses with varying amounts of precipitation could be related to the competitive abilities of different functional groups. Mueggler (1967) found that forb growth benefited more from increased soil moisture than grass growth and suggested that forbs grazed during a

wet year would be damaged less than those grazed during a dry year. In our study, end of season forb biomass similarly showed greater recovery from grazing in the wet year (2011) than in the dry year (2012). This result suggests that grazing in a wet year could potentially increase forb biomass more so than grass biomass and possibly shift plant community composition over time.

We found that many end of season arthropod responses were reduced by grazing in both study years, regardless of the timing of grazing or the amount of precipitation. End of growing season densities were reduced for all grazing treatments in both years for Hemiptera, and in the relatively wetter year for Araneae. This indicates a higher amount of rainfall in 2011 did not aid either arthropod order in recovery from grazing. Even though our two study years varied in precipitation and soil moisture availability, it is possible there were other ecological drivers influencing the responses of plants and arthropods to grazing, such as site differences attributed to fine-scale topography (Milchunas et al. 1989) or variability in timing of rainfall (Perez-Camacho et al. 2012).

Management Implications

Having a better understanding of how timing of grazing affects plants and arthropods will be useful for similar grassland systems interested in conservation grazing, and in particular, how potential changes in forage availability will affect species of concern. Management decisions about when to initiate grazing in high-elevation grasslands should consider that grazing earlier in the growing season may temporarily affect plant communities and the most common arthropod order

(Hemiptera). Our results demonstrate that the effects of timing of grazing are not uniform during the growing season and that early grazing may impact higher trophic levels that are reliant on forb biomass and Hemiptera density in late June. Even though forbs made up less than 10% of the plant community biomass in our system, key temporal differences between treatments may affect breeding sage-grouse (Gregg 2006) and pollinators (Gilgert and Vaughan 2011), that depend on forbs during certain times of the season for life history requirements. Other studies have similarly suggested that temporal variation in bird forage may have important implications for post-fledgling survival (Paquette et al. 2013). Further studies are needed to determine the long-term effects of timing of grazing, and if effects of herbivory are amplified if grazing occurs in consecutive growing seasons.

Proper planning of grazing regimes may aid in reducing possible effects on higher trophic levels with early season grazing. Early season grazing could take place outside of core bird nesting and foraging areas in the future, which may help mediate potential impacts on higher trophic levels. One of the most beneficial grazing strategies may include a matrix of grazing plots, with varying initiation graze dates and years of rest in-between grazing periods. Doing so will aid certain areas of the grassland in recovery from grazing at any point during the growing season, and provide the necessary structure and forage availability for higher trophic levels.

Table 1: Repeated-measures ANOVA results comparing response variables among treatments (control, early graze, and late graze) for 2012 data. Sampling event is the repeated measure. Significant p-values at $\alpha < 0.05$ are in bold. All plant variables and one insect variable, Hemiptera density, differed significantly across grazing treatments, but these effects depended on the sampling event. All other arthropod orders were unaffected by grazing treatments, but certain orders did vary among sampling events.

Variable	df	F	p-value	Arthropod order variable	df	F	p-value	Arthropod order variable	df	F	p-value
<i>Total plant biomass</i>				<i>Araneae density</i>				<i>Araneae total biomass</i>			
Treatment	2,7	2.22	0.179	Treatment	2,6	0.04	0.9653	Treatment	2,7	0.81	0.4844
Event	3,5	5.17	0.0542	Event	3,4	7.45	0.0409	Event	3,5	16.35	0.0051
Treatment:Event	6,10	8.75	0.0017	Treatment:Event	6,8	1.17	0.4078	Treatment:Event	6,10	0.12	0.9915
<i>Forb biomass</i>				<i>Hemiptera density</i>				<i>Hemiptera total biomass</i>			
Treatment	2,7	7.87	0.0162	Treatment	2,6	3.18	0.1143	Treatment	2,7	0.51	0.6238
Event	3,5	7.2	0.0291	Event	3,4	9.28	0.03	Event	3,5	0.59	0.648
Treatment:Event	6,10	9.74	0.0011	Treatment:Event	6,8	5.92	0.0125	Treatment:Event	6,10	1.45	0.2884
<i>Plant height</i>				<i>Hymenoptera density</i>				<i>Hymenoptera total biomass</i>			
Treatment	2,7	31.53	0.0003	Treatment	2,6	0.91	0.4522	Treatment	2,7	0.83	0.4751
Event	2,6	0.74	0.52	Event	3,4	0.75	0.5763	Event	3,5	1.84	0.2576
Treatment:Event	4,12	21.40	<0.0001	Treatment:Event	6,8	0.43	0.8376	Treatment:Event	6,10	0.98	0.4875
<i>Arthropod density</i>				<i>Diptera density</i>				<i>Diptera total biomass</i>			
Treatment	2,6	2.31	0.1805	Treatment	2,6	1.06	0.4024	Treatment	2,7	0.65	0.5508
Event	3,4	1.65	0.3128	Event	3,4	12.98	0.0157	Event	3,5	4.48	0.0701
Treatment:Event	6,8	1.75	0.2277	Treatment:Event	6,8	3.31	0.0609	Treatment:Event	6,10	1.56	0.2556
				<i>Coleoptera density</i>				<i>Coleoptera total biomass</i>			
				Treatment	2,6	0.34	0.7232	Treatment	2,7	0.28	0.763
				Event	3,4	34.87	0.0025	Event	3,5	3.29	0.1164
				Treatment:Event	6,8	1.70	0.239	Treatment:Event	6,10	0.72	0.6423
				<i>Orthoptera density</i>				<i>Orthoptera total biomass</i>			
				Treatment	2,6	1.49	0.2989	Treatment	2,7	0.34	0.7235
				Event	3,4	1.62	0.3192	Event	3,5	7.15	0.0294
				Treatment:Event	6,8	1.79	0.2188	Treatment:Event	6,10	0.26	0.9444

Table 2: Univariate one-way ANOVAs for each sampling event and Tukey's Honestly Significant Difference multiple comparisons when a significant treatment main effect was present within each sampling event for 2012 data. Significant p-values at $\alpha < 0.05$ are in bold. The treatment letters sharing a line are not statistically different from one another. Treatments are indicated as follows: C=Control, E=Early, L=Late.

Variable	Sampling event	df	F	p-value	Tukey's		
<i>Total plant biomass</i>							
	Early June	2	0.09	0.9133			
	Late June	2	16.83	0.0021	C	E	L
	Late July	2	3.72	0.0795			
	Late August	2	2.27	0.1736			
<i>Forb biomass</i>							
	Early June	2	0.87	0.4596			
	Late June	2	29.23	0.0004	C	E	L
	Late July	2	22.68	0.0009	C	E	L
	Late August	2	8.67	0.0128	C	E	L
<i>Plant height</i>							
	Late June	2	54.18	<.001	C	E	L
	Late July	2	16.37	0.0023	C	E	L
	Late August	2	40.95	0.0001	C	E	L
<i>Hemiptera density</i>							
	Early June	2	0.26	0.7795			
	Late June	2	11.02	0.0098	C	E	L
	Late July	2	6.53	0.0251	C	E	L
	Late August	2	3.24	0.1008			

Table 3: Univariate one-way ANOVAs for each treatment and Tukey's Honestly Significant Difference multiple comparisons when a significant sampling event main effect was present within each treatment for 2012 data. Significant p-values at $\alpha < 0.05$ are in bold. The sampling event numbers sharing a line are not statistically different from one another. Sampling events are indicated as follows: 1=Sampling event 1 (early June), 2=Sampling event 2 (late June), 3= Sampling event 3 (late July), 4= Sampling event 4 (Late August). If arthropod orders did not vary according to treatment, analysis was done on means across all treatments (Diptera density, Araneae density, Coleoptera density, Orthoptera total biomass, and Araneae total biomass).

Variable	Treatment	df	F	p-value	Tukey's			
Total plant biomass	Control	3	0.06	0.9794				
	Early	3	4.04	0.0508	1	2	3	4
	Late	3	6.52	0.0073	1	2	3	4
Forb biomass	Control	3	1.31	0.3366				
	Early	3	22.22	0.0003	1	2	3	4
	Late	3	9.49	0.0017	1	2	3	4
Plant height	Control	2	0.93	0.4458				
	Early	2	26.35	0.0011	NA	2	3	4
	Late	2	30.60	<0.0001	NA	2	3	4
Hemiptera density	Control	3	0.20	0.8967				
	Early	3	1.62	0.2598				
	Late	3	4.41	0.0288	1	2	3	4
Diptera density	NA	3	17.30	<0.0001	1	2	3	4
Araneae density	NA	3	6.75	0.001	1	2	3	4
Coleoptera density	NA	3	12.72	<0.0001	1	2	3	4
Orthoptera total biomass	NA	3	6.23	0.0016	1	2	3	4
Araneae total biomass	NA	3	6.11	0.0018	1	2	3	4

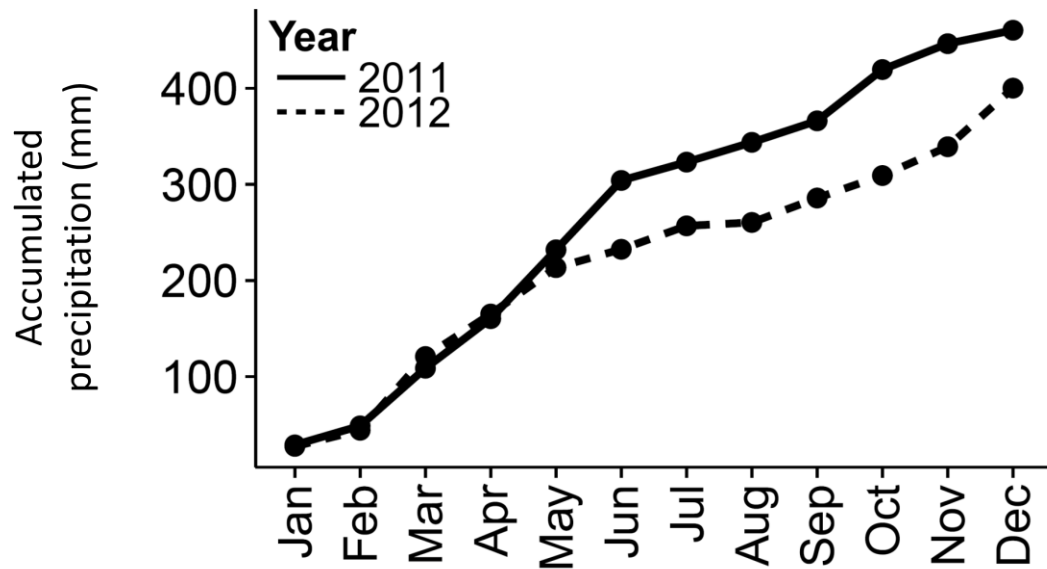


Figure 1: Accumulated precipitation from January to December in 2011 and 2012 on Red Rock Lakes National Wildlife Refuge. 2011 was wetter, with accumulated annual precipitation of 460 mm, while 2012 was drier, with accumulated annual precipitation of 400 mm. The major differences in precipitation across years emerged from June onwards. Precipitation data are from PRISM (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 24 July 2013).

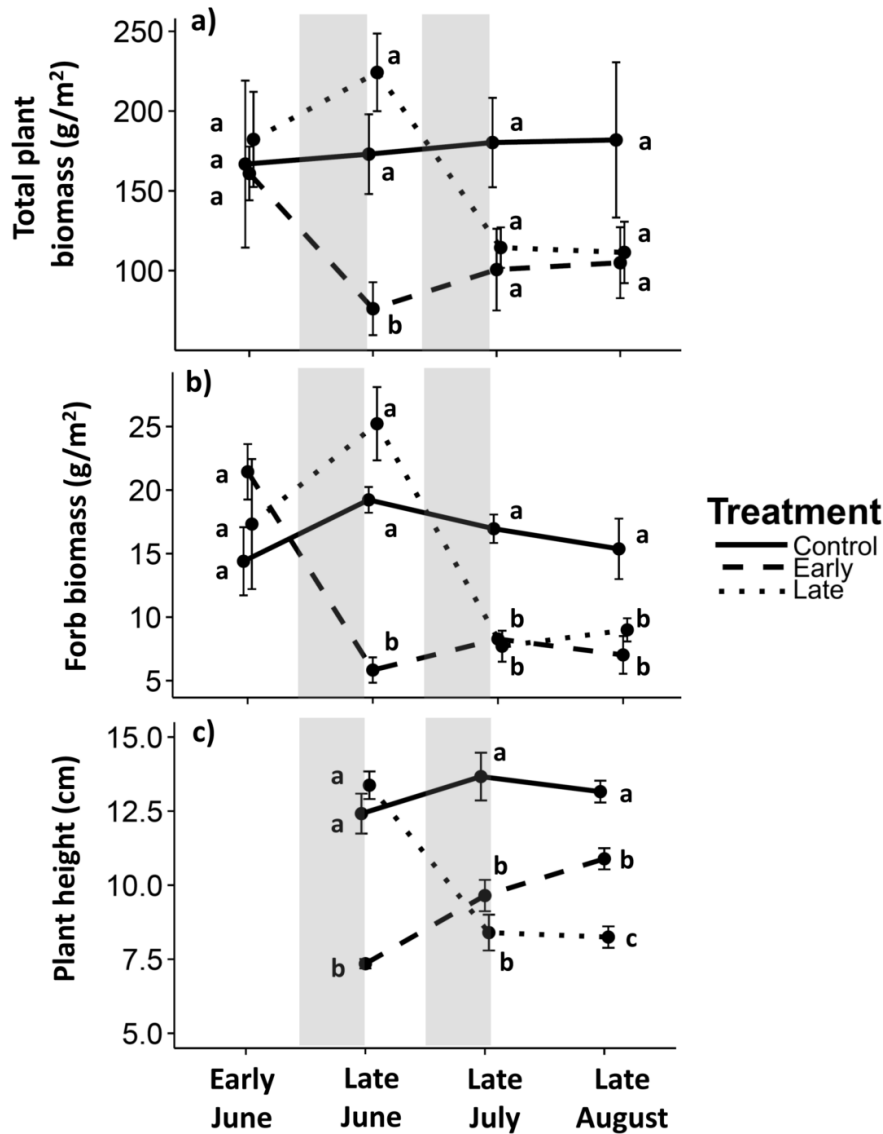


Figure 2: Temporal changes in a) total plant biomass, b) forb biomass, c) plant height in response to grazing treatments (all values are untransformed means $\pm$ SE). Duration of early and late grazing treatments are shown by shaded grey boxes. Significant treatment differences within a sampling event are indicated by differing letters. Tukey's HSD results for significant sampling event differences within a treatment are shown in Table 3. Immediately after early grazing was the only time that total plant biomass from any grazing treatment differed from control plots (a). Immediately after early grazing was the only time that forb biomass from early plots differed from late plots (b). Early-grazed plots had reduced plant height immediately after early grazing but then increased in plant height and were taller than late-grazed plots at the end of the growing season (c).

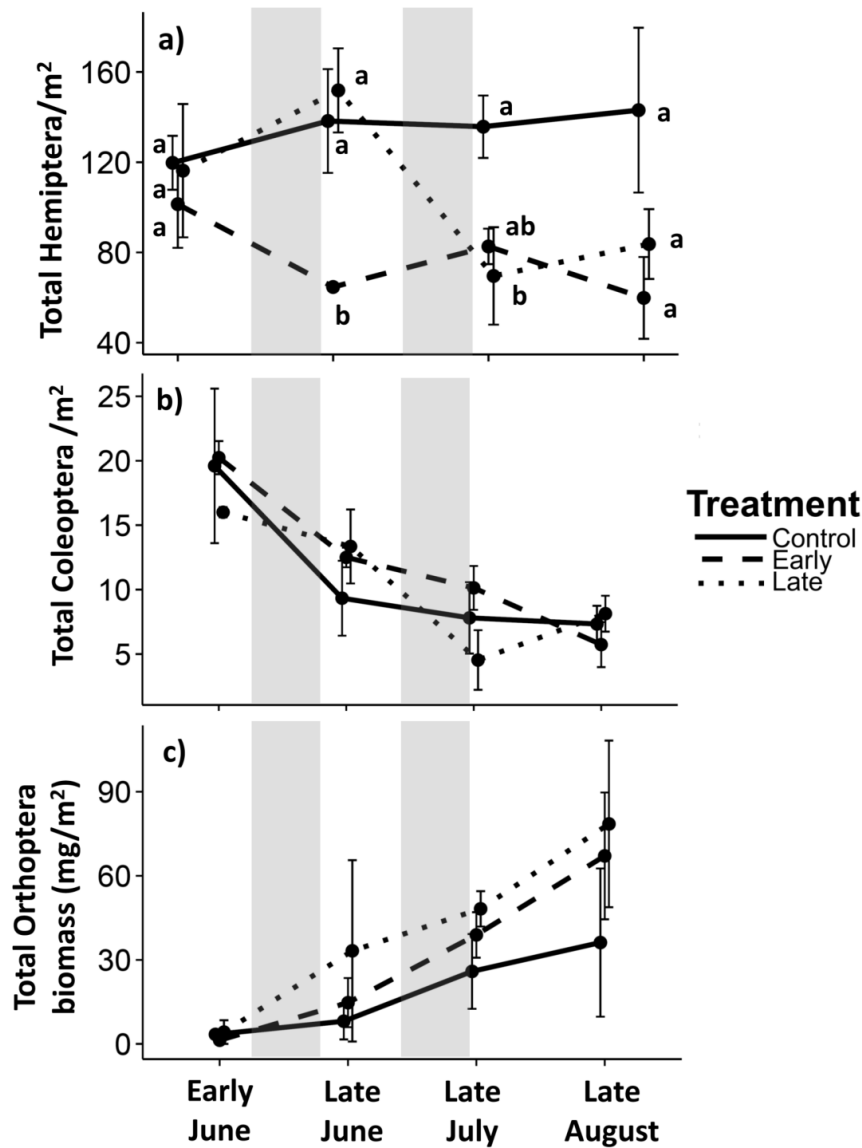


Figure 3: Temporal changes in a) Hemiptera density, b) Coleoptera density, and c) Total Orthoptera biomass in response to grazing treatments (all values are untransformed means $\pm$ SE). Duration of early and late grazing treatments are shown by shaded grey boxes. Significant treatment differences within a sampling event are indicated by differing letters. Tukey's HSD results for significant sampling event differences within a treatment are shown in Table 3. Immediately after early grazing was the only time that Hemiptera density in early plots differed from late plots (a). Coleoptera density was unaffected by grazing treatments but steadily declined throughout the growing season (b). Orthoptera total biomass was unaffected by grazing treatments but steadily increased throughout the growing season (c).

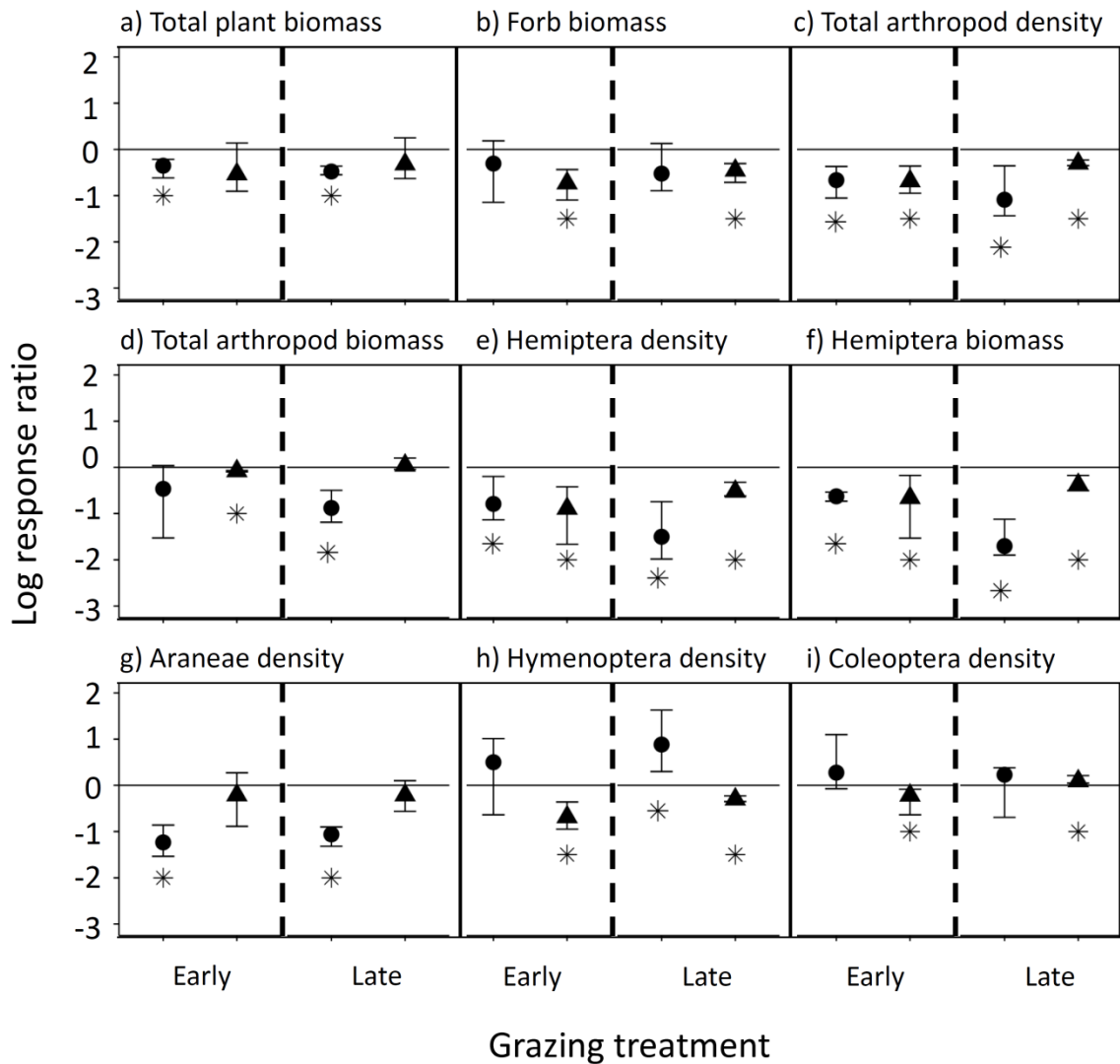


Figure 4: Mean effect size (log response ratio comparing grazing treatments to control) of 2011 (circle) and 2012 (triangle) end of growing season plant and arthropod responses. Error bars are bias-corrected 95% confidence intervals. Asterisks (*) denote significant effect sizes at $\alpha=0.05$. Due to similar results for density and biomass for Araneae, Hymenoptera, and Coleoptera, we only report effect sizes for arthropod density. Diptera and Orthoptera density and biomass in grazed treatments were not significantly different from controls.

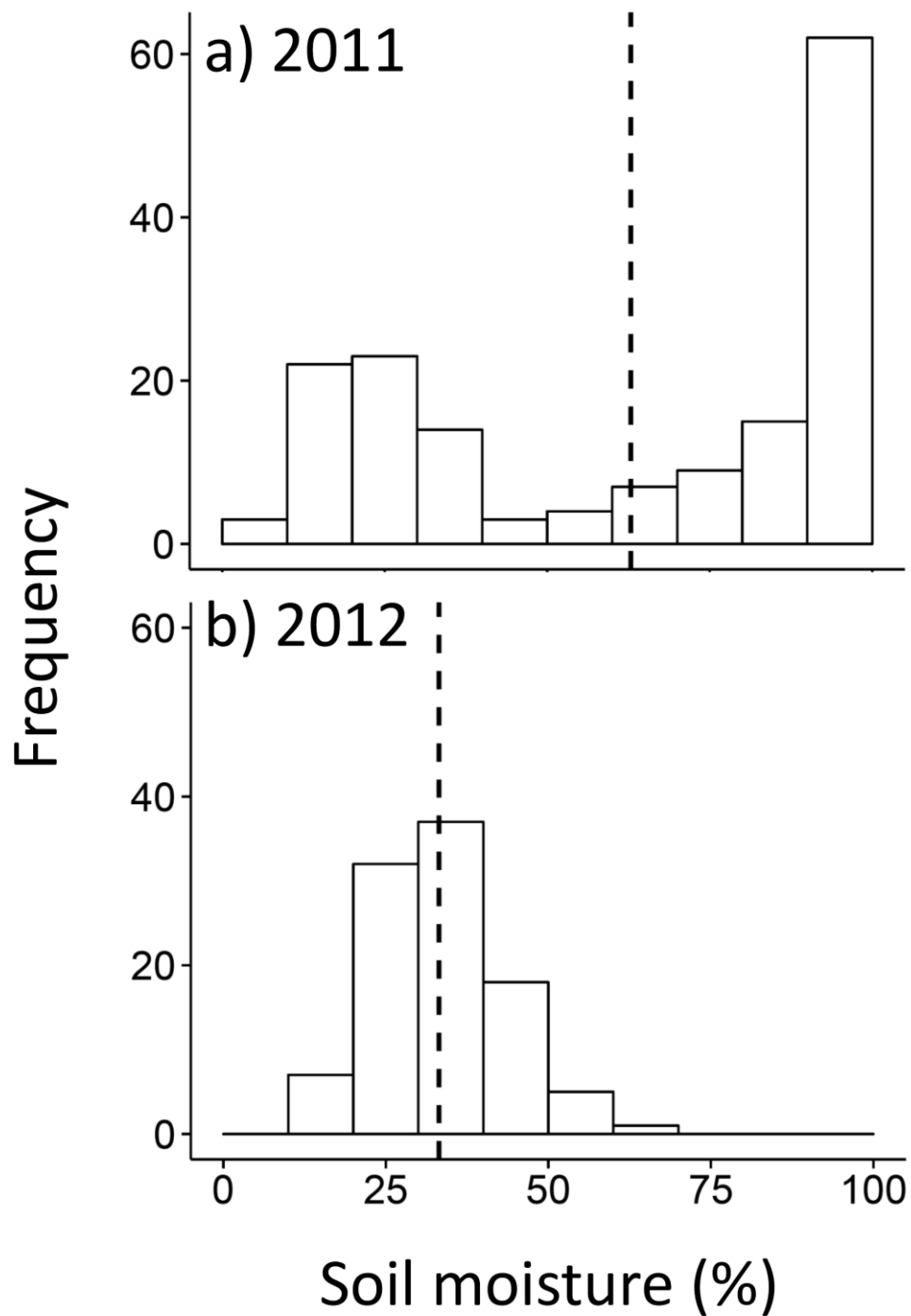


Figure 5: End of season (late August) histograms for soil moisture across all treatments for a) 2011 and b) 2012. The dashed line indicates mean soil moisture for each year. The study site in 2011 had greater mean soil moisture, a greater range of soil moisture values, and more of a bimodal distribution when compared to the study site in 2012.

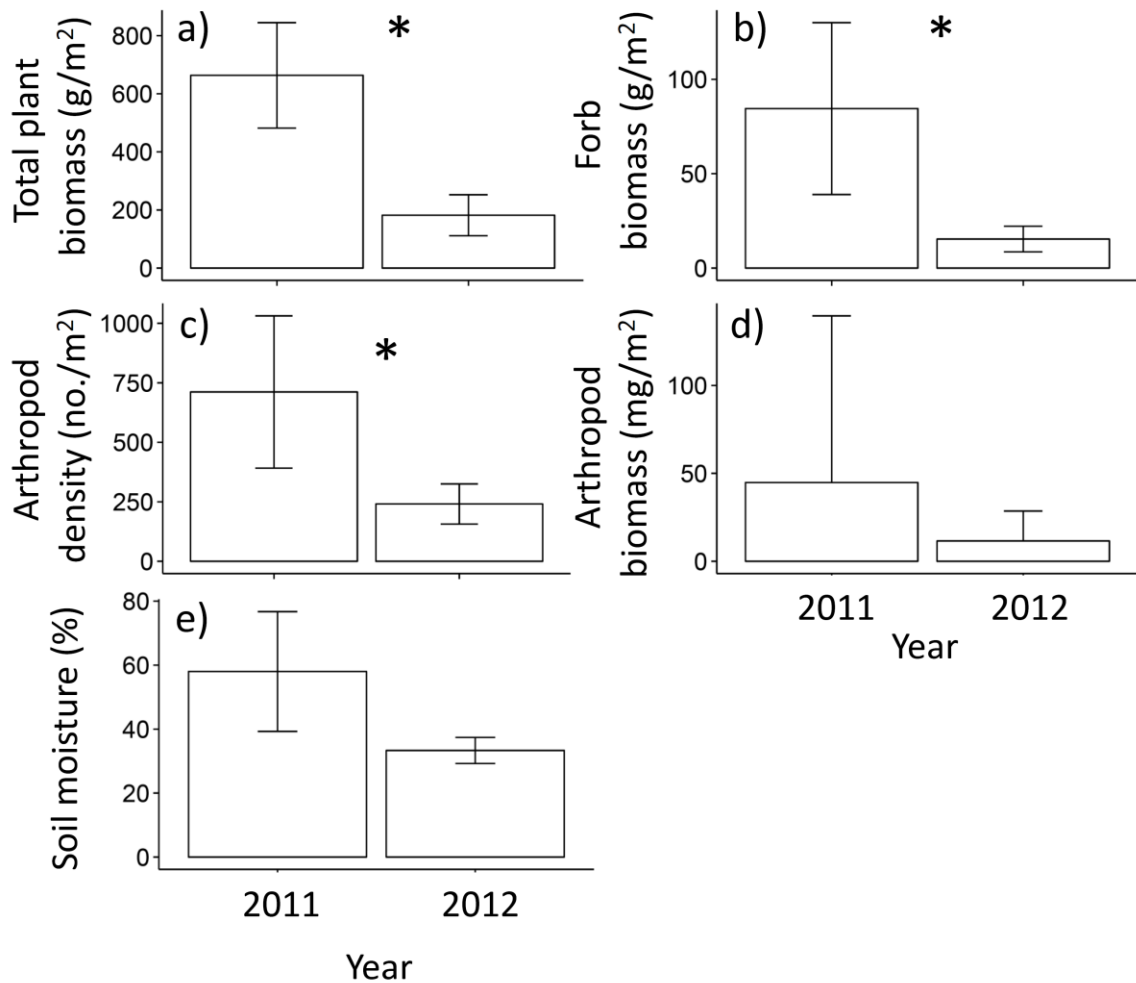


Figure 6: End of season (late August) bar graph comparisons for a) total plant biomass, b) forb biomass, c) arthropod density, d) arthropod biomass, and e) soil moisture across all treatments between 2011 and 2012 (untransformed means $\pm$ SE). Only one-sided error bar is shown for arthropod biomass due to negative values. * Indicates significant differences between 2011 and 2012 ($p < 0.05$ from paired t-tests, $n=3$). All variables were square-root transformed $+0.5$ for t-tests. The 2011 study year had significantly greater total plant biomass, forb biomass, and arthropod density than the 2012 study year.

LITERATURE CITED

- Anderson, M.T., Frank, D.A., 2003. Defoliation effects on reproductive biomass: importance of scale and timing. *Journal of Range Management* 56, 501–516.
- Bai, Y., Wu, J., Clark, C.M., Pan, Q., Zhang, L., Chen, S., Wang, Q., Han, X., 2012. Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. *Journal of Applied Ecology* 49, 1204–1215.
- Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G., Knops, J.M.H., 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9, 780–788.
- Bell, J.R., Wheeler, C.P., Cullen, W., 2001. The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of zoology* 255, 377–387.
- Briske, D. D. 1991. Developmental morphology and physiology of grasses. Pages 85-108 in R. K. Heitschmidt and J. W. Stuth, editors. *Grazing management: an ecological perspective*. Timber Press, Portland, Oregon, USA.
- Burkhardt, J.W., Sanders, K., 2012. Management of Growing-Season Grazing in the Sagebrush Steppe: A Science Review of Management Tools Appropriate for Managing Early-Growing-Season Grazing. *Rangelands* 34, 30–35.
- Cagnolo, L., Molina, S.I., Valladares, G.R., 2002. Diversity and guild structure of insect assemblages under grazing and exclusion regimes in a montane grassland from Central Argentina. *Biodiversity & Conservation* 11, 407–420.
- Cayan, D.R., Kammerdiener, S.A., Dettinger, M.D., Caprio, J.M., Peterson, D.H., 2001. Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society* 82, 399–416.
- Chase, J.M., Leibold, M.A., Downing, A.L., Shurin, J.B., 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology* 81, 2485–2497.
- Cingolani, A.M., Cabido, M.R., Renison, D., Solís Neffa, V., 2003. Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *Journal of Vegetation Science* 14, 223–232.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280, 745–

747.

- Davidson, A.D., Ponce, E., Lightfoot, D.C., Fredrickson, E.L., Brown, J.H., Cruzado, J., Brantley, S.L., Sierra-Corona, R., List, R., Toledo, D., Ceballos, G., 2010. Rapid response of a grassland ecosystem to an experimental manipulation of a keystone rodent and domestic livestock. *Ecology* 91, 3189–3200.
- Dennis, P., Young, M.R., Gordon, I.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological Entomology* 23, 253–264.
- Derner, J.D., Lauenroth, W.K., Stapp, P., Augustine, D.J., 2009. Livestock as Ecosystem Engineers for Grassland Bird Habitat in the Western Great Plains of North America. *Rangeland Ecology and Management* 62, 111–118.
- Drut, M.S., Pyle, W.H., Crawford, J.A., 1994. Diets and food selection of sage grouse chicks in Oregon. *Journal of Range Management* 47, 90–93.
- Frank, D.A., Kuns, M.M., Guido, D.R., 2002. Consumer control of grassland plant production. *Ecology* 83, 602–606.
- Gibson, C.W.D., Brown, V.K., Losito, L., McGavin, G.C., 1992. The response of invertebrate assemblies to grazing. *Ecography* 15, 166–176.
- Gibson, C.W.D., Hamblin, C., Brown, V.K., 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology* 29, 132–142.
- Gilgert, W., Vaughan, M., 2011. The Value of Pollinators and Pollinator Habitat to Rangelands: Connections Among Pollinators, Insects, Plant Communities, Fish, and Wildlife. *Rangelands* 33, 14–19.
- Glenn, S.M., Collins, S.L., Gibson, D.J., 1992. Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. *Landscape Ecology* 7, 243–251.
- Gotelli, N.J. and A.M. Ellison. 2004. *A Primer of Ecological Statistics*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Gregg, M.A., 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival. Thesis, Oregon State University, Corvallis, Oregon, USA.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in

experimental ecology. *Ecology* 80, 1150–1156.

Hendrickson, J. and B. Olson. 2006. Understanding plant response to grazing. Pages 32-39 *in* Targeted Grazing: a Natural Approach to Vegetation Management and Landscape Enhancement. American Sheep Industry Association.

JMP, Version 10. SAS Institute Inc., Cary, NC, 1989-2013.

Joern, A., Laws, A.N., 2013. Ecological Mechanisms Underlying Arthropod Species Diversity in Grasslands. *Annual Review of Entomology* 58, 19–36.

Knapp, A.K., Hoover, D.L., Blair, J.M., Buis, G., Burkepile, D.E., Chamberlain, A., Collins, S.L., Fynn, R.W.S., Kirkman, K.P., Smith, M.D., 2012. A test of two mechanisms proposed to optimize grassland aboveground primary productivity in response to grazing. *Journal of Plant Ecology*.

Kőrösi, ádám, Batáry, P., Orosz, A., Rédei, D., Báldi, A., 2012. Effects of grazing, vegetation structure and landscape complexity on grassland leafhoppers (Hemiptera: Auchenorrhyncha) and true bugs (Hemiptera: Heteroptera) in Hungary. *Insect Conservation and Diversity* 5, 57–66.

Kruess, A., Tscharrntke, T., 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological conservation* 106, 293–302.

Lenoir, L., Lennartsson, T., 2010. Effects of timing of grazing on arthropod communities in semi-natural grasslands. *Journal of Insect Science* 10, 1–24.

Maschinski, J., Whitham, T.G., 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *The American Naturalist* 134, 1–19.

McNaughton, S.J., 1986. Grazing lawns: on domesticated and wild grazers. *The American Naturalist* 128, 937–939.

McNaughton, S.J., 1993. Grasses and grazers, science and management. *Ecological Applications* 3, 17–20.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L., Kazempour, M.K., 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80, 11–23.

Morris, M.G., 1973. The Effects of Seasonal Grazing on the Heteroptera and Auchenorrhyncha (Hemiptera) of Chalk Grassland. *Journal of Applied Ecology* 10, 761–780.

- Morris, M.G., Lakhani, K.H., 1979. Responses of Grassland Invertebrates to Management by Cutting. I. Species Diversity of Hemiptera. *Journal of Applied Ecology* 16, 77–98.
- Mueggler, W.F., 1967. Response of mountain grassland vegetation to clipping in southwestern Montana. *Ecology* 48, 942–949.
- Mysterud, A., Ove Hansen, L., Peters, C., Austrheim, G., 2005. The short-term effect of sheep grazing on selected invertebrates (Diptera and Hemiptera) relative to other environmental factors in an alpine ecosystem. *Journal of Zoology* 266, 411–418.
- Oosterheld, M., McNaughton, S.J., 1991. Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85, 305–313.
- Olf, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13, 261–265.
- Paquette, S.R., Garant, D., Pelletier, F., Bélisle, M., 2013. Seasonal patterns in Tree Swallow prey (Diptera) abundance are affected by agricultural intensification. *Ecological Applications* 23, 122–133.
- Peñuelas, J., Filella, I., Zhang, X., Llorens, L., Ogaya, R., Lloret, F., Comas, P., Estiarte, M., Terradas, J., 2004. Complex spatiotemporal phenological shifts as a response to rainfall changes. *New Phytologist* 161, 837–846.
- Pérez-Camacho, L., Rebollo, S., Hernández-Santana, V., García-Salgado, G., Pavón-García, J., Gómez-Sal, A., 2012. Plant functional trait responses to interannual rainfall variability, summer drought and seasonal grazing in Mediterranean herbaceous communities. *Functional Ecology* 26, 740–749.
- Peterson, J.G., 1970. The food habits and summer distribution of juvenile sage grouse in central montana. *The Journal of Wildlife Management* 34, 147–155.
- Post, E., Stenseth, N.C., 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* 80, 1322–1339.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 24 July 2013.
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>

- Rambo, J.L., Faeth, S.H., 1999. Effect of vertebrate grazing on plant and insect community structure. *Conservation Biology* 13, 1047–1054.
- Ritchie, M.E., 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* 81, 1601–1612.
- Rogers, L.E., Buschbom, R.L., Watson, C.R., 1977. Length-Weight Relationships of Shrub-steppe invertebrates. *Annals of the Entomological Society of America* 70, 51–53.
- Romme, W.H., Turner, M.G., 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conservation Biology* 5, 373–386.
- Rosenberg, M.S., D.C. Adams, and J. Gurevitch. 2000. *MetaWin: Statistical Software for Meta-Analysis. Version 2.* Sinauer Associates, Sunderland, Massachusetts.
- Samson, D.A., Werk, K.S., 1986. Size-Dependent Effects in the Analysis of Reproductive Effort in Plants. *The American Naturalist* 127, 667–680.
- Schaffers, A.P., Raemakers, I.P., Sykora, K.V., J.F. ter Braak, C., 2008. Arthropod assemblages are best predicted by plant species composition. *Ecology* 89, 782–794.
- Sims, P.L., Singh, J.S., 1978. The structure and function of ten western north american grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* 66, 573–597.
- Sjödin, N.E., Bengtsson, J., Ekbom, B., 2008. The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology* 45, 763–772.
- Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D., Kigel, J., 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *Journal of Applied Ecology* 37, 224–237.
- Stewart, K.E.J., Bourn, N.A.D., Thomas, J.A., 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. *Journal of Applied Ecology* 38, 1148–1154.
- Sullivan, A.T., Howe, H.F., 2009. Prairie forb response to timing of vole herbivory. *Ecology* 90, 1346–1355.

- Sveum, C.M., Crawford, J.A., Edge, W.D., 1998. Use and selection of brood-rearing habitat by sage grouse in south central Washington. *Western North American Naturalist* 58, 344–351.
- United States Department of Agriculture, N.R.C.S., 2013. Tepee Creek (813) SNOTEL Site Information.
<http://www.wcc.nrcs.usda.gov/nwcc/site?sitenum=813&state=mt>
 Accessed: July 24, 2013.
- United States Fish and Wildlife Service. 2009. Comprehensive Conservation Plan, Red Rock Lakes National Wildlife Refuge.
- United States Department of Agriculture, N.R.C.S., 2011. Flattop Mountain (482) SNOTEL Site Information.
<http://www.wcc.nrcs.usda.gov/nwcc/site?Sitenum=482&state=mt2011>
 Accessed: July 14, 2011.
- Wallace, L.L., 1990. Comparative photosynthetic responses of big bluestem to clipping versus grazing. *Journal of Range Management* 43, 58–61.
- WallisDeVries, M.F., 1998. Large herbivores as key factors for nature conservation. Pages 1-20 *in* WallisDeVries, M.F., J.P. Bakker, and S.E. van Wieren, editors. *Grazing and Conservation Management*. Kluwer Academic Publishers, Dordrecht, the Netherlands.
- Williamson, S.C., Detling, J.K., Dodd, J.L., Dyer, M.I., 1989. Experimental evaluation of the grazing optimization hypothesis. *Journal of Range Management* 149–152.