Grasshopper Responses to Fire and Postfire Grazing in the Northern Great Plains Vary Among Species

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ABSTRACT

Rangeland management practices such as burning and grazing may affect the development, survival, and reproduction of grasshopper populations. Experiments in the northern Great Plains that examine effects of fire and grazing utilization on grasshoppers are lacking. As part of a larger study examining vegetation responses to late summer fire and postfire grazing utilization in semiarid mixed prairie in eastern Montana to aid in postfire management decisions, we examined grasshopper responses to late summer fire and postfire grazing intensity. The experiment was repeated using adjacent blocks, with blocks receiving fire treatment in either 2003 or 2004 and grazing in the following year. Treatments were no fire and no grazing, and summer fire followed by grazing at 0%, 17%, or 50% forage utilization on a biomass basis. Grasshopper sampling was conducted before fire and for 2 years post fire. Fire reduced grasshopper density 36–53% across experiments, sampling periods, and postfire grazing treatments, but the effects of grazing and fire were species dependent. The two most abundant grasshopper species, *Ageneotettix deorum* (Scudder) and *Opeia obscura* (Thomas), were reduced 80% and 84% the first year after the 2003 fire, but only *O. obscura* was affected following the 2004 fire. Late summer fire appears to be a useful management tool to reduce populations of some grasshopper species in the northern Great Plains, while other species appear more responsive to food limitation from increased postfire grazing utilization. Fire effects were largely driven by two species, indicating that late-season fire impacts could be species dependent.

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Introduction

Grasshoppers in the western United States often reach high densities and are economically important rangeland pests when abundant (Branson et al., 2006; Joern, 2000). During grasshopper outbreaks, grasshoppers often exceed livestock grazers in herbivore biomass and plant biomass removed (Belovsky, 2000; Belovsky and Slade, 2000; Branson and Haferkamp, 2014). The population dynamics of grasshoppers remain poorly understood (Joern, 2000). Although grasshopper outbreaks often lead to chemical control efforts, habitat management approaches to reduce grasshopper populations have received little attention (Branson et al., 2006). As grasshoppers are highly responsive to factors such as altered habitat structure and food availability (Joern, 2004; Onsager and Olfert, 2000), rangeland management practices may affect grasshopper populations by affecting development, survival, and reproduction.

Livestock grazing has been shown to positively and negatively affect grasshopper population densities, with relationships often differing between ecosystems in the western United States (reviewed in Branson et al., 2006; O'Neill et al., 2003). Foraging by livestock can directly reduce food availability for grasshoppers and indirectly affect populations through longer-term changes in plant community composition (Branson and Haferkamp, 2014; Fielding and Brusven, 1996; O'Neill et al., 2003, 2010). In addition, both grazing and trampling can affect a grasshopper's structural habitat and affect development and predation rates (Joern, 2004, 2005; Onsager, 2000; Pitt, 1999). For example, many pest grasshopper species in the northern Great Plains appear to increase in abundance when they can thermoregulate in microhabitats with habitat heterogeneity including bare soil (Onsager, 2000). Relationships between livestock grazing patterns and grasshopper populations in the northern plains remain unclear, although Onsager (2000), in a study lacking ideal replication, found grasshopper densities were five to nine times lower in rotational grazing pastures than in season-long grazing pastures.

Burning has been shown to frequently influence grasshopper densities and community composition in multiple ecosystems (Branson et al., 2006). Changes in grasshopper populations following fire can result from direct mortality of eggs, nymphs, or adults, as well as direct and indirect effects of vegetation and habitat changes (Bock and Bock, 1991; Joern, 2004, 2005; Porter and Redak, 1996; Vermeire et al., 2004). Although spring burning can positively affect grasshopper densities in tallgrass prairie (Joern, 2004), fall fire may be useful as a management tool to reduce populations of some pest grasshopper species in the northern Great Plains (Branson, 2005). In mechanistic laboratory

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studies, Branson and Vermeire (2007, 2013) showed that elevated soil temperatures associated with fire occurring under fuel loads typically found in the northern Great Plains could cause grasshopper egg mortality for species laying shallow egg pods but not for species laying deeper egg pods.

No experiments in the northern Great Plains have examined the combined effects of fire and postfire grazing utilization on grasshopper populations. Only one large-scale study has simultaneously examined fire and grazing management effects on grasshopper populations in the northern Great Plains, but low grasshopper densities combined with variability between replicate blocks limited the ability to detect treatment effects (Branson and Sword, 2010). We examined the responses of grasshoppers to late summer fire and postfire sheep grazing utilization. The objectives of the study were to examine if late-summer fire affected grasshopper densities and species composition and if postfire grazing utilization influenced the effect of burning on grasshopper densities and species composition. The grasshopper work was part of a larger set of studies examining vegetation responses to late summer fire and postfire grazing utilization to aid in postfire rangeland management (Vermeire et al., 2011, 2014).

Study Site

Research was conducted in semiarid mixed prairie, at the Fort Keogh Livestock and Range Research Laboratory located near Miles City, Montana (lat 46°24′N, long 105°56′W; 815 m above sea level). The freeze-free period ranges from 110 to 135 d. July is the hottest month, with an average maximum of 32°C, and January is coldest, with an average minimum of –14°C. The 30-yr average annual precipitation is 319 mm, with April to May precipitation being the greatest controlling factor for plant productivity (Heitschmidt and Vermeire, 2006; Vermeire et al., 2008, 2009).

The study site is rolling upland on Pinehill loam soil (fine, montmorillonitic Typic Eutroboralfs) with some patches of a Pinehill-Absher complex. Absher soil is a clay loam (fine, smectitic, frigid Leptic Torrertic Natrustalfs). The site had a decades-long history of moderate grazing by cattle until May 2003, when livestock were excluded. Vegetation was dominated by perennial graminoids, with *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Pascopyrum smithii* (Rydb.) A. Löve, *Carex filifolia* Nutt., *Bouteloua gracilis* (Willd. Ex Kunth) Lag. ex Griffiths, and *Poa secunda* J. Presl contributing most to biomass. Annual grasses *Bromus japonicus* Thunb., *B. tectorum* L., and *Vulpia octoflora* (Walter) Rydb. were always present and variable in abundance. *Artemisia frigida* Willd. occurred frequently, whereas *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young was common but widely spaced. The most common forbs were *Plantago patagonica* Jacq., *Logfia arvensis* (L.) Holub, *Alyssum alyssoides* L., *Sphaeralcea coccinea* (Nutt.) Rydb., and *Phlox hoodii* Richardson.

There are three main subfamilies of rangeland grasshoppers in the area of the study, slant-faced (Gomphocerinae), band-winged (Oedipodinae), and spur-throated (Melanoplinae). The majority of species in the slant-faced and band-winged subfamilies are grass feeders, whereas the spur-throated subfamily includes grass, mixed, and forb feeders (Pfadt, 2002). Although all grasshoppers found in the area of the study are univoltine, the four most abundant grasshopper species at the study site differ in phenology and egg-laying habits (Pfadt, 2002). *Ageneotettix deorum* (Scudder), the white-whiskered grasshopper, is a small-bodied early hatching species laying small egg pods of three to five eggs just below the soil surface. It is a common economic species in the slant-faced subfamily and is a grass generalist. *Opeia obscura* (Thomas), the obscure grasshopper, is another small-bodied slant-faced species that is later hatching. It lays egg pods of ~eight eggs and typically prefers blue grama *(Bouteloua gracilis)*. *Melanoplus sanguinipes* (Fabricius), the migratory grasshopper, was the most common spur-throated species. It begins hatching after *A. deorum* and lays much larger egg pods up to 4 cm deep. It is a highly

polyphagous feeder on grasses and forbs and is a dominant economic species in the spur-throated subfamily. *Trachyrhachys kiowa* (Thomas), the kiowa grasshopper, is an intermediate hatching species in the band-winged subfamily that feeds on grasses and sedges and lays vertical egg pods up to 3 cm deep.

Methods

Thirty-two 0.75-ha plots (75×100 m) were randomly assigned four treatments, with four replications within each of two fire treatment years. The experiment was repeated using two adjacent blocks of 16 plots, with blocks receiving fire treatment in either 2003 (Experiment 1) or 2004 (Experiment 2) and grazing treatment in 2004 or 2005, respectively. The repeated experiments are described as Experiments 1 and 2, following Vermeire et al. (2011, 2014). Treatments were no fire and no grazing, and summer fire followed by grazing the next year at one of three levels of forage utilization on a biomass basis (0%, 17%, or 50%), hereafter referred to as fire-grazing treatments.

Fires were applied to individual plots 29 August 2003 and 24 and 25 August 2004. Plots receiving grazing treatments were stocked during late June and early July of the first growing season after fire using 3 or 9 sheep *Ovis aries* in 2004 and 6 or 18 sheep in 2005 to achieve 17% and 50% utilization, respectively, by mid-July. Resulting stocking rates for 17% and 50% utilization were 4.3 and 12.2 animal unit days·ha^{-1} (1 AUD = 9.08 kg dry-matter forage) during 2004 and 25.4 and 77.7 AUD·ha^{-1} during 2005 because of differences in forage production between years. Additional details of fuel loads, fire weather, sheep management, and plant response to treatments were reported by Vermeire et al. (2011, 2014). The on-site U.S. Department of Agriculture Livestock and Range Research Laboratory Institutional Animal Care and Use Committee considered sheep handling in this study as a standard management practice requiring no official approval for experimental procedures.

Grasshopper sampling was conducted before each fire and for 2 years after each fire treatment. As the study was designed to generate grazing utilization recommendations in the year following fire, livestock grazing occurred only during the first year post fire. Grasshopper populations were sampled for an additional year after livestock grazing to determine if fire and grazing impacts were persistent, given grasshoppers univoltine life cycles. Total grasshopper population density was estimated every 2–4 weeks by counting the number of grasshoppers within 40, 0.1-m^2 aluminum wire rings between ~late May and August (Belovsky and Joern, 1995; Joern, 2004; Onsager and Henry, 1977). Rings were permanently placed in three or four transects in each replicate plot and were spaced about 5 m from each other. Grasshopper sampling periods varied between years on the basis of the timing of grasshopper hatching and population declines (Table 1). Sampling took place on days when air temperature was above 23°C. Grasshopper community composition was determined through random catch samples of ~50–60 individuals taken two or three times each summer. Low grasshopper population densities of < 2 per m^2 in all plots during the study limited the number of grasshoppers that could be removed from plots without potentially depleting populations. Individuals

Table 1
Sampling dates by assessment period for Experiment 1 (fires applied 29 August 2003) and Experiment 2 (fires applied 24 and 25 August 2004) on silty ecological sites in southeastern Montana.

Period	Sampling Dates	
	Experiment 1	Experiment 2
Prefire	28 Jul, 26 Aug 2003	14 Jul, 4, 18 Aug 2004
Postfire	3 Sep 2003	31 Aug 2004
Pregraze	27 May, 16 Jun 2004	20 Jun 2005
Graze	29 Jun, 13 Jul 2004	30 Jun, 18 Jul 2005
2 yr postfire	30 Jun, 8, 29 Jul, 22 Aug 2005	6, 22, 28 Jul, 19 Jul 2006

walked transects through plots with insect sweep nets and caught individual grasshoppers when observed. Grasshoppers that escaped were identified to species when possible. Grasshoppers were frozen for later identification to species and developmental instar.

Total grasshopper density, density by subfamily, density of the seven most abundant species, subfamily species richness, and Margalef's diversity (D = (S-1/ln N, S = species number and N = total individuals; Magurran, 2004) were analyzed with the use of SAS MIXED analysis of covariance with repeated measures to determine effects of summer fire and postfire grazing utilization. Models included the main effects of experiment, fire-grazing treatment, period, and their interactions. Pretreatment data were tested as covariates but were only retained in the model for band-winged species richness because pretreatment data were not significant for any other variables. Sampling period (post-fire, pregraze, graze, 2 yr postfire) was the repeated measure. Only total density included the immediate postfire sampling period. Significance of tests and interactions was declared at α = 0.05 unless otherwise indicated and followed by tests of simple effects.

Results

Temperature and precipitation were near average at the start of the study, followed by cool and very dry conditions during 2004 (Table 2). Growing degree-day accumulation at the time of burning was lower than the long-term average in Experiment 2 and near the long-term average in Experiment 1. Spring precipitation was more than 40% greater than average during 2005 and 2006, with 2006 also being hotter than average. The variability in temperature and precipitation combined with intra-annual population fluctuations resulted in experiment by sampling period interactions for most variables measured. However, total grasshopper density on nonburned, nongrazed plots was similar between experiments for all but the prefire sampling period (Fig. 1). Therefore experiment and sampling periods are only discussed when they interacted with fire-grazing treatment.
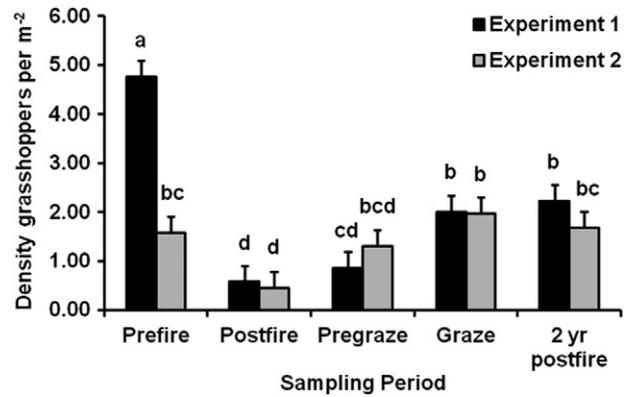
Fire reduced grasshopper density 36–53% across experiments, sampling periods, and postfire grazing treatments (Table 3). Spur-throated grasshoppers followed a similar pattern, with reduced densities on all burned plots compared with nonburned plots. Slant-faced grasshopper density varied by the interacting effects of experiment and treatment but was reduced by fire in every case (Table 4). Treatment effects on band-winged grasshopper density differed among sampling periods (Table 5). Band-winged grasshopper density increased between each of the sampling periods on nonburned plots and did so less consistently for the burned plots (see Table 5). Before and during grazing, the treatment with 17% grazing utilization by sheep resulted in greater band-winged grasshopper density than nonburned, nongrazed pastures. Fire with no grazing reduced band-winged grasshopper density, relative to nonburned plots, by the second year postfire.

The seven most common grasshopper species were *Opeia obscura* (Thomas), *Melanoplus sanguinipes* (Fabricius), *Ageneotettix deorum* (Scudder), *Trachyrhachys kiowa* (Thomas), *Phlibostroma quadrimaculatum* (Thomas), *Spharagemon equale* (Say), and *Aulocara femoratum* (Scudder). *Melanoplus sanguinipes* density was reduced by postfire grazing at 17% and 50% utilization levels; *T. kiowa* density was reduced by grazing to 50% utilization after fire; and *P. quadrimaculatum* showed trends of being reduced by fire with no grazing and fire followed by 50% utilization

Fig. 1. Grasshopper density in nonburned, nongrazed pastures by sampling period and experiment. Experiment-by-sampling period means with a common letter above bars are similar (P > 0.05).

(see Table 3). Densities of *S. equale* and *A. femoratum* were similar among fire-grazing treatments. *Ageneotettix deorum* density was reduced about 80% with fire across postfire grazing utilization levels in Experiment 1 (see Table 4). However, in Experiment 2, *A. deorum* density was lower for nonburned plots than in Experiment 1 and similar across all treatments.

Opeia obscura density varied with interacting effects of experiment and fire-grazing treatment (see Table 4), as well as the interaction of sampling period and fire-grazing treatment (see Table 5). Fire reduced *O. obscura* density across grazing utilization levels for each experiment, and burned plot values were similar between experiments, but *O. obscura* was less abundant in nonburned plots during Experiment 2 than Experiment 1. Before grazing commenced, *O. obscura* density was low and similar across treatments, but fire effects were later apparent, with an 84% reduction during the grazing period and a 60% reduction 2 years after fire (see Table 5).

Species richness was similar across treatments for slant-faced and spur-throated grasshoppers (see Table 3). However, fire increased band-winged grasshopper species richness, regardless of postfire grazing utilization. Fire increased overall grasshopper diversity relative to nonburned plots when fire was followed by no grazing or 50% grazing utilization. Fire followed by 17% utilization resulted in grasshopper diversity that was intermediate and similar to nonburned and the other burned treatments.

Discussion

Fire reduced grasshopper densities 43% across experiments and sampling periods; however, few shifts in species diversity and richness were noted between treatments. Less abundant species were less likely to be detected due to restricted sampling to avoid population depletion. Although slant-faced and spur-throated species diversity was not affected by burning, band-winged species richness was higher in burned plots. Band-winged species are more mobile than the other two subfamilies and typically prefer open bare patches of soil (Pfadt, 2002). Reductions in densities due to fire were larger than those observed with fall fires by Branson (2005) and Branson and Sword (2010), where most grasshoppers had already died. Species-specific responses to fire were evident, indicating that density shifts following late summer fire in the northern Great Plains need to be linked to the underlying species composition. Although the small plot size could allow grasshopper movement between plots, the sustained postfire treatment impacts indicate that this was not a major issue for the most abundant species.

Context-dependent and species-specific effects of burning were evident, with densities of the two most abundant grasshopper species, *A. deorum* and *O. obscura*, reduced 80% and 84%, respectively, the first year after fire in Experiment 1. The reduction in *A. deorum* and

Table 2
Mean May through July temperature and total April through May precipitation during the study period and 30-yr averages for each.

Period	May-Jul Temperature (°C)	Apr-May Precipitation (mm)
2003	18.8	91.9
2004	17.3	27.4
2005	17.9	121.0
2006	20.3	119.8
1977-2006	18.9	85.0

Table 3

Treatment effects on grasshopper density, richness (S), and diversity. Treatments are nonburned and nongrazed (NB), summer-burned and nongrazed (BN + 0%), and summer-burned and grazed the first year after fire to achieve 17% (BN + 17%), or 50% (BN + 50%) utilization and nongrazed the second year after fire. Fire-grazing treatment means within a component with a common letter are similar (*P* > 0.05). As there was a trend for treatment differences in *P. quadrimaculatum* (*P* = 0.07), treatment means were compared but are designated with an asterisk.

Component	NB + 0%	BN + 0%	BN + 17%	BN + 50%	Stderr	P value
Total density (no. per m^{-2})	1.38 a	0.81 b	0.88 b	0.65 b	0.08	<0.001
Spur-throated (no. per m^{-2})	0.47 a	0.31 b	0.27 b	0.17 b	0.06	0.004
M. sanguinipes (no. per m^{-2})	0.42 a	0.28 ab	0.25 b	0.15 b	0.06	0.012
T. kiowa (no. per m^{-2})	0.22 ab	0.16 bc	0.23 a	0.15 c	0.02	0.031
P. quadrimaculatum (no. per m^{-2})	0.07 *a	0.04 *b	0.05 *ab	0.03 *b	0.01	0.068
S. equale (no. per m^{-2})	0.07	0.11	0.12	0.08	0.02	0.082
A. femoratum (no. per m^{-2})	0.03	0.03	0.02	0.02	0.01	0.745
Slant-faced S (no. sp)	4.8	5.0	5.1	5.0	0.24	0.816
Band-winged S (no. sp)	2.0 b	2.5 a	2.5 a	2.8 a	0.16	0.004
Spur-throated S (no. sp)	1.4	1.5	1.3	1.5	0.14	0.772
Margalef's diversity	1.79 b	2.03 a	1.95 ab	2.13 a	0.09	0.046

Table 4

Slant-faced subfamily grasshopper density (no. per m^{-2}) by experiment and fire-grazing treatment. Treatments are nonburned and nongrazed (NB), summer-burned and nongrazed (BN + 0%), and summer-burned and grazed the first year after fire to achieve 17% (BN + 17%), or 50% (BN + 50%) utilization and nongrazed the second year after fire. Fire-grazing treatment means within a component and experiment with a common lowercase letter are similar (*P* > 0.05) and experiment means within a component and fire-grazing treatment with a common uppercase letter are similar (*P* > 0.05).

Component	Experiment	NB + 0%	BN + 0%	BN + 17%	BN + 50%	Stderr	P value
Slant-faced	1	1.47 a A	0.30 b B	0.36 b B	0.32 b A	0.09	<0.001
	2	0.93 a B	0.62 b A	0.66 b A	0.43 b A		
O. obscura	1	0.71 a A	0.12 b A	0.13 b A	0.09 b A	0.06	0.005
	2	0.48 a B	0.27 b A	0.29 b A	0.18 b A		
A. deorum	1	0.46 a A	0.07 b B	0.09 b B	0.12 b A	0.04	<0.001
	2	0.23 a B	0.21 a A	0.23 a A	0.14 a A		

O. obscura densities persisted for 2 yr in Experiment 1, but only *O. obscura* experienced postfire population declines in Experiment 2. Vermeire et al. (2004) and Branson (2005) observed reductions in *A. deorum* densities the year following fall fire in the southern and northern Great Plains, indicating fire frequently reduces this common economic species. Varied responses of *A. deorum* and *O. obscura* in Experiment 2, as well as weaker fire effects on *M. sanguinipes* and *T. kiowa* densities, indicate different mechanisms likely affected each species. Density shifts could result from a combination of egg mortality, adult mortality, and indirect vegetation and habitat changes.

Postfire changes in grasshopper populations have been linked to shifts in habitat structure, plant production, quality, or species composition (Joern, 2004, 2005; Jonas and Joern, 2007; Porter and Redak, 1996). Although precipitation altered plant production between experiments, there was no effect of burning on vegetation production the first year post fire in either experiment (Vermeire et al., 2011, 2014). Three of the four most abundant grasshopper species feed nearly exclusively on grasses, and grass production increased on burned sites by the second year post fire. Burning increased western wheatgrass while reducing annual grasses, which are not a significant food source for grasshoppers. Although vegetation quality data were not available, indirect fire effects on vegetation quality do not appear as strong in this system as in tallgrass systems (Branson, 2005) and were not likely

a strong determinant of grasshopper density shifts post fire. Although not assessed, structural changes from burning could impact effectiveness or abundance of vertebrate predators (Pitt, 1999). Invertebrate predators, such as spiders, can affect grasshopper population dynamics. Although spiders were not assessed, a late summer fire would likely result in spider mortality.

Litter was reduced for 2 yr following fire when comparing nongrazed burned and nonburned plots, indicating more bare ground with fire (Vermeire et al., 2011, 2014). Although band-winged diversity was higher in burned plots, density increased over time on nonburned plots while density increased less consistently in burned plots the second year postfire. It is unclear if these differences in directional shifts over time were a random result or due to band-winged species responses to fire. Although removal of litter could increase soil temperature and accelerate hatching as in tallgrass prairie (Meyer et al., 2002), Vermeire et al. (2011) noted that the light soil color, limited postburn black residue, and lower litter cover led to smaller soil temperature differences between burned and nonburned plots than more productive systems.

The dominant context-dependent and species-specific responses to fire may be related to species differences in phenology and egg pod depth. Heat from fire increases with fuel load, with shallow subsurface temperatures capable of reaching lethal levels for grasshopper eggs

Table 5

Grasshopper density (no. per m^{-2}) by sampling period and fire-grazing treatment for band-winged species and the slant-faced species *O. obscura*. Treatments are nonburned and nongrazed (NB), summer-burned and nongrazed (BN + 0%), and summer-burned and grazed the first year after fire to achieve 17% (BN + 17%), or 50% (BN + 50%) utilization and nongrazed the second year after fire. Fire-grazing treatment means within a component and sampling period with a common lowercase letter are similar (*P* > 0.05) and sampling period means within a component and fire-grazing treatment with a common uppercase letter are similar (*P* > 0.05).

Component	Period	NB + 0%	BN + 0%	BN + 17%	BN + 50%	Stderr	P value
Band-winged	Pregraze	0.11 b C	0.15 ab B	0.27 a B	0.16 ab B	0.05	0.045
	Graze	0.30 b B	0.37 ab A	0.46 a A	0.22 b B		
	2 yr postfire	0.52 a A	0.35 b A	0.39 ab AB	0.39 ab A		
O. obscura	Pregraze	0.18 a B	0.09 a B	0.07 a B	0.07 a A	0.07	0.002
	Graze	0.74 a A	0.10 b B	0.18 b AB	0.08 b A		
	2 yr postfire	0.86 a A	0.39 b A	0.38 b A	0.25 b A		

(Branson and Vermeire, 2007; Whelan, 1995; Wright and Bailey, 1982). *Ageneotettix deorum* lays small horizontal egg pods just below the soil surface, exposing eggs to potentially lethal temperatures during fire (Vermeire et al., 2004; Branson and Vermeire, 2007), whereas *O. obscura* and *M. sanguinipes* lay deeper egg pods and are less vulnerable to fire-induced egg mortality (Branson and Vermeire, 2007, 2013). Although *A. deorum* densities declined strongly following fire in Experiment 1, fire did not affect densities in Experiment 2. Branson and Vermeire (2007, 2013) observed increased heat dosage created significant egg mortality for *A. deorum* eggs laid in intact sod cores. The results are consistent with predictions from Branson and Vermeire (2007) because only the greater fire continuity (less patchy combustion of fuels) in Experiment 1 yielded reductions in *A. deorum* density. As egg mortality cannot be assessed under field conditions, adult mortality for the early hatching *A. deorum* could have also contributed to the postfire population reduction in Experiment 1 through reduced reproduction. The lower proportional reduction of *O. obscura* in Experiment 2 with burning could have partially resulted from low late summer reproduction in nonburned plots because of drought.

As fire directly kills grasshoppers (Bock and Bock, 1991), species differences in risk from late summer fires exist on the basis of hatching phenology. *Opeia obscura* was the latest hatching of common species at the site, and a few nymphs were present shortly before fire in Experiment 1. Densities of *O. obscura* declined with burning in both experiments. Before grazing, *O. obscura* density was similar across treatments, but fire effects led to an 84% reduction during the grazing period after hatching was complete and a 60% reduction 2 yr after fire. The consistent 2-yr reductions in *O. obscura* post fire likely resulted primarily from adult mortality leading to reduced reproduction, as eggs are not vulnerable to fire-induced egg mortality and adults are capable of only short flights (Branson and Vermeire, 2013). By contrast, *A. deorum,* the other species strongly reduced by fire, is an early hatching species.

Postfire grazing utilization had few direct effects when burning led to low densities in all postfire grazing utilization treatments. The low postfire densities, combined with detrimental drought effects, constrained the examination of postfire grazing utilization. Band-winged densities did not exhibit a consistent response to postfire grazing utilization, which could be affected by their greater mobility given the plot sizes and preference for bare ground (Pfadt, 2002). Although not significant, densities of the abundant species were least with 50% utilization plus fire, with the exception of *A. deorum*. After grazing was initiated, densities of *M. sanguinipes* and *T. kiowa* were lower with 50% utilization than nongrazed, nonburned controls, indicating the reductions were only expressed by fire plus grazing. Strong density-dependent food limitation was not expected with the low densities observed. Current-year plant production did not differ among utilization treatments during the drought for Experiment 1, whereas biomass declined with increasing utilization in Experiment 2, which was preceded by a wet spring (Vermeire et al., 2014). Postfire grazing utilization reduced forb biomass, particularly in year 2 of Experiment 1 and year 1 of Experiment 2 (Vermeire et al., 2014), indicating mixed feeding species such as *M. sanguinipes* could be affected by food limitation from grazing utilization. Lack of an interaction for *M. sanguinipes* with time period matched the sustained effect of grazing on forbs (Vermeire et al, 2014). Grazing also opens up the canopy and might allow more effective avian predation in a productive year (Pitt, 1999). As grazing has been shown to increase food limitation with higher grasshopper densities (Branson and Haferkamp, 2014), additional investigation of postfire grazing utilization is necessary.

In the only other study to date in northern mixed prairie examining fire-grazing interactions, fire and grazing interacted to affect grasshopper density and community composition but conclusions were limited by low grasshopper densities (Branson and Sword, 2010). Most effects in this study were direct fire effects, with few interactions between fire and postfire grazing. The relatively weak interaction between fire

and postfire grazing likely results from the dominant effects of fire on *A. deorum* and *O. obscura* densities, combined with the low grasshopper densities. These results differ from the vegetation data collected as part of this experiment, where fire-grazing treatment and time since fire interacted on most biomass components (Vermeire et al., 2014). Similar to these results, in tallgrass prairie both fire and grazing directly affected grasshopper densities but no interactions were evident (Joern, 2004).

Precipitation differed between the experiments and likely affected grasshopper populations independent of treatments. Experiment 1 had near-average precipitation during the burn year, followed by the second driest spring in 70 yr during the postfire grazing year (Vermeire et al., 2011, 2014). The Experiment 2 burn occurred during the drought, with postfire grazing occurring during the fifth wettest spring in 70 yr. Precipitation had a stronger effect on productivity than either fire or postfire grazing, with five times greater postfire grass production in Experiment 2 than Experiment 1 (Vermeire et al, 2011, 2014). Low production during drought likely led to a reduction in grasshopper densities from 2004 to 2005, with late summer drought conditions in the northern Great Plains frequently limiting survival and reproduction (Branson, 2008; Branson and Haferkamp, 2014). The strongly contrasting weather conditions between Experiments 1 and 2 were informative, as with 2 similar years study implications would have been limited to a narrow range of growing conditions.

Grasshopper populations were more strongly affected by late summer fire than postfire grazing while densities were low and impacted by a severe drought. Joern (2004) and Branson et al. (2006) argued that a better understanding of grazing and fire impacts is needed to facilitate better grasshopper management. The context dependent effects of fire were likely affected by fire intensity and continuity and species composition. Because populations of the two dominant species, *A. deorum* and *O. obscura*, were nearly eliminated in Experiment 1, more than 1 yr was required for populations to rebound. Previous studies in the northern Great Plains examining fall fire documented only a 1-yr effect on grasshopper densities (Branson, 2005; Branson and Sword, 2010). Grasshopper species-specific responses have constrained the ability to predict population responses following burning (Branson and Vermeire, 2007, 2013; Joern, 2004), with both fire intensity and grasshopper phenology important in determining fire impacts in this study. Fire intensity and continuity should affect whether late summer fire controls populations of *A. deorum*. By contrast, fire timing will likely determine the level of control for species laying deeper egg pods, such as *O. obscura*. Based on the response of the late hatching species *O. obscura* to a late August fire, burning earlier would likely reduce egg production for additional species. As fire strongly reduced already low grasshopper densities, effects of postfire grazing utilization rates on grasshopper populations could differ during periods of higher grasshopper densities. In addition, since late season fire effects in this study were driven by two species, impacts could be weaker with a different species complex. The responses in this study differ from those observed in mesic tallgrass prairies and other systems, which extends the understanding of how fire and grazing affect grasshopper populations.

Management Implications

Late season fires are the most common natural fire timing in the northern Great Plains, in contrast to managed spring burning in tallgrass prairie. Late summer fire appears to be a useful management tool to reduce populations of some grasshopper species in the northern Great Plains, while other species appear more responsive to food limitation from increased postfire grazing utilization. Knowledge of grasshopper species composition, standing biomass at the time of fire, and the timing of fire relative to grasshopper phenology, are likely required to allow managers to accurately predict impacts on grasshoppers (Branson and Vermeire, 2007, 2013; Branson et al., 2006). As reductions in grasshopper populations were sustained for 2 yr postfire, late summer fire can provide extended grasshopper control in the northern Great Plains.

Vermeire et al. (2011, 2014) observed fire led to a reduction of non-native plants and increased native grass production, indicating that late season fire can have complementary positive effects on both grass production and grasshopper control. Although widespread burning of rangeland to deal with a current outbreak is unlikely to be practical for the control of grasshoppers, incorporating a system of rotating fire among pastures and years to dampen the potential for outbreaks in the first place may be an option. To allow generalized management recommendations, additional research is needed examining effects of the seasonal timing of fire on grasshopper populations in the northern Great Plains.

Acknowledgments

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