

Attracted by higher crude protein, grasshopper abundance and offtake increase after prescribed fire*

Nicholas Gregory Heimbuch^{1*}, Devan Allen
McGranahan², Carissa L. Wonkka³, Lance T. Vermeire²
and David H. Branson³

^{1*}University of Pittsburgh, 4200 Fifth Ave, Pittsburgh, 15260,
Pennsylvania, USA.

²USDA Agricultural Research Service, Livestock & Range
Research Laboratory, 243 Ft. Keogh Rd., Miles City, 59301,
Montana, USA.

³USDA Agricultural Research Service, Northern Plains
Agricultural Research Laboratory, 1500 N Central Ave, Sidney,
59270, Montana, USA.

*Corresponding author(s). E-mail(s): ngh11@pitt.edu;

Contributing authors: Devan.McGranahan@usda.gov;

Carissa.Wonkka@usda.gov ; Lance.Vermiere@usda.gov;

Dave.Branson@usda.gov ;

* Author contributions: *This Highlighted Student Paper represents a novel approach to both fire-grazing interaction research—by focusing on invertebrate herbivores in an ungulate-dominated ecosystem—and research on fire effects on grasshoppers—most grasshopper research focuses on direct fire effects on grasshopper mortality.* NGH collected data. NGH and DAM analyzed data. NGH wrote the initial draft of the paper, which DAM and CLW edited with input from LV and DB. LV was responsible for the prescribed fire treatments from which data were collected. DB provided grasshopper expertise and sampling equipment.

Abstract

Grasshoppers are critical components of open ecosystems, such as grasslands and savannas, worldwide. While often seen as pest species competing with domestic livestock for forage resources and damaging crops, many species never reach abundances that result in economic damage and can provide essential ecosystem services. Grasshopper population and community dynamics are modulated by the processes that determine plant structural and community dynamics in a given ecosystem; in open ecosystems, fire is one of the most ubiquitous. This study examined how indirect fire effects (improved forage quality) affect the density of and offtake by grasshoppers at two different times since fire and in unburned plots. Both offtake and density were significantly higher in burned plots compared to unburned plots. Burned plot grasshopper density increased over time, with greater rates of increase in recently burned plots, while density remained constant in unburned locations. These density and offtake patterns appear to be the result of higher crude protein content in burned plots, on account of them having a much higher proportion of recent growth after fire removed aboveground senesced material. These findings present a mechanism by which fire interacts with grasshopper abundance and distribution in open ecosystems. Long term assessments of fire and its interaction with grazing and weather patterns are necessary to determine if attraction to and consumption of post-fire vegetation will result in greater performance of pest grasshopper species or enhance community diversity, regulating pest species outbreaks.

Keywords: Fire-grazing interaction; Magnet effect; Orthoptera: Acrididae; Prescribed fire; Pyric herbivory; Rangeland forage quality; Rangeland pest management

Introduction

As globally-ubiquitous herbivores, grasshoppers (Orthoptera: Acrididae) contribute to ecosystem function around the world. Historically, interest in grasshoppers has generally increased with their local density, as grasshopper outbreaks and locust swarms have wrought economic damage for centuries (Cease et al, 2015). While such outbreaks were long considered to be primarily driven by environmental conditions beyond human control, research has described close interactions between land management and grasshopper dynamics (Le Gall et al, 2019). Although the utility of this broader understanding of grasshoppers and human land use has mostly been realized within the context of pest control (Branson et al, 2006), grasshoppers also contribute to ecosystem dynamics including nutrient cycling and plant community composition (Meyer et al, 2002; Zhang et al, 2011; Kietzka et al, 2021; Belovsky and Slade, 2000).

Grasshoppers are particularly important in *open ecosystems*—rangeland biomes such as grasslands and savannas because herbaceous plant communities are regulated by frequent disturbances and their interaction, especially herbivory and fire (Bond, 2022). Interactions between grasshoppers, fire, and other herbivores drive interconnected plant, nutrient, and soil microbial dynamics, impacting ecosystem services derived from open ecosystems. For instance, grasshoppers are widely seen as pests in competition with economically-valuable livestock for herbaceous primary productivity (Zhang et al, 2019). Hewitt and Onsager (1983) estimated

4 *Rangeland grasshoppers and prescribed fire*

grasshoppers consume nearly US\$400 million (US\$1.7 billion
inflation-adjusted) worth of livestock forage per year in the western United
States. Meanwhile, fire interacts with grasshoppers via direct and indirect
effects, which are variable among species depending on their biology (e.g.
[Vermeire et al, 2004](#)). Direct effects include mortality of adults and eggs from
heat exposure, while indirect effects include alterations to host plant
availability, vegetation structure, and microclimate. Thus the fire-grasshopper
interaction also has implications for grasshopper-livestock competition.

Because the nutritive value of vegetation in open ecosystems often varies
depending on the time since it last burned, fire likely also affects
grasshoppers by modulating their food resources. Perennial, fire-adapted
plants resprout using energy stored in organs protected from heat damage,
and post-fire plant tissue is typically higher in crude protein and lower in
structural carbohydrates than the mature or senescent tissue that was
consumed by the fire ([McGranahan and Wonkka, 2021](#)). Thus, despite overall
lower plant biomass on account of the fire, grasshopper abundance on
recently-burned areas is often higher than unburned areas, especially for
graminivorous (grass-eating) species ([Meyer et al, 2002](#)). More broadly,
post-disturbance succession and plant nutritive value have been identified as
important factors in grasshopper abundance ([Fartmann et al, 2012](#); [Schirmel
et al, 2019](#)). Yet explicit examinations between time-since-fire, plant nutritive
value, and grasshopper abundance have not been conducted.

We measured grasshopper abundance and forage consumption, along with
grass protein content, in a replicated experiment that created a
time-since-fire gradient in temperate grassland. Because grasshoppers are
morphologically capable of much more precise herbivory than most
vertebrate grazers, we measured protein content of grass leaves and stems

separately. We predicted that more-recently burned plots would have both higher protein content—especially in leaves—and greater grasshopper abundance. As such, we predicted a greater degree of vegetation removal by grasshoppers from recently-burned plots, as determined by comparing aboveground plant biomass against that from within grasshopper exclosures.

Methods

Study location & design

Our study was conducted at the USDA-Agricultural Research Service Livestock and Range Research Laboratory in Miles City, Montana, USA (46.40 N, 105.95 W). Vegetation is typical mixed-grass prairie, and the study site was dominated by western wheatgrass *Pascopyrum smithii*. The overwhelming majority of grasshoppers on the study site, as determined by mid-season sweep netting and identification at the USDA-ARS Pest Management Research Unit in Sidney, Montana, consisted of the migratory grasshopper *Melanoplus sanguinipes*, a native species of spur-throated grasshopper in the family Acrididae.

Within a larger prescribed fire experiment, we selected nine, 300-m² plots to test three different time-since-fire treatments (n=3 each): Fire the previous autumn, fire the previous spring, and a control treatment left unburned for several years. Livestock were excluded from the entire study area and had been for several years. While the study area was open to wildlife such as deer *Odocoileus* spp., pronghorn *Antilocapra americana*, and lagomorphs including *Sylvilagus floridanus* and *Lepus* spp, we observed no evidence of their presence on any plots during the sampling period.

Sample collection

To measure the amount of vegetation removed by foraging grasshoppers, we established two pairs of sample points within each plot. Each pair of 0.25-m² sample points consisted of one full mesh grasshopper enclosure alongside another structure with a similar footprint and shade factor that was open to grasshopper herbivory. Each type of structure consisted of a polyvinyl chloride tube frame with heavy nylon netting, which when fully wrapped and zipped around the frame and weighted down with sand-filled tubes, effectively kept grasshoppers out (Parker and Salzman, 1985). Because the mesh reduced sunlight intensity by 400 w m⁻² compared to the surrounding area, we designed control structures that remain open on the north and south faces to allow grasshoppers to enter while still producing shade conditions that matched the enclosures during peak photosynthetic activity. These paired structures ensured that shade would not influence grass development, skewing offtake measurements. Structures were monitored at least every 48 hr and after any substantial weather event to ensure they remained intact; in the few instances grasshoppers had crawled under the enclosures, they were removed upon discovery.

On all plots, the first pair of structures was established 1 July 2021, and the second pair 1 week later. On 9 August—40 d after the first pair of structures were erected—all aboveground biomass, standing dead and current year's growth, within each 0.25 m² frame footprint was clipped to ground level. Within the recently-burned plots, individual grass tiller counts were recorded—because structures were placed randomly and tiller density was observed to be variable, we prepared to express biomass on both a per-tiller basis as well as by area. Clipped biomass was dried at 60°C for 48 hr and weighed to the nearest 0.001 g.

We collected forage quality samples on the 26th day of the study, roughly halfway through the study period. For each plot, samples were comprised of 40 western wheatgrass tillers randomly selected by tossing a marker flag in the air and clipping, to ground level, the tiller nearest to where it landed, regardless of phenology or live/dead status. Tillers were separated into leaf blades and stems (which included leaf sheaths) prior to drying at 60°C for 48 hr and grinding into fine powder. Protein content was determined with a Thermo Scientific Flash 2000 combustion analyzer.

To determine grasshopper density, we employed a standard ring count methodology (Onsager, 1977; Joern and Laws, 2013). One week after the initial pairs of structures were established, we placed 5, 0.1 m² rings on the ground in a \times pattern centered on each plot, with rings approximately 1.5 m apart and at least 2 m from plot edges. Nineteen observations were made over the course of the study period, between 9 July and 6 August. All plots were sampled in each round of observations by a single observer (N.G.H.), and all observations were conducted between 1000 and 1200 for consistent solar conditions. Sampling consisted of walking slowly through the plot and agitating the area near each ring with a long stick, and recording the number of grasshoppers that jumped from the ring.

Data analysis

To determine whether accessibility to grasshoppers affected the amount of aboveground vegetation, we subtracted the dried biomass values from control structures from that of their paired grasshopper exclosures and calculated the mean of these two differences for each plot ($n = 3$ experimental units per treatment). To account for the different lengths of deployments among the two pairs of structures, offtake was expressed as daily rate of removal by dividing

the difference in biomass between paired structures by the number of days each structure pair was deployed. We used a linear model with the intercept term removed to test each of the three difference values against 0 (null hypothesis: no difference in standing crop between grasshopper exclosures and control frames) using the `lm` function in the R statistical environment (R Core Team, 2020). We tested pairwise contrasts in standing crop differences across each treatment with a post-hoc Tukey test using `TukeyHSD`.

We determined whether crude protein content varied with fire treatment and plant organs (leaf blades vs. stems) by fitting each term and their interaction in an ANOVA. Pairwise contrasts among fire treatments were again tested with `TukeyHSD`.

To determine if there were general linear trends in grasshopper abundance patterns over the course of the study, we conducted a nonparametric test of the Kendall's tau (τ) statistic fit to the grasshopper count data within each burn treatment using the `kendallTrendTest` function in the *EnvStats* package for R (Millard, 2013). To compare the relative rates of change over the study period, we plotted the estimated slope of the trend for each burn treatment and the associated 95% confidence intervals as returned by `kendallTrendTest`.

Results

Overall, aboveground plant biomass was lower outside of exclosures in both fire treatments ($64 \pm 4\%$ less in fall burn plots and $55 \pm 9\%$ less in spring burn plots), but did not differ between exclosures and accessible unburned plots ($1 \pm 8\%$). Biomass removal by grasshoppers accounted for statistically-significantly lower biomass outside of grasshopper exclosures in both fall and spring burns ($t = -7.6$, $P < 0.001$ and $t = -6$, $P < 0.001$, respectively). But

there was no difference in offtake among spring and fall burns ($P > 0.05$), with grasshoppers removing approximately $1.0 (\pm 0.2) \text{ kg ha}^{-1} \text{ d}^{-1}$ in each (Fig. 1). Aboveground biomass was not different between grasshopper exclosures and areas accessible to grasshoppers in unburned plots ($t = -0.12$, $P > 0.05$). Offtake was significantly lower in unburned plots than plots burned in both the previous fall and spring ($P < 0.01$ and $P = 0.01$, respectively).

Crude protein content varied among the fire treatments ($t = 57$, $P < 0.001$; Fig. 2). Crude protein content in fall and spring burns averaged $6.4\% \pm 0.2 \text{ s.e.}$ and did not differ from one another ($P > 0.05$). But crude protein content in unburned plots—which included a substantial amount of senesced material from previous growing seasons—was lower than in both fall and spring burns plots ($t = -2.7$, $P < 0.001$ and $t = -3.1$, $P < 0.001$, respectively).

Across all samples, crude protein content did not vary among leaves and stems ($t = 2.7$, $P > 0.05$). Despite a trend towards higher crude protein in leaf tissue in unburned plots (Fig. 2), the pattern was not influential enough to create a significant fire treatment \times organ interaction ($t = 2.1$, $P > 0.05$).

Grasshopper abundance was similar across plots at the beginning of the study period (early July) but increased significantly over the next month in fall and spring burn plots ($\tau = 0.29$, $P < 0.01$ and $\tau = 0.62$, $P < 0.001$; Fig. 3). Grasshopper abundance remained constant over the study period in unburned plots ($\tau = 0.039$, $P > 0.05$). While grasshopper abundance increased in both burn treatments, the rate of increase was approximately three times greater in plots that had been most recently burned in the spring than those that had been burned in the previous fall (Fig. 3, *bottom*), which represented more than a five-fold increase in density from approximately 5 to 25 grasshoppers m^{-2} (Fig. 3, *top*).

Discussion

Insect herbivore abundance and distribution are extremely spatially and temporally variable (Cappuccino and Price, 1995). This variability is often tied to variability in plant biomass and nutrient content (Joern et al, 2012). Insect herbivores often select plant species or suites of species based on specific nutritional needs (Ibanez et al, 2013; Behmer and Joern, 2008) and will actively seek a diet that contains a specific ratio of nutrients (Behmer, 2009). Therefore, the distribution of plant nutritional quality on the landscape can be a strong determinant of grasshopper abundance and distribution (White, 2012; Joern et al, 2012; Ozment et al, 2021).

In the present study, grasshoppers removed over half of available biomass over the study period in burned plots but had no detectable effect in unburned plots. This is likely related to crude protein content which was elevated in burned plots and the resultant increase in grasshopper abundance over time in plots that had been burned in either the spring or previous fall. Grasshoppers in other systems have been shown to select burned vegetation: grasshoppers feeding in willow selected resprouting burned willow shoots, consuming them completely, while rejecting unburned willow after a taste (Stein et al, 1992) and in the Brazilian Cerrado, leaf chewing insects including grasshoppers selected resprouting burned shrubs, causing 30-60 percent greater damage to resprouting leaves than unburned leaves (Lopes and Vasconcelos, 2011).

Time since last fire is a driver of spatial and temporal variability in the distribution of plant nutritional quality. Resprouting plant tissues typically have higher protein content than their mature counterparts on account of having a lower proportion of structural carbohydrates (McGranahan and Wonkka, 2021). At the stand level, fire removes low-quality, senesced material from previous season's growth, allowing high-quality regrowth to dominate

the sward. This elevated protein content in burned areas can be maintained over longer periods by repeated grazing (Wanchuk et al, 2021), even during drought (Spiess et al, 2020). Higher nutritional quality attracts herbivores to an area after fire and they maintain the high nutritional quality by remaining in that area to continue consuming high quality plant tissues that must then regrow and this feedback has been documented for a range of herbivores in open ecosystems worldwide (Allred et al, 2011; Archibald et al, 2005; Sensenig et al, 2010). The dominant grasshopper species in our plots, *Melanoplus sanguinipes*, shows preference for current year's growth and standing dead material makes up only a small proportion of its diet (Anderson and Wright, 1952; Mulkern et al, 1962). In the present study, burned plots with overall higher crude protein content as a result of higher proportions of resprouting, green tissue, attracted *M. sanguinipes* from surrounding unburned vegetation.

In this study, the rate of increase in grasshopper abundance was greater in spring burn plots, which were burned most recently. Although there were no differences in absolute abundance between fall and spring burn plots, the differences in rate of increase over the course of the study suggests that divergence of grasshopper abundance between spring and fall burned plots likely became significant by the end of the growing season. This points to a fire-grazing nutrient feedback —the most recently burned plots maintained that strong feedback over the course of the study while the attraction was not as strong to fall burn plots. Crude protein content did not differ between fall and spring burn plots at the time it was measured —halfway through the study in mid July. However, given the differential rate of increase in spring and fall burn plots, crude protein between those treatments likely diverged later in the growing season, along with grasshopper abundances.

Grasshopper population dynamics and resultant community composition are impacted by many drivers simultaneously. In addition to plant nutritional status, predation risk (Schmitz et al, 1997), dispersal limitation (Hawlena and Schmitz, 2010), and microclimatic conditions (Bauer and Kenyeres, 2007; Gardiner and Dover, 2008) are strong determinants of grasshopper dynamics. Because of the role it plays in each of these, vegetation structure often correlates with grasshopper distribution and density, although the strongest correlations have occurred in highly productive grasslands such as tallgrass prairies (Joern, 2004). In the present study, fire altered both vegetation nutritional status and structure, making it difficult to parse which drove increases in grasshopper abundance. And both likely play some roll in driving grasshopper habitat selection. The dominant species found during our study has been shown to respond positively to nitrogen in this ecosystem (Branson, 2003). In addition, grasshoppers showed similar attraction to high nutrient grazing lawns in tallgrass prairie (Ozment et al, 2021). While there is a similar conflation of structure and nutrient content to that in the present study, they found the attraction weaker when the nutritional contrast between grazing lawns and surrounding areas lessened during drought, supporting nutritional quality as an important driver. Regardless of the mechanism, recently burned plots clearly attracted more grasshoppers and subsequently had more aboveground biomass removal than unburned plots, which has potential implications for management.

Because grasshoppers can be economic pests in grasslands used for livestock production when at high densities, improved survival and reproduction resulting from nutrient enhancement in burned vegetation (Branson, 2003) could intensify competition between livestock and grasshoppers in burned areas. Loss of livestock forage to grasshoppers is

most problematic during grasshopper outbreaks or during droughts, when plant productivity is low (Belovsky and Slade, 1995; Joern, 2000; Branson and Haferkamp, 2014). The dominant grasshopper at our study area, the migratory grasshopper *Melanoplus sanguinipes*, is commonly viewed as one of the most frequent economic pest species in the central and western US, making it especially damaging to farmers and ranchers throughout the Great Plains (Onsager, 2000; Olfert et al, 2021). However, many grasshopper species do not cause economic harm and instead enhance ecosystem service delivery by increasing nutrient cycling, providing food for rangeland wildlife, exerting some control over unwanted rangeland plants, and in some cases increasing overall rangeland productivity (Branson et al, 2006). In addition, greater grasshopper diversity can reduce the likelihood of pest species outbreaks as beneficial grasshoppers compete for resources and enhance the efficacy of grasshopper predators (Branson et al, 2006). Fire at appropriate scales could enhance diversification of grasshopper communities because they exhibit a breadth of species-specific habitat requirements and fire can enhance structural and nutritive heterogeneity in vegetation.

Gains in grasshopper performance from nutritive enhancement could be offset by negative fire effects, as fire alone can result in short-lived reductions in grasshopper abundance by up to 75% (Branson and Vermeire, 2016), although the effects are often short-lived. Direct effects of fire include adult and nymphal mortality (Bock and Bock, 1991), and egg mortality due to soil heating (Branson and Vermeire, 2013, 2016; Vermeire et al, 2004). Indirect effects related to microclimate, soil properties, and plant community compositional changes can also alter grasshopper abundance in burned areas (Van Wingerden et al, 1991; Schirmel et al, 2011; Evans et al, 1983; Matenaar et al, 2014; Meyer et al, 2002), although other drivers, such as

livestock grazing, likely interact with fire in most grasslands (McGranahan
and Wonkka, 2021; Fuhlendorf et al, 2009; Joern, 2005). Given these
wide-ranging impacts on diversity and mortality, fire could be a sustainable
low-cost alternative to conventional control of economically-damaging
grasshopper outbreaks —broad-scale chemical applications (Branson et al,
2006), which are expensive, unreliable, and have non-target effects on
beneficial arthropods. In addition, ecosystem services provided by non-pest
grasshopper species are lost when insecticides are used to control grasshopper
outbreaks (Joern, 2000). Longer-term assessment of grasshopper dynamics in
burned and unburned areas is needed to determine the potential for fire to
reduce outbreaks of economically damaging grasshopper species.

Future research should also assess the impacts of fire at larger scales and
the interaction of fire with other disturbances such as drought and livestock
grazing. Grasshopper responses observed in this study likely reflect
movement patterns and attraction to burned plots, which might differ at
large scales. Studies of fire-herbivore feedbacks at multiple scales show that
small-scale fires result in positive feedbacks, creating grazing hotspots with
high crude protein for long durations, similar to our findings here (Cromsigt
and Olff, 2008). In contrast, large-scale fires can result in more dispersed
herbivore distribution that can homogenize plant nutritional status and
structure as grazing pressure is dispersed, resulting in more ungrazed areas
within a burn perimeter that do not maintain high nutrient content
(Archibald et al, 2005) and lessening the attraction of the burned area to
herbivores (Donaldson et al, 2018). However, it is uncertain whether
heterogeneity in protein content distribution within a broader fire could
result in the creation of similar small-scale nutrient hotspots in the presence
of grasshoppers or if the additional grazing pressure from grasshoppers could

enhance livestock attraction to burned areas at larger scales. Regardless of scale, livestock grazing-fire interactions (Onsager, 2000; O'Neill et al, 2003) and drought likely play a role in fire-grasshopper dynamics by either enhancing or diminishing contrast in protein content between unburned and burned vegetation (Augustine and Derner, 2014; Yoganand and Owen-Smith, 2014; Ozment et al, 2021), and our findings suggest that this contrast is an important driver of grasshopper distribution and offtake.

Acknowledgments. We appreciate the general assistance of D.F. Watson from NPARL in organizing field equipment, the assistance of Cheryl Murphy, with protein analysis at LARRL, and Nicole Davidson, with grasshopper identification at NPARL.

Conflict of Interest. The authors declare that they have no conflict of interest.

Funding. NGH received salary support from the USDA-ARS Plains Area co-funded internship with matching funds from LARRL and NPARL.

Ethics statement. This article does not contain any studies with human participants or animals performed by any of the authors.

Availability of data and code. Data and R script used herein are available under a U.S. Public Domain license at the USDA Ag Data Commons (doi.org/10.15482/USDA.ADC/1528475).

References

Allred BW, Fuhlendorf SD, Engle DM, et al (2011) Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution* 1(2):132–144. <https://doi.org/10.1002/ece3.12>

Anderson NL, Wright JC (1952) Grasshopper Investigations on Montana Range Lands. Bulletin 486. Bulletin 486, Montana State College Agricultural Experiment Station, Bozeman MT

Archibald S, Bond W, Stock W, et al (2005) Shaping the landscape: Fire–grazer interactions in an African savanna. *Ecological Applications* 15(1):96–109

Augustine DJ, Derner JD (2014) Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. *Journal of Applied Ecology* 51(1):242–250

Bauer N, Kenyeres Z (2007) Seasonal changes of microclimatic conditions in grasslands and its influence on orthopteran assemblages. *Biologia* 62(6):742–748

Behmer ST (2009) Insect Herbivore Nutrient Regulation. *Annual Review of Entomology* 54(1):165–187. <https://doi.org/10.1146/annurev.ento.54.110807.090537>

Behmer ST, Joern A (2008) Coexisting generalist herbivores occupy unique nutritional feeding niches. *Proceedings of the National Academy of Sciences* 105(6):1977–1982. <https://doi.org/10.1073/pnas.0711870105>

Belovsky G, Slade J (2000) Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences* 97(26):14,412–14,417

Belovsky GE, Slade JB (1995) Dynamics of two Montana grasshopper populations: Relationships among weather, food abundance and intraspecific competition. *Oecologia* 101(3):383–396. <https://doi.org/10.1007/BF00328826>

- Bock CE, Bock JH (1991) Response of grasshoppers (Orthoptera: Acrididae) to wildfire in a Southeastern Arizona grassland. *The American Midland Naturalist* 125(1):162–167. <https://doi.org/10.2307/2426379>
- Bond WJ (2022) Out of the shadows: Ecology of open ecosystems. *Plant Ecology & Diversity* pp 1–18. <https://doi.org/10.1080/17550874.2022.2034065>
- Branson DH (2003) Reproduction and survival in *Melanoplus sanguinipes* (Orthoptera: Acrididae) in response to resource availability and population density: The role of exploitative competition. *The Canadian Entomologist* 135(3):415–426
- Branson DH, Haferkamp MA (2014) Insect herbivory and vertebrate grazing impact food limitation and grasshopper populations during a severe outbreak. *Ecological Entomology* 39(3):371–381. <https://doi.org/10.1111/een.12114>
- Branson DH, Vermeire LT (2013) Heat Dosage and Oviposition Depth Influence Egg Mortality of Two Common Rangeland Grasshopper Species. *Rangeland Ecology & Management* 66(1):110–113. <https://doi.org/10.2111/REM-D-11-00187.1>
- Branson DH, Vermeire LT (2016) Grasshopper responses to fire and post-fire grazing in the Northern Great Plains vary among species. *Rangeland Ecology & Management* 69(2):144–149
- Branson DH, Joern A, Sword GA (2006) Sustainable Management of Insect Herbivores in Grassland Ecosystems: New Perspectives in Grasshopper Control. *BioScience* 56(9):743–755. [https://doi.org/10.1641/0006-3568\(2006\)56\[743:SMOIHJ\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[743:SMOIHJ]2.0.CO;2)

Cappuccino N, Price PW (1995) Population Dynamics: New Approaches and Synthesis. Academic Press, SanDiego, CA, USA

Cease AJ, Elser JJ, Fenichel EP, et al (2015) Living With Locusts: Connecting Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets. *BioScience* 65(6):551–558. <https://doi.org/10.1093/biosci/biv048>

Cromsigt JP, Olff H (2008) Dynamics of grazing lawn formation: An experimental test of the role of scale-dependent processes. *Oikos* 117(10):1444–1452

Donaldson JE, Archibald S, Govender N, et al (2018) Ecological engineering through fire-herbivory feedbacks drives the formation of savanna grazing lawns. *Journal of Applied Ecology* 55(1):225–235. <https://doi.org/10.1111/1365-2664.12956>

Evans EW, Rogers RA, Opfermann DJ (1983) Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: Night trapping vs. sweeping. *Environmental Entomology* 12(5):1449–1454

Fartmann T, Krämer B, Stelzner F, et al (2012) Orthoptera as ecological indicators for succession in steppe grassland. *Ecological Indicators* 20:337–344. <https://doi.org/10.1016/j.ecolind.2012.03.002>

Fuhlendorf SD, Engle DM, Kerby J, et al (2009) Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. *Conservation Biology* 23(3):588–598. <https://doi.org/10.1111/j.1523-1739.2008.01139.x>

Gardiner T, Dover J (2008) Is microclimate important for Orthoptera in open landscapes? *Journal of Insect Conservation* 12(6):705–709

- Hawlena D, Schmitz OJ (2010) Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences* 107(35):15,503–15,507
- Hewitt GB, Onsager JA (1983) Control of grasshoppers on rangeland in the United States—a perspective. *Journal of Range Management* 36(2):202–207
- Ibanez S, Manneville O, Miquel C, et al (2013) Plant functional traits reveal the relative contribution of habitat and food preferences to the diet of grasshoppers. *Oecologia* 173(4):1459–1470
- Joern A (2000) What are the consequences of non-linear ecological interactions for grasshopper control strategies? In: Lockwood JA, Latchininsky AV, Sergeev MG (eds) *Grasshoppers and Grassland Health: Managing Grasshopper Outbreaks without Risking Environmental Disaster*, NATO Science Series, vol 73. Springer, Dordrecht, p 131–144
- Joern A (2004) Variation in Grasshopper (Acrididae) Densities in Response to Fire Frequency and Bison Grazing in Tallgrass Prairie. *Environmental Entomology* 33(6):1617–1625. <https://doi.org/10.1603/0046-225X-33.6.1617>
- Joern A (2005) Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86(4):861–873. <https://doi.org/10.1890/04-0135>
- Joern A, Laws AN (2013) Ecological Mechanisms Underlying Arthropod Species Diversity in Grasslands. *Annual Review of Entomology* 58(1):19–36. <https://doi.org/10.1146/annurev-ento-120811-153540>

Joern A, Provin T, Behmer ST (2012) Not just the usual suspects: Insect herbivore populations and communities are associated with multiple plant nutrients. *Ecology* 93(5):1002–1015

Kietzka GJ, Lecoq M, Samways MJ (2021) Ecological and Human Diet Value of Locusts in a Changing World. *Agronomy* 11(9). <https://doi.org/10.3390/agronomy11091856>

Le Gall M, Overson R, Cease A (2019) A Global Review on Locusts (Orthoptera: Acrididae) and Their Interactions With Livestock Grazing Practices. *Frontiers in Ecology and Evolution* 7

Lopes CT, Vasconcelos HL (2011) Fire increases insect herbivory in a Neotropical savanna. *Biotropica* 43(5):612–618

Matenaar D, Bröder L, Bazelet CS, et al (2014) Persisting in a windy habitat: Population ecology and behavioral adaptations of two endemic grasshopper species in the Cape region (South Africa). *Journal of Insect Conservation* 18(3):447–456. <https://doi.org/10.1007/s10841-014-9654-4>

McGranahan DA, Wonkka CL (2021) *Ecology of Fire-Dependent Ecosystems: Wildland Fire Science, Policy, and Management*. CRC Press, Boca Raton, FL

Meyer CK, Whiles MR, Charlton RE (2002) Life History, Secondary Production, and Ecosystem Significance of Acridid Grasshoppers in Annually Burned and Unburned Tallgrass Prairie. *American Entomologist* 48(1):52–61. <https://doi.org/10.1093/ae/48.1.52>

Millard SP (2013) *EnvStats: An R Package for Environmental Statistics*. Springer, New York

Mulkern GB, Anderson JF, Brusven MA (1962) Biology and Ecology of North Dakota Grasshoppers. 1. Food Habits and Preferences of Grasshoppers Associated with Alfalfa Fields. North Dakota Agricultural Experiment Station, Fargo ND

Olfert O, Weiss RM, Giffen D, et al (2021) Modeling Ecological Dynamics of a Major Agricultural Pest Insect (*Melanoplus sanguinipes* ; Orthoptera: Acrididae): A Cohort-Based Approach Incorporating the Effects of Weather on Grasshopper Development and Abundance. Journal of Economic Entomology 114(1):122–130. <https://doi.org/10.1093/jee/toaa254>

O’Neill KM, Olson BE, Rolston MG, et al (2003) Effects of livestock grazing on rangeland grasshopper (Orthoptera: Acrididae) abundance. Agriculture, Ecosystems & Environment 97(1):51–64. [https://doi.org/10.1016/S0167-8809\(03\)00136-1](https://doi.org/10.1016/S0167-8809(03)00136-1)

Onsager JA (1977) Comparison of Five Methods for Estimating Density of Rangeland Grasshoppers. Journal of Economic Entomology 70(2):187–190. <https://doi.org/10.1093/jee/70.2.187>

Onsager JA (2000) Suppression of grasshoppers in the Great Plains through grazing management. Journal of Range Management 53(6):592–602

Ozment KA, Welti EA, Shaffer M, et al (2021) Tracking nutrients in space and time: Interactions between grazing lawns and drought drive abundances of tallgrass prairie grasshoppers. Ecology and Evolution 11(10):5413–5423

Parker MA, Salzman AG (1985) Herbivore Exclosure and Competitor Removal: Effects on Juvenile Survivorship and Growth in the Shrub *Gutierrezia Microcephala*. Journal of Ecology 73(3):903–913. <https://doi.org/10.>

2307/2260156

R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Schirmel J, Mantilla-Contreras J, Blindow I, et al (2011) Impacts of succession and grass encroachment on heathland Orthoptera. *Journal of Insect Conservation* 15(5):633–642

Schirmel J, Gerlach R, Buhk C (2019) Disentangling the role of management, vegetation structure, and plant quality for Orthoptera in lowland meadows. *Insect Science* 26(2):366–378. <https://doi.org/10.1111/1744-7917.12528>

Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78(5):1388–1399

Sensenig RL, Demment MW, Laca EA (2010) Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology* 91(10):2898–2907. <https://doi.org/10.1890/09-1673.1>

Spiess JW, McGranahan DA, Geaumont B, et al (2020) Patch-Burning Buffers Forage Resources and Livestock Performance to Mitigate Drought in the Northern Great Plains. *Rangeland Ecology & Management* 73(4):473–481. <https://doi.org/10.1016/j.rama.2020.03.003>

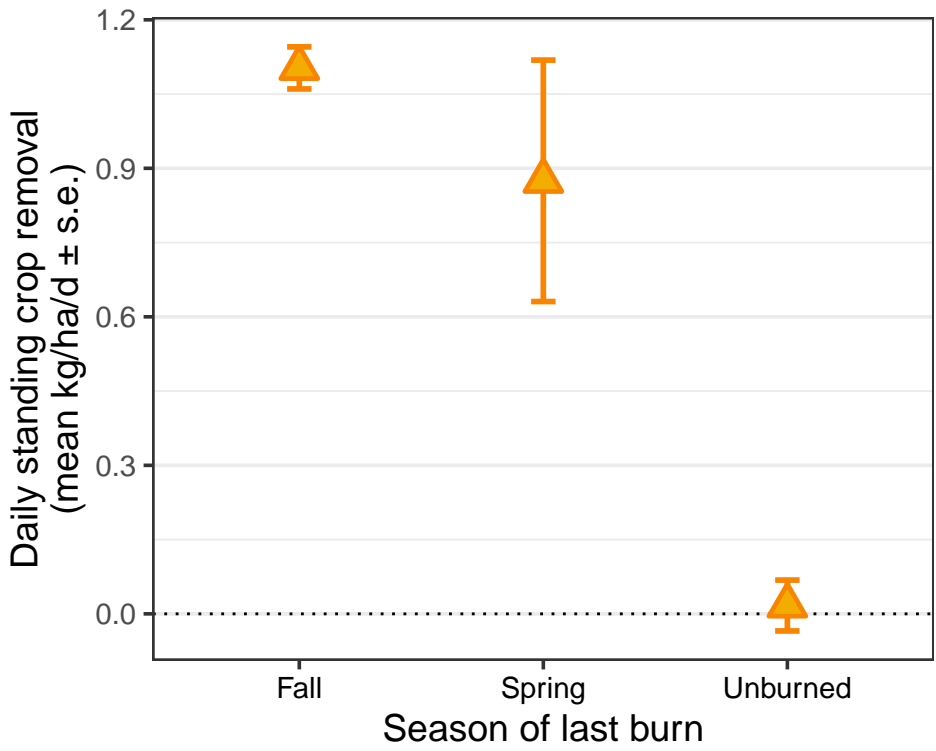
Stein SJ, Price PW, Abrahamson WG, et al (1992) The effect of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk. *Oikos* pp 190–196

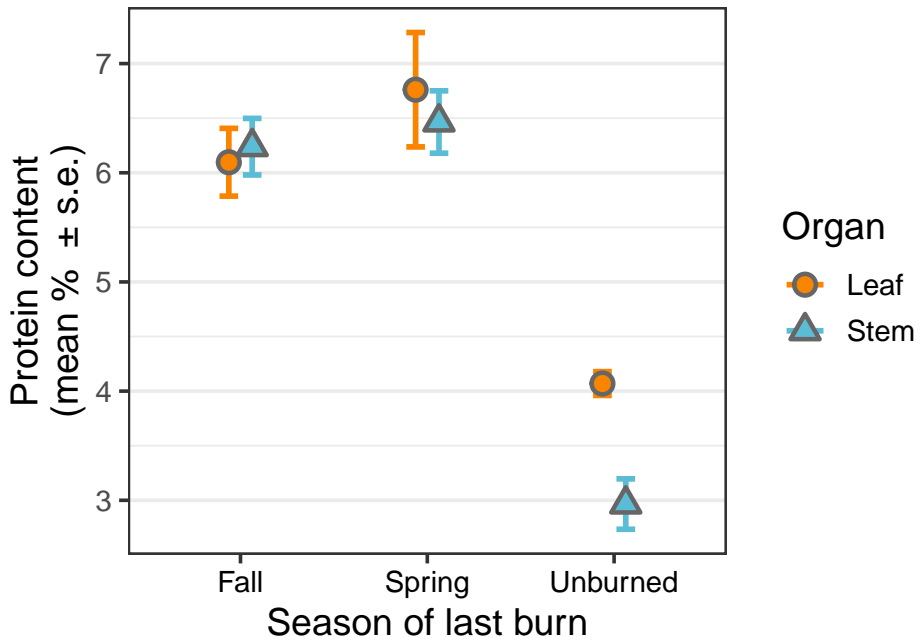
- Van Wingerden W, Musters J, Maaskamp F (1991) The influence of temperature on the duration of egg development in West European grasshoppers (Orthoptera: Acrididae). *Oecologia* 87(3):417–423
- Vermeire LT, Mitchell RB, Fuhlendorf SD, et al (2004) Selective control of rangeland grasshoppers with prescribed fire. *Journal of Range Management* 57(1):29–33. [https://doi.org/10.2111/1551-5028\(2004\)057\[0029:SCORGW\]2.0.CO;2](https://doi.org/10.2111/1551-5028(2004)057[0029:SCORGW]2.0.CO;2)
- Wanchuk MR, McGranahan DA, Sedivec KK, et al (2021) Contrasts in forage mineral concentration with patch-burn grazing: A preliminary analysis. *Translational Animal Science* 5(Supplement_S1):S75–S79. <https://doi.org/10.1093/tas/txab173>
- White TC (2012) *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer Science & Business Media, Berlin, Germany
- Yoganand K, Owen-Smith N (2014) Restricted habitat use by an African savanna herbivore through the seasonal cycle: Key resources concept expanded. *Ecography* 37(10):969–982
- Zhang G, Han X, Elser JJ (2011) Rapid top-down regulation of plant C:N:P stoichiometry by grasshoppers in an Inner Mongolia grassland ecosystem. *Oecologia* 166(1):253–264. <https://doi.org/10.1007/s00442-011-1904-5>
- Zhang L, Lecoq M, Latchininsky A, et al (2019) Locust and grasshopper management. *Annual Review of Entomology* 64(1):15–34. <https://doi.org/10.1146/annurev-ento-011118-112500>

Figure 1 Mean differences in biomass removal rate between grasshopper enclosures and control frames in plots with three different fire treatments. Standing crop was determined by clipping at the end of the four-week study period and differences attributable to grasshopper removal are expressed as mean kg ha⁻¹ day⁻¹.

Figure 2 Mean protein content of western wheatgrass *Pascopyrum smithii* sampled from three burn treatments as a percentage of total dry matter. Orange circles indicate the protein content of leaf blades; blue triangles are stems (which include leaf sheaths).

Figure 3 Observed grasshopper counts per square meter. Orange indicates data taken from fall burn treatments, blue from spring burn treatments, and red from unburned (control) plots. *Bottom* shows data from Kendall's Tau statistic which assessed the observed count trendline consistency over time. Our tau values were compared against the null hypothesis that there was no trend in our data. 95% confidence intervals were calculated to show the possible variance in slope for the data over time. Most grasshoppers observed were the migratory grasshopper *Melanoplus sanguinipes*.

**Fig. 1**

**Fig. 2**

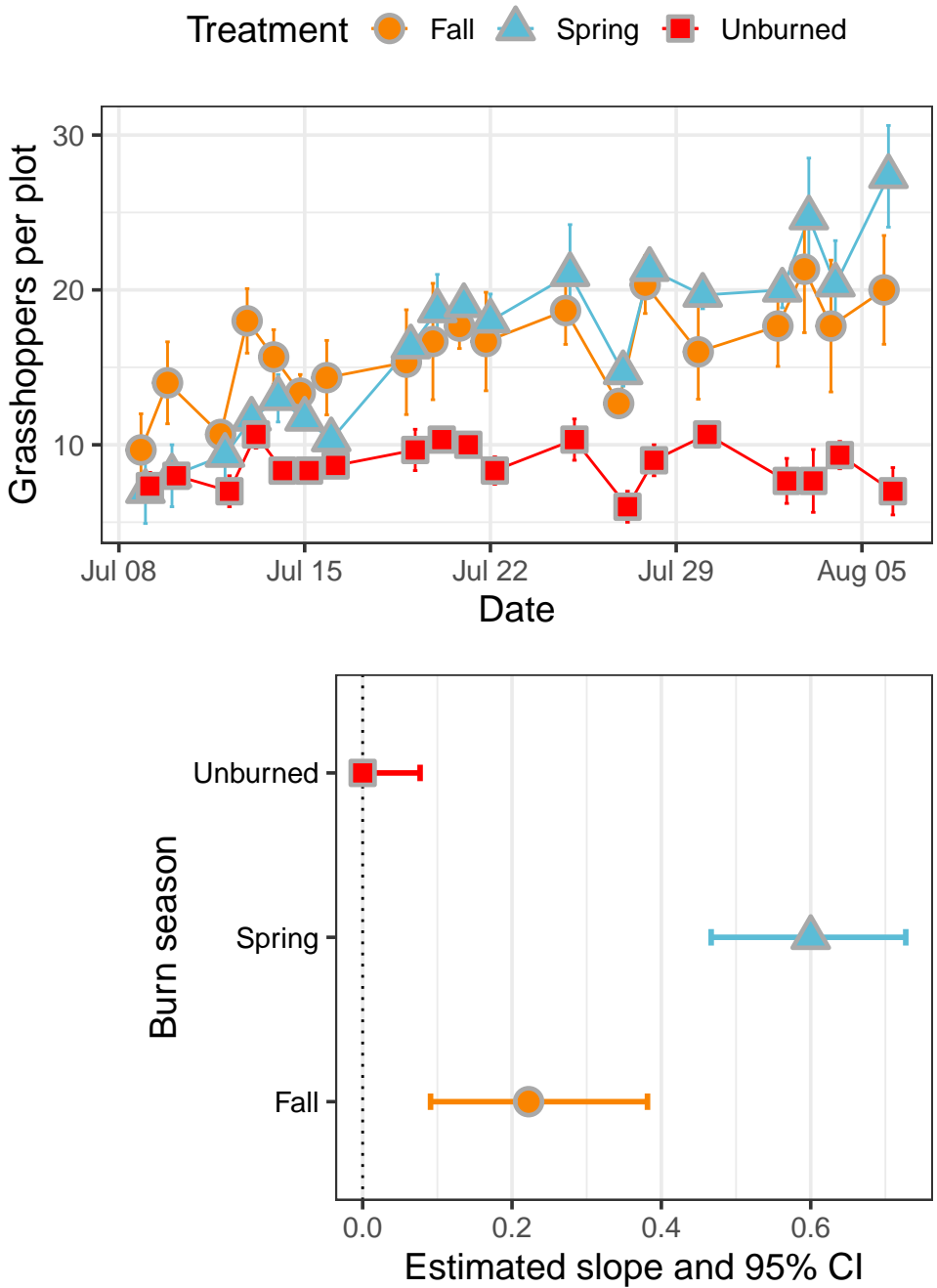


Fig. 3