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

Nicholas Gregory HeimbuchA Devan Allen McGranahanB,D Carissa L. WonkkaC Lance VermeireB David BransonC

A University of Pittsburg, Pittsburg, PA, USA

B USDA Agricultural Research Service, Livestock and Range Research Laboratory, Miles City, MT, USA

C USDA Agricultural Research Service, Northern Plains Agricultural Research Laboratory, Sidney, MT, USA

D Corresponding author. Email: [Devan.McGranahan@usda.gov](mailto:Devan.McGranahan@usda.gov)

# Abstract

Little research has been done to examine the influences of fire and drought on grasshopper herbivory patterns. Climate warming is producing more frequent and more intense droughts in the Northern Great Plains region of the United States, affecting herbivore resource availability and stressing the range ecosystem. This study created three different time since fire treatments to examine how indirect fire effects (improved forage quality) affect the density and offtake of local grasshoppers. Both offtake and density were significantly higher in burned locations compared to unburned control plots. Burned plot grasshopper density increased greatly over time, while density remained constant in unburned locations. These density patterns appear to be the direct result of the high protein content found in burned locations. The results raise further questions into the mechanism that produces the magnet effect in range grasshoppers. These results also highlight the importance of understanding how fire will interact with future climate conditions to affect range herbivore interactions.

# Introduction

Fire and herbivory are interactive ecological disturbances that affect grassland dynamics around the world.

With global climate continuing to warm, rangeland herbivores must adapt to flaring environmental disturbances. Drought and fire are among the most prevalent disturbances occurring in the American Midwest. As anthropogenic climate change continues to shift weather patterns, rainfall in the northern Great Plains is predicted to increase in the spring and fall, with annual droughts developing through summer months (Derner et al. 2018). Aboveground net primary productivity (ANPP) in grassland ecosystems is severely reduced by drought conditions (Hoover et al. 2014). Legacy effects from these droughted summers are not clearly understood on long timescales, giving range herbivores variable forage availability in the years to come (Hoover et al. 2014).

As droughts continue to worsen in summer months, fire will become even more frequent in range ecosystems (Donovan et al. 2017, 2020). In fact, mean wildfire frequency more than tripled from 2005-2014 compared to the previous 9 year mean (Donovan et al. 2017). Despite the ANPP reduction, patch burning treatments are able to buffer the drought losses through improved forage protein content (Spiess et al. 2020). Fire produces a spike in crude protein, the benchmark measurement for forage quality, which then decreases over time (Allred et al. 2011). Even in homogeneous fire regimes, fire still improves protein content and removes accumulated grass detritus, however it can also weaken the biodiversity of the region, creating inconsistent annual forage production (McGranahan et al. 2016).

The effects of these disturbances on rangeland ungulates are well understood. Drought reduces plant biomass and leads to an exodus of herbivores out of the droughted location and into wetter, more productive environments (Trisos et al. 2021). Due to lowered productivity, livestock who are unable to leave the droughted rangeland experience reduced weight gain (Allred et al. 2014). On burned rangeland, ungulate species follow a pyric herbivory feeding pattern, spending more time grazing in burned patches compared to unburned pasture (Fuhlendorf et al. 2009; Parrini and Owen-Smith 2010).

Grasshopper response to fire and drought, on the other hand, still has many open ended questions. Drought depresses reproductive fitness of grasshoppers remaining in warm, droughted locations compared to grasshoppers in undroughted locations (Rosenblatt 2018). Fire’s relationship with herbivorous insect species is more complicated. Large fires can easily kill adult grasshoppers and destroy eggs laid in shallow soil (Branson and Vermeire 2013). Whether grasshoppers experience the same improved growth that livestock experience from burning treatments is still the subject of ongoing research. Grasshoppers prefer high nitrogen content forage to spur growth and development and improve fecundity (Schmitz 2010). While feeding on plants, grasshoppers are able to monitor their protein and carbohydrate intake to maintain ideal nutrient ratios (Behmer and Joern 2008; Behmer 2009). For instance, grasshoppers will choose to forage on plants high in carbon content to increase metabolism and respiratory function (Schmitz 2010). More research is required to understand whether a low nutrient, droughted range ecosystem will produce the same magnet effect on grasshoppers that draws ungulates to recently burned prairie.

We designed this study to determine whether grasshoppers consume more herbaceous biomass in recently-burned grassland with higher nutritive value. We expected that (hypothesis on grasshoppers and fire) and (hypothesis on crude protein and fire). The primary indirect effect examined in this study is the improved forage quality produced after fire events (Allred et al. 2011). Previous research into fire’s effect on grasshopper density have been conducted on relatively large burn areas (Vermeire et al. 2004; Branson 2005). Thus, it is currently unclear how grasshoppers react to and utilize small patches of heightened resource quality within a low quality, droughted landscape. The summer of 2021 was incredibly dry in eastern Montana, producing the necessary droughted forage conditions for us to examine this research question.

# Methods

## Study site and experimental design

Our study was conducted at the USDA Agricultural Research Service’s Livestock and Range Research Laboratory in Miles City, Montana (46°24' N, 105°57' W), within the Northwestern Great Plains ecoregion. The region has a temperate climate with [annual average temps and rainfall] and is dominated by mixed-grass prairie and shortgrass-*Artemisia* sagebrush steppe. The specific study location is on clayey and shallow-silty soils and is dominated by western wheatgrass (*Pascopyrum smithii*) and green needlegrass (*Nassella viridula*). , during the summer of 2021, the migratory grasshopper (Melanoplus sanguinipes). These grasshoppers are frequently responsible for the largest outbreaks, making the migratory grasshopper especially damaging to farmers and ranchers throughout the Great Plains (Onsager and Olfert 2000; Olfert et al. 2021).

We selected nine, 375 m2 plots to test three different time-since-fire treatments with three repetitions each: a fall burn treatment, a spring burn treatment, and an unburned control treatment. These plots were situated in a large ungrazed pasture with a two meter buffer zone between plots. The plots, established in [year], are part of a larger, on-going study on vegetation dynamics in response to seasonality and frequency of prescribed fire [find a paper from Lance from these plots?].

## Data collection

### Grasshopper consumption of standing crop

To measure grasshopper removal of herbaceous vegetation, we established two pairs of exclosures and control frames within each of the 9 different plots around vegetation that reflected the overall grass assemblage of the pasture, avoiding areas of substantial bare ground. Following previous grasshopper herbivory studies, our 0.25 m2 exclosures consisted of a PVC pipe skeleton with heavy nylon netting weighted with sandbags to keep grasshoppers from flying or crawling into the exclosure area (Parker and Salzman 1985). Because the exclosure netting reduced sunlight intensity by 400 w m-2 (as determined by [give model number/relevant info about the LiCor here], 0.25 m2 control structures were constructed from identical PVC frames and covered on three sides with hardware cloth of a mesh size sufficient to produce a similar 400 w m-2 shade effect, which we confirmed with the LiCor. The control structures remained open on the north and south faces to allow grasshoppers access while still producing shaded conditions during peak photosynthesis hours. We erected one pair of exclosure-control structures in each plot on July 1st, and a second pair of structures in each plot on July 7th.

Exclosures were routinely checked for grasshopper breaches with no more than 48 hours elapsing between inspection. One substantial breach occurred 19 days into the experiment timeline, when a storm right after an inspection caused damage to a single exclosure and allowed grasshoppers access to the exclosure for a maximum of two days.

After 40 days, on August 9th, standing crop was measured by clipping to within 2 cm of ground level all aboveground biomass within the 0.25 m2footprint of all structures. During clipping, I counted and recorded individual grass tillers in the burn treatment plots to compare data on per tiller offtake across burn treatments. In the lab, I dried samples at 60C for 48 h and weighed them to the nearest 0.0001 gram.

### Crude protein content

On the 26th day of the study period, roughly halfway through the experiment, I randomly selected 40 tillers of western wheatgrass from each plot by tossing a marker flag in the air and clipping the aboveground biomass of the tiller nearest to where it landed. Tillers were separated into leaves and stems to assess forage quality differences between the two plant organs. I dried the stems and leaves and ground them into fine powders which I then analyzed in a Carbon/Nitrogen analysis machine in the lab.

### Grasshopper density

I assessed grasshopper density on each plot using ring count methodology (Onsager 1977; Joern and Laws 2013). On July 8th, I placed 5, 0.1 m rings on each plot in an “X” shaped pattern, spaced approximately 1.5 m to keep rings away from plot edges but far enough apart to ensure grasshoppers within weren’t disturbed until they could be counted.. Between July 9th and August 6th, abundance on each plot was measured 19 times by a single observer (NGH). Each count consisted of walking slowly through the plot and agitating the area near each ring with a 1 m stick and recorded the number of grasshoppers to leap out from within the ring. All counts were conducted between 1000 and 1200 for consistent solar conditions, and the temperature was recorded at the beginning of each count.

## Data analysis

To determine whether accessibility to grasshoppers affected standing crop, we subtracted the dried biomass values of control frames from that of their paired grasshopper exclosure frames (n = 6 observational units per treatment) and found the mean of these two differences for each plot (n = 3 experimental units per treatment). 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 (leaves 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 () 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

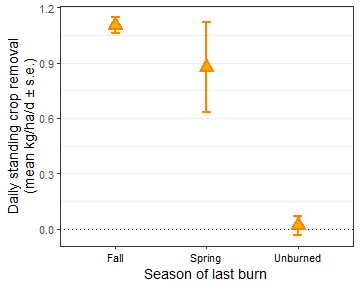


Fig. 1: Mean differences in standing crop between grasshopper exclosures and control frames in plots with three different fire treatments. Standing crop was determined by clipping at the end of the four-week study period and differences attributable to grasshopper removal are expressed as mean kg per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

Standing crop was statistically-significantly lower outside of grasshopper exclosures in both fall and spring burns ( -7.6, < 0.001 and -6, < 0.001, respectively). There was no difference in offtake among spring and fall burns ( > 0.05), with grasshoppers removing approximately 1.0 (± 0.2) kg ha-1 d-1 in each (Fig. 1). Standing crop was not different between grasshopper exclosures and areas accessible to grasshoppers in unburned plots ( -0.12, > 0.05). Offtake was significantly lower in unburned plots than plots burned in both the previous fall and spring ( < 0.01 and = 0.01, respectively).

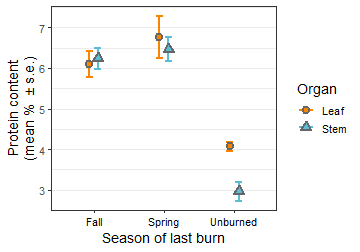


Fig. 2: Mean protein content of western wheatgrass *Pascopyrum smithii* sampled from three burn treatments as a percentage of total dry matter. Red circles indicate the protein content of leaves; blue triangles are stems.

Crude protein content varied among the fire treatments ( 57, < 0.001; Fig. 2). Crude protein content in fall and spring burns averaged 6.4% ± 0.2 s.e. and did not differ among each other ( > 0.05). But crude protein content in unburned plots was lower than in both fall and spring burns plots (-2.7, < 0.001 and -3.1, < 0.001, respectively).

Across all samples, crude protein content did not vary among leaves and stems ( 2.7, > 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 organ interaction ( 2.1, > 0.05).

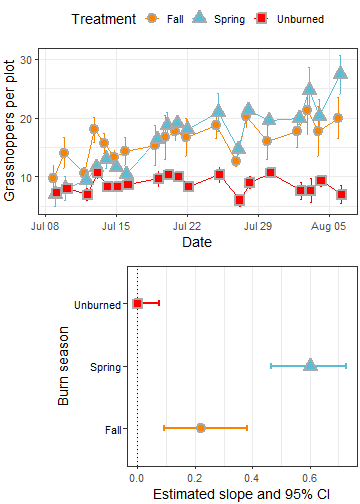


Fig. 3: Observed grasshopper counts on a per square meter basis. Red indicates data taken from fall burn treatments, green is spring burn treatments, and blue is the unburned control treatment count data. Figure 3B shows data from Kendall’s Tau statistic which assessed the observed count trendline consistency 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.

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 ( 0.29, < 0.01 and 0.62, < 0.001; Fig. 3). Grasshopper abundance remained constant over the study period in unburned plots ( 0.039, > 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 10 to 55 grasshoppers m-2 (Fig. 3, *top*).

# Discussion

Previous research indicates that prescribed fire reduces grasshopper density (Vermeire et al. 2004; Joern 2004), our study, however, saw heightened density in small patch burning treatments which could have massive implications for predicting rangeland herbivore competition. Fire as a method of control varies greatly in effectiveness from species to species; certain species, such as Hesperotettix viridis, can be reduced by as much as 88% (Vermeire et al. 2004). Flightless species of grasshopper and species that are heavily reliant on specific plant hosts are especially susceptible to fire disturbances (Matenaar et al. 2014). Thanks to nutrient buffering produced by fire treatment (Spiess et al. 2020), protein availability produced a magnet effect which we believe caused the heightened density and offtake in burned plots (Meyer et al. 2002). These findings indicate fire disturbance can produce pockets of extreme competition between range herbivores, with much less forage for ungulates than what is seemingly available.

M. sanguinipes’ preferred diet is a nitrogen and carbohydrate ratio of 1:1, making them especially robust and better able to adapt to nutritionally variable seasons (Behmer and Joern 2008). Furthermore, these grasshoppers have the fastest egg production rate at intermediate dietary nitrogen levels of around 4% (Joern and Behmer 1998) and use nitrogen to maintain their health and function (Schmitz 2010). Due to their robust qualities, these grasshoppers were incredibly abundant on the Northern Great Plains in the summer of 2021. Although our burned plots had higher nitrogen than what is ideal for egg production, the competition between grasshoppers and the overall low nitrogen content of the landscape pushed M. sanguinipes to our plots to supplement their diets. Primary productivity in the Northern Great Plains is directly linked to rainfall (Padbury et al. 2002), therefore the steady increase in grasshopper density on our burn treatment plots is most likely attributable to an intensification of the magnet effect as the summer long drought progressed given that emergence typically peaks in late June (Belovsky and Slade 1995; Humphreys et al. 2022). While other research suggests that grasshoppers can be attracted to heterogeneous areas for thermoregulatory microhabitats (Joern and Laws 2013), the rapid increase in grasshopper density and the worsening of the drought over the summer points to a nutrient pull rather than a beneficial microhabitat. High temperatures, which we experienced consistently throughout the summer heat wave, weaken M. sanguinipes ability to fight infection (Srygley and Jaronski 2022), further indicating that these grasshoppers are drawn by nitrogen content and not thermoregulation when shade was nearly completely absent in the burned plots.

Our study differs from other pyric herbivory studies because it was conducted with small, clustered areas of burn. Because density increased so greatly with burn in this study, it indicates a need for further research into small burn resource utilization by range grasshoppers. Future directions for our study can examine how grasshopper density changes with distance from a burn edge for a large burn area. This information could provide a clearer picture of recolonization effects created by burn scars combined with magnet effects. Recolonization presents an avenue for this research to be applied to larger burns in the Great Plains region, which are becoming more and more common. Grasshopper density changes could also be further examined through the offtake rate over time. Further research is needed to see if the offtake rate increased in burned plots over the duration of the drought. This would show that offtake is directly related to the quality of the surrounding forage. Because climate change is intensifying drought conditions (Derner et al. 2018), understanding how offtake will change will better inform ranching practices to ensure sustainable competition between grasshoppers and livestock.

Our study has important implications for ranch practices in the Northern Great Plains. Because prescribed fire is so often used as a forage buffer for cattle ranching (Spiess et al. 2020), it is important to know how much of the available forage will go to cattle and how much will be consumed by grasshoppers. Our research already goes against the population dynamics between grasshoppers and prescribed previously described (Vermeire et al. 2004; Joern 2004), so it is very likely that grasshopper abundances are being underestimated when determining how many cattle can be put out to pasture without overgrazing the landscape. Furthermore, because the density changed so much over the course of the study, ranchers must reevaluate the level of competition at the beginning of the season compared to the end of the season when resources are even more scarce in a drought.

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Thanks bugs.

# References

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

Allred BW, Scasta JD, Hovick TJ, et al (2014) Spatial heterogeneity stabilizes livestock productivity in a changing climate. Agriculture, Ecosystems & Environment 193:37–41. <https://doi.org/10.1016/j.agee.2014.04.020>

Behmer ST (2009) Insect Herbivore Nutrient Regulation. Annual Review of Entomology 54:165–187. <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 105:1977–1982. <https://doi.org/10.1073/pnas.0711870105>

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

Branson DH (2005) Effects of Fire on Grasshopper Assemblages in a Northern Mixed-grass Prairie. Environmental Entomology 34:1109–1113. <https://doi.org/10.1093/ee/34.5.1109>

Branson DH, Vermeire LT (2013) Heat Dosage and Oviposition Depth Influence Egg Mortality of Two Common Rangeland Grasshopper Species. Rangeland Ecology & Management 66:110–113. <https://doi.org/10.2111/REM-D-11-00187.1>

Derner J, Briske D, Reeves M, et al (2018) Vulnerability of grazing and confined livestock in the Northern Great Plains to projected mid- and late-twenty-first century climate. Climatic Change 146:19–32. <https://doi.org/10.1007/s10584-017-2029-6>

Donovan VM, Wonkka CL, Twidwell D (2017) Surging wildfire activity in a grassland biome. Geophysical Research Letters 44:5986–5993. <https://doi.org/10.1002/2017GL072901>

Donovan VM, Wonkka CL, Wedin DA, Twidwell D (2020) Land-Use Type as a Driver of Large Wildfire Occurrence in the U.S. Great Plains. Remote Sensing 12:1869. <https://doi.org/10.3390/rs12111869>

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

Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland ecosystem to climate extremes. Ecology 95:2646–2656. <https://doi.org/10.1890/13-2186.1>

Humphreys JM, Srygley RB, Branson DH (2022) Geographic Variation in Migratory Grasshopper Recruitment under Projected Climate Change. Geographies 2:12–30. <https://doi.org/10.3390/geographies2010003>

Joern A (2004) Variation in Grasshopper (Acrididae) Densities in Response to Fire Frequency and Bison Grazing in Tallgrass Prairie. Environmental Entomology 33:1617–1625. <https://doi.org/10.1603/0046-225X-33.6.1617>

Joern A, Behmer ST (1998) Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. Ecological Entomology 23:174–184. <https://doi.org/10.1046/j.1365-2311.1998.00112.x>

Joern A, Laws AN (2013) Ecological Mechanisms Underlying Arthropod Species Diversity in Grasslands. Annual Review of Entomology 58:19–36. <https://doi.org/10.1146/annurev-ento-120811-153540>

Matenaar D, Bröder L, Bazelet CS, Hochkirch A (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 18:447–456. <https://doi.org/10.1007/s10841-014-9654-4>

McGranahan DA, Hovick TJ, Dwayne Elmore R, et al (2016) Temporal variability in aboveground plant biomass decreases as spatial variability increases. Ecology 97:555–560. <https://doi.org/10.1890/15-0906.1>

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 48:52–61. <https://doi.org/10.1093/ae/48.1.52>

Millard SP (2013) [EnvStats: An R Package for Environmental Statistics](https://www.springer.com). Springer, New York

Olfert O, Weiss RM, Giffen D, Vankosky MA (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 114:122–130. <https://doi.org/10.1093/jee/toaa254>

Onsager JA (1977) Comparison of Five Methods for Estimating Density of Rangeland Grasshoppers1. Journal of Economic Entomology 70:187–190. <https://doi.org/10.1093/jee/70.2.187>

Onsager JA, Olfert O (2000) [What Tools have Potential for Grasshopper Pest Management?](https://doi.org/10.1007/978-94-011-4337-0_10) In: Lockwood JA, Latchininsky AV, Sergeev MG (eds) Grasshoppers and Grassland Health: Managing Grasshopper Outbreaks without Risking Environmental Disaster. Springer Netherlands, Dordrecht, pp 145–156

Padbury G, Waltman S, Caprio J, et al (2002) Agroecosystems and Land Resources of the Northern Great Plains. Agronomy Journal 94:251–261. <https://doi.org/10.2134/agronj2002.2510>

Parker MA, Salzman AG (1985) Herbivore Exclosure and Competitor Removal: Effects on Juvenile Survivorship and Growth in the Shrub Gutierrezia Microcephala. Journal of Ecology 73:903–913. <https://doi.org/10.2307/2260156>

Parrini F, Owen-Smith N (2010) The importance of post-fire regrowth for sable antelope in a Southern African savanna. African Journal of Ecology 48:526–534. <https://doi.org/10.1111/j.1365-2028.2009.01143.x>

R Core Team (2020) [R: A language and environment for statistical computing](https://www.R-project.org/). R Foundation for Statistical Computing, Vienna, Austria

Rosenblatt AE (2018) Shifts in plant nutrient content in combined warming and drought scenarios may alter reproductive fitness across trophic levels. Oikos 127:1853–1862. <https://doi.org/10.1111/oik.05272>

Schmitz OJ (2010) [Resolving Ecosystem Complexity (MPB-47)](https://press.princeton.edu/books/paperback/9780691128498/resolving-ecosystem-complexity-mpb-47)

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 73:473–481. <https://doi.org/10.1016/j.rama.2020.03.003>

Srygley RB, Jaronski ST (2022) Increasing temperature reduces cuticular melanism and immunity to fungal infection in a migratory insect. Ecological Entomology 47:109–113. <https://doi.org/10.1111/een.13088>

Trisos MO, Parr CL, Davies AB, et al (2021) Mammalian herbivore movement into drought refugia has cascading effects on savanna insect communities. Journal of Animal Ecology 90:1753–1763. <https://doi.org/10.1111/1365-2656.13494>

Vermeire LT, Mitchell RB, Fuhlendorf SD, Wester DB (2004) Selective control of rangeland grasshoppers with prescribed fire. Journal of Range Management 5