1 Attracted by higher crude protein,

2 grasshopper abundance and offtake increase

after prescribed fire?!<

3

4 Nicholas Gregory Heimbuch

1\*, Devan Allen

5 McGranahan2, Carissa L. Wonkka3, Lance T. Vermeire2

6 and David H. Branson3

7 1\*University of Pittsburgh, 4200 Fifth Ave, Pittsburgh, 15260,

8 Pennsylvania, USA.

9 2USDA Agricultural Research Service, Livestock & Range

10 Research Laboratory, 243 Ft. Keogh Rd., Miles City, 59301,

11 Montana, USA.

12 3USDA Agricultural Research Service, Northern Plains

13 Agricultural Research Laboratory, 1500 N Central Ave, Sidney,

14 59270, Montana, USA.

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

16 Contributing authors: Devan.McGranahan@usda.gov;

17 [Carissa.Wonkka@usda.gov](mailto:Carissa.Wonkka@usda.gov) ; Lance.Vermiere@usda.gov;

18 [Dave.Branson@usda.gov](mailto:Dave.Branson@usda.gov) ;

19

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 col- lected 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.

1

\*

|  |  |
| --- | --- |
| 2 | *Rangeland grasshoppers and prescribed fire* |
| 20 | **Abstract** |
| 21 | Grasshoppers are critical components of open ecosystems, such |
| 22 | as grasslands and savannas, worldwide. While often seen as pest |
| 23 | species competing with domestic livestock for forage resources and |
| 24 | damaging crops, many species never reach abundances that result |
| 25 | in economic damage and can provide essential ecosystem services. |
| 26 | Grasshopper population and community dynamics are modulated |
| 27 | by the processes that determine plant structural and community |
| 28 | dynamics in a given ecosystem; in open ecosystems, fire is one |
| 29 | of the most ubiquitous. This study examined how indirect fire |
| 30 | effects (improved forage quality) affect the density of and offtake |
| 31 | by grasshoppers at two different times since fire and in unburned |
| 32 | plots. Both offtake and density were significantly higher in burned |
| 33 | plots compared to unburned plots. Burned plot grasshopper den- |
| 34 | sity increased over time, with greater rates of increase in recently |
| 35 | burned plots, while density remained constant in unburned loca- |
| 36 | tions. These density and offtake patterns appear to be the result |
| 37 | of higher crude protein content in burned plots, on account of |
| 38 | them having a much higher proportion of recent growth after fire |
| 39 | removed aboveground senesced material. These findings present a |
| 40 | mechanism by which fire interacts with grasshopper abundance and |
| 41 | distribution in open ecosystems. Long term assessments of fire and |
| 42 | its interaction with grazing and weather patterns are necessary |
| 43 | to determine if attraction to and consumption of post-fire vegeta- |
| 44 | tion will result in greater performance of pest grasshopper species |
| 45 | or enhance community diversity, regulating pest species outbreaks. |

*Rangeland grasshoppers and prescribed fire* 3

46 **Keywords:** Fire-grazing interaction; Magnet effect; Orthoptera: Acrididae;

47 Prescribed fire; Pyric herbivory; Rangeland forage quality; Rangeland pest

48 management

49 **Introduction**

50 As globally-ubiquitous herbivores, grasshoppers (Orthoptera: Acrididae)

51 contribute to ecosystem function around the world. Historically, interest in

52 grasshoppers has generally increased with their local density, as grasshopper

53 outbreaks and locust swarms have wrought economic damage for centuries

54 ([Cease et al](#_bookmark17), [2015](#_bookmark17)). While such outbreaks were long considered to be

55 primarily driven by environmental conditions beyond human control,

56 research has described close interactions between land management and

57 grasshopper dynamics ([Le Gall et al](#_bookmark33), [2019](#_bookmark33)). Although the utility of this

58 broader understanding of grasshoppers and human land use has mostly been

59 realized within the context of pest control ([Branson et al](#_bookmark15), [2006](#_bookmark15)),

60 grasshoppers also contribute to ecosystem dynamics including nutrient

61 cycling and plant community composition ([Meyer et al](#_bookmark37), [2002](#_bookmark37); [Zhang et al](#_bookmark58),

62 [2011](#_bookmark58); [Kietzka et al](#_bookmark32), [2021](#_bookmark32); [Belovsky and Slade](#_bookmark7), [2000](#_bookmark7)).

63 Grasshoppers are particularly important in *open ecosystems* —rangeland

64 biomes such as grasslands and savannas because herbaceous plant

65 communities are regulated by frequent disturbances and their interaction,

66 especially herbivory and fire ([Bond](#_bookmark10), [2022](#_bookmark10)). Interactions between

67 grasshoppers, fire, and other herbivores drive interconnected plant, nutrient,

68 and soil microbial dynamics, impacting ecosystem services derived from open

69 ecosystems. For instance, grasshoppers are widely seen as pests in

70 competition with economically-valuable livestock for herbaceous primary

71 productivity ([Zhang et al](#_bookmark59), [2019](#_bookmark59)). [Hewitt and Onsager](#_bookmark25) ([1983](#_bookmark25)) estimated

4 *Rangeland grasshoppers and prescribed fire*

72 grasshoppers consume nearly US$400 million (US$1.7 billion

73 inflation-adjusted) worth of livestock forage per year in the western United

74 States. Meanwhile, fire interacts with grasshoppers via direct and indirect

75 effects, which are variable among species depending on their biology (e.g.

76 [Vermeire et al](#_bookmark54), [2004](#_bookmark54)). Direct effects include mortality of adults and eggs from

77 heat exposure, while indirect effects include alterations to host plant

78 availability, vegetation structure, and microclimate. Thus the fire-grasshopper

79 interaction also has implications for grasshopper-livestock competition.

80 Because the nutritive value of vegetation in open ecosystems often varies

81 depending on the time since it last burned, fire likely also affects

82 grasshoppers by modulating their food resources. Perennial, fire-adapted

83 plants resprout using energy stored in organs protected from heat damage,

84 and post-fire plant tissue is typically higher in crude protein and lower in

85 structural carbohydrates than the mature or senescent tissue that was

86 consumed by the fire ([McGranahan and Wonkka](#_bookmark36), [2021](#_bookmark36)). Thus, despite overall

87 lower plant biomass on account of the fire, grasshopper abundance on

88 recently-burned areas is often higher than unburned areas, especially for

89 graminivorous (grass-eating) species ([Meyer et al](#_bookmark37), [2002](#_bookmark37)). More broadly,

90 post-disturbance succession and plant nutritive value have been identified as

91 important factors in grasshopper abundance ([Fartmann et al](#_bookmark21), [2012](#_bookmark21); [Schirmel](#_bookmark48)

92 [et al](#_bookmark48), [2019](#_bookmark48)). Yet explicit examinations between time-since-fire, plant nutritive

93 value, and grasshopper abundance have not been conducted.

94 We measured grasshopper abundance and forage consumption, along with

95 grass protein content, in a replicated experiment that created a

96 time-since-fire gradient in temperate grassland. Because grasshoppers are

97 morphologically capable of much more precise herbivory than most

98 vertebrate grazers, we measured protein content of grass leaves and stems

*Rangeland grasshoppers and prescribed fire* 5

99 separately. We predicted that more-recently burned plots would have both

100 higher protein content—especially in leaves—and greater grasshopper

101 abundance. As such, we predicted a greater degree of vegetation removal by

102 grasshoppers from recently-burned plots, as determined by comparing

103 aboveground plant biomass against that from within grasshopper exclosures.

104 **Methods**

105 **Study location & design**

106 Our study was conducted at the USDA-Agricultural Research Service

107 Livestock and Range Research Laboratory in Miles City, Montana, USA

108 (46.40 N, 105.95 W). Vegetation is typical mixed-grass prairie, and the study

109 site was dominated by western wheatgrass *Pascopyrum smithii*. The

110 overwhelming majority of grasshoppers on the study site, as determined by

111 mid-season sweep netting and identification at the USDA-ARS Pest

112 Management Research Unit in Sidney, Montana, consisted of the migratory

113 grasshopper *Melanoplus sanguinipes*, a native species of spur-throated

114 grasshopper in the family Acrididae.

115 Within a larger prescribed fire experiment, we selected nine, 300-m2 plots

116 to test three different time-since-fire treatments (n=3 each): Fire the

117 previous autumn, fire the previous spring, and a control treatment left

118 unburned for several years. Livestock were excluded from the entire study

119 area and had been for several years. While the study area was open to

120 wildlife such as deer *Odocoileus* spp., pronghorn *Antilocapra americana*, and

121 lagomorphs including *Sylvilagus floridanus* and *Lepus* spp, we observed no

122 evidence of their presence on any plots during the sampling period.

6 *Rangeland grasshoppers and prescribed fire*

123 **Sample collection**

124 To measure the amount of vegetation removed by foraging grasshoppers, we

125 established two pairs of sample points within each plot. Each pair of 0.25-m2

126 sample points consisted of one full mesh grasshopper exclosure alongside

127 another structure with a similar footprint and shade factor that was open to

128 grasshopper herbivory. Each type of structure consisted of a polyvinyl

129 chloride tube frame with heavy nylon netting, which when fully wrapped and

130 zipped around the frame and weighted down with sand-filled tubes,

131 effectively kept grasshoppers out ([Parker and Salzman](#_bookmark45), [1985](#_bookmark45)). Because the

132 mesh reduced sunlight intensity by 400 w m-2 compared to the surrounding

133 area, we designed control structures that remain open on the north and

134 south faces to allow grasshoppers to enter while still producing shade

135 conditions that matched the exclosures during peak photosynthetic activity.

136 These paired structures ensured that shade would not influence grass

137 development, skewing offtake measurements. Structures were monitored at

138 least every 48 hr and after any substantial weather event to ensure they

139 remained intact; in the few instances grasshoppers had crawled under the

140 exclosures, they were removed upon discovery.

141 On all plots, the first pair of structures was established 1 July 2021, and

142 the second pair 1 week later. On 9 August—40 d after the first pair of

143 structures were erected—all aboveground biomass, standing dead and current

144 year’s growth, within each 0.25 m2 frame footprint was clipped to ground

145 level. Within the recently-burned plots, individual grass tiller counts were

146 recorded—because structures were placed randomly and tiller density was

147 observed to be variable, we prepared to express biomass on both a per-tiller

148 basis as well as by area. Clipped biomass was dried at 60*◦*C for 48 hr and

149 weighed to the nearest 0.001 g.

*Rangeland grasshoppers and prescribed fire* 7

150 We collected forage quality samples on the 26th day of the study, roughly

151 halfway through the study period. For each plot, samples were comprised of

152 40 western wheatgrass tillers randomly selected by tossing a marker flag in

153 the air and clipping, to ground level, the tiller nearest to where it landed,

154 regardless of phenology or live/dead status. Tillers were separated into leaf

155 blades and stems (which included leaf sheaths) prior to drying at 60*◦*C for 48

156 hr and grinding into fine powder. Protein content was determined with a

157 Thermo Scientific Flash 2000 combustion analyzer.

158 To determine grasshopper density, we employed a standard ring count

159 methodology ([Onsager](#_bookmark42), [1977](#_bookmark42); [Joern and Laws](#_bookmark30), [2013](#_bookmark30)). One week after the

160 initial pairs of structures were established, we placed 5, 0.1 m2 rings on the

161 ground in a *×* pattern centered on each plot, with rings approximately 1.5 m

162 apart and at least 2 m from plot edges. Nineteen observations were made

163 over the course of the study period, between 9 July and 6 August. All plots

164 were sampled in each round of observations by a single observer (N.G.H.),

165 and all observations were conducted between 1000 and 1200 for consistent

166 solar conditions. Sampling consisted of walking slowly through the plot and

167 agitating the area near each ring with a long stick, and recording the number

168 of grasshoppers that jumped from the ring.

169 **Data analysis**

170 To determine whether accessibility to grasshoppers affected the amount of

171 aboveground vegetation, we subtracted the dried biomass values from control

172 structures from that of their paired grasshopper exclosures and calculated

173 the mean of these two differences for each plot (n = 3 experimental units per

174 treatment). To account for the different lengths of deployments among the two

175 pairs of structures, offtake was expressed as daily rate of removal by dividing

8 *Rangeland grasshoppers and prescribed fire*

176 the difference in biomass between paired structures by the number of days

177 each structure pair was deployed. We used a linear model with the intercept

178 term removed to test each of the three difference values against 0 (null

179 hypothesis: no difference in standing crop between grasshopper exclosures

180 and control frames) using the lm function in the R statistical environment ([R](#_bookmark46)

181 [Core Team](#_bookmark46), [2020](#_bookmark46)). We tested pairwise contrasts in standing crop differences

182 across each treatment with a post-hoc Tukey test using TukeyHSD.

183 We determined whether crude protein content varied with fire treatment

184 and plant organs (leaf blades vs. stems) by fitting each term and their

185 interaction in an ANOVA. Pairwise contrasts among fire treatments were

186 again tested with TukeyHSD.

187 To determine if there were general linear trends in grasshopper

188 abundance patterns over the course of the study, we conducted a

189 nonparametric test of the Kendall’s tau (*τ* ) statistic fit to the grasshopper

190 count data within each burn treatment using the kendallTrendTest

191 function in the *EnvStats* package for R ([Millard](#_bookmark38), [2013](#_bookmark38)). To compare the

192 relative rates of change over the study period, we plotted the estimated slope

193 of the trend for each burn treatment and the associated 95% confidence

194 intervals as returned by kendallTrendTest.

195 **Results**

196 Overall, aboveground plant biomass was lower outside of exclosures in both

197 fire treatments (64 *±* 4% less in fall burn plots and 55 *±* 9% less in spring

198 burn plots), but did not differ between exclosures and accessible unburned

199 plots (1 *±* 8%). Biomass removal by grasshoppers accounted for statistically-

200 significantly lower biomass outside of grasshopper exclosures in both fall and

201 spring burns (*t* = -7.6, *P <* 0.001 and *t* = -6, *P <* 0.001, respectively). But

*Rangeland grasshoppers and prescribed fire* 9

202 there was no difference in offtake among spring and fall burns (*P >* 0.05),

203 with grasshoppers removing approximately 1.0 (*±* 0.2) kg ha-1 d-1 in each

204 (Fig. [1](#_bookmark60)). Aboveground biomass was not different between grasshopper

205 exclosures and areas accessible to grasshoppers in unburned plots (*t* = -0.12,

206 *P >* 0.05). Offtake was significantly lower in unburned plots than plots burned

207 in both the previous fall and spring (*P <* 0.01 and *P* = 0.01, respectively).

208 Crude protein content varied among the fire treatments (*t* = 57, *P <*

209 0.001; Fig. [2](#_bookmark61)). Crude protein content in fall and spring burns averaged 6.4%

210 ± 0.2 s.e. and did not differ from one another (*P >* 0.05). But crude protein

211 content in unburned plots—which included a substantial amount of senesced

212 material from previous growing seasons—was lower than in both fall and

213 spring burns plots (*t* = -2.7, *P <* 0.001 and *t* = -3.1, *P <* 0.001, respectively).

214 Across all samples, crude protein content did not vary among leaves and

215 stems (*t* = 2.7, *P >* 0.05). Despite a trend towards higher crude protein in

216 leaf tissue in unburned plots (Fig. [2](#_bookmark61)), the pattern was not influential enough

217 to create a significant fire treatment *×* organ interaction (*t* = 2.1, *P >* 0.05).

218 Grasshopper abundance was similar across plots at the beginning of the

219 study period (early July) but increased significantly over the next month in

220 fall and spring burn plots (*τ* = 0.29, *P <* 0.01 and *τ* = 0.62, *P <* 0.001;

221 Fig. [3](#_bookmark62)). Grasshopper abundance remained constant over the study period in

222 unburned plots (*τ* = 0.039, *P >* 0.05). While grasshopper abundance

223 increased in both burn treatments, the rate of increase was approximately

224 three times greater in plots that had been most recently burned in the spring

225 than those that had been burned in the previous fall (Fig. [3](#_bookmark62), *bottom*), which

226 represented more than a five-fold increase in density from approximately 5 to

227 25 grasshoppers m-2 (Fig. [3](#_bookmark62), *top*).

10 *Rangeland grasshoppers and prescribed fire*

228 **Discussion**

229 Insect herbivore abundance and distribution are extremely spatially and

230 temporally variable ([Cappuccino and Price](#_bookmark16), [1995](#_bookmark16)). This variability is often

231 tied to variability in plant biomass and nutrient content ([Joern et al](#_bookmark31), [2012](#_bookmark31)).

232 Insect herbivores often select plant species or suites of species based on

233 specific nutritional needs ([Ibanez et al](#_bookmark26), [2013](#_bookmark26); [Behmer and Joern](#_bookmark6), [2008](#_bookmark6)) and

234 will actively seek a diet that contains a specific ratio of nutrients ([Behmer](#_bookmark5),

235 [2009](#_bookmark5)). Therefore, the distribution of plant nutritional quality on the

236 landscape can be a strong determinant of grasshopper abundance and

237 distribution ([White](#_bookmark56), [2012](#_bookmark56); [Joern et al](#_bookmark31), [2012](#_bookmark31); [Ozment et al](#_bookmark44), [2021](#_bookmark44)).

238 In the present study, grasshoppers removed over half of available biomass

239 over the study period in burned plots but had no detectable effect in unburned

240 plots. This is likely related to crude protein content which was elevated in

241 burned plots and the resultant increase in grasshopper abundance over time in

242 plots that had been burned in either the spring or previous fall. Grasshoppers

243 in other systems have been shown to select burned vegetation: grasshoppers

244 feeding in willow selected resprouting burned willow shoots, consuming them

245 completely, while rejecting unburned willow after a taste ([Stein et al](#_bookmark52), [1992](#_bookmark52))

246 and in the Brazilian Cerrado, leaf chewing insects including grasshoppers

247 selected resprouting burned shrubs, causing 30-60 percent greater damage to

248 resprouting leaves than unburned leaves ([Lopes and Vasconcelos](#_bookmark34), [2011](#_bookmark34)).

249 Time since last fire is a driver of spatial and temporal variability in the

250 distribution of plant nutritional quality. Resprouting plant tissues typically

251 have higher protein content than their mature counterparts on account of

252 having a lower proportion of structural carbohydrates ([McGranahan and](#_bookmark36)

253 [Wonkka](#_bookmark36), [2021](#_bookmark36)). At the stand level, fire removes low-quality, senesced material

254 from previous season’s growth, allowing high-quality regrowth to dominate

*Rangeland grasshoppers and prescribed fire* 11

255 the sward. This elevated protein content in burned areas can be maintained

256 over longer periods by repeated grazing ([Wanchuk et al](#_bookmark55), [2021](#_bookmark55)), even during

257 drought ([Spiess et al](#_bookmark51), [2020](#_bookmark51)). Higher nutritional quality attracts herbivores to

258 an area after fire and they maintain the high nutritional quality by remaining

259 in that area to continue consuming high quality plant tissues that must then

260 regrow and this feedback has been documented for a range of herbivores in

261 open ecosystems worldwide ([Allred et al](#_bookmark0), [2011](#_bookmark0); [Archibald et al](#_bookmark2), [2005](#_bookmark2); [Sensenig](#_bookmark50)

262 [et al](#_bookmark50), [2010](#_bookmark50)). The dominant grasshopper species in our plots, *Melanoplus*

263 *sanguinipes*, shows preference for current year’s growth and standing dead

264 material makes up only a small proportion of its diet ([Anderson and Wright](#_bookmark1),

265 [1952](#_bookmark1); [Mulkern et al](#_bookmark39), [1962](#_bookmark39)). In the present study, burned plots with overall

266 higher crude protein content as a result of higher proportions of resprouting,

267 green tissue, attracted *M. sanguinipes* from surrounding unburned vegetation.

268 In this study, the rate of increase in grasshopper abundance was greater

269 in spring burn plots, which were burned most recently. Although there were

270 no differences in absolute abundance between fall and spring burn plots, the

271 differences in rate of increase over the course of the study suggests that

272 divergence of grasshopper abundance between spring and fall burned plots

273 likely became significant by the end of the growing season. This points to a

274 fire-grazing nutrient feedback —the most recently burned plots maintained

275 that strong feedback over the course of the study while the attraction was

276 not as strong to fall burn plots. Crude protein content did not differ between

277 fall and spring burn plots at the time it was measured —halfway through the

278 study in mid July. However, given the differential rate of increase in spring

279 and fall burn plots, crude protein between those treatments likely diverged

280 later in the growing season, along with grasshopper abundances.

12 *Rangeland grasshoppers and prescribed fire*

281 Grasshopper population dynamics and resultant community composition

282 are impacted by many drivers simultaneously. In addition to plant nutritional

283 status, predation risk ([Schmitz et al](#_bookmark49), [1997](#_bookmark49)), dispersal limitation ([Hawlena](#_bookmark24)

284 [and Schmitz](#_bookmark24), [2010](#_bookmark24)), and microclimatic conditions ([Bauer and Kenyeres](#_bookmark4),

285 [2007](#_bookmark4); [Gardiner and Dover](#_bookmark23), [2008](#_bookmark23)) are strong determinants of grasshopper

286 dynamics. Because of the role it plays in each of these, vegetation structure

287 often correlates with grasshopper distribution and density, although the

288 strongest correlations have occurred in highly productive grasslands such as

289 tallgrass prairies ([Joern](#_bookmark28), [2004](#_bookmark28)). In the present study, fire altered both

290 vegetation nutritional status and structure, making it difficult to parse which

291 drove increases in grasshopper abundance. And both likely play some roll in

292 driving grasshopper habitat selection. The dominant species found during

293 our study has been shown to respond positively to nitrogen in this ecosystem

294 ([Branson](#_bookmark11), [2003](#_bookmark11)). In addition, grasshoppers showed similar attraction to high

295 nutrient grazing lawns in tallgrass prairie ([Ozment et al](#_bookmark44), [2021](#_bookmark44)). While there

296 is a similar conflation of structure and nutrient content to that in the present

297 study, they found the attraction weaker when the nutritional contrast

298 between grazing lawns and surrounding areas lessened during drought,

299 supporting nutritional quality as an important driver. Regardless of the

300 mechanism, recently burned plots clearly attracted more grasshoppers and

301 subsequently had more aboveground biomass removal than unburned plots,

302 which has potential implications for management.

303 Because grasshoppers can be economic pests in grasslands used for

304 livestock production when at high densities, improved survival and

305 reproduction resulting from nutrient enhancement in burned vegetation

306 ([Branson](#_bookmark11), [2003](#_bookmark11)) could intensify competition between livestock and

307 grasshoppers in burned areas. Loss of livestock forage to grasshoppers is

*Rangeland grasshoppers and prescribed fire* 13

308 most problematic during grasshopper outbreaks or during droughts, when

309 plant productivity is low ([Belovsky and Slade](#_bookmark8), [1995](#_bookmark8); [Joern](#_bookmark27), [2000](#_bookmark27); [Branson](#_bookmark12)

310 [and Haferkamp](#_bookmark12), [2014](#_bookmark12)). The dominant grasshopper at our study area, the

311 migratory grasshopper *Melanoplus sanguinipes*, is commonly viewed as one of

312 the most frequent economic pest species in the central and western US,

313 making it especially damaging to farmers and ranchers throughout the Great

314 Plains ([Onsager](#_bookmark43), [2000](#_bookmark43); [Olfert et al](#_bookmark40), [2021](#_bookmark40)). However, many grasshopper

315 species do not cause economic harm and instead enhance ecosystem service

316 delivery by increasing nutrient cycling, providing food for rangeland wildlife,

317 exerting some control over unwanted rangeland plants, and in some cases

318 increasing overall rangeland productivity ([Branson et al](#_bookmark15), [2006](#_bookmark15)). In addition,

319 greater grasshopper diversity can reduce the likelihood of pest species

320 outbreaks as beneficial grasshoppers compete for resources and enhance the

321 efficacy of grasshopper predators ([Branson et al](#_bookmark15), [2006](#_bookmark15)). Fire at appropriate

322 scales could enhance diversification of grasshopper communities because they

323 exhibit a breadth of species-specific habitat requirements and fire can

324 enhance structural and nutritive heterogeneity in vegetation.

325 Gains in grasshopper performance from nutritive enhancement could be

326 offset by negative fire effects, as fire alone can result in short-lived reductions

327 in grasshopper abundance by up to 75% ([Branson and Vermeire](#_bookmark14), [2016](#_bookmark14)),

328 although the effects are often short-lived. Direct effects of fire include adult

329 and nymphal mortality ([Bock and Bock](#_bookmark9), [1991](#_bookmark9)), and egg mortality due to soil

330 heating ([Branson and Vermeire](#_bookmark13), [2013](#_bookmark13), [2016](#_bookmark14); [Vermeire et al](#_bookmark54), [2004](#_bookmark54)). Indirect

331 effects related to microclimate, soil properties, and plant community

332 compositional changes can also alter grasshopper abundance in burned areas

333 ([Van Wingerden et al](#_bookmark53), [1991](#_bookmark53); [Schirmel et al](#_bookmark47), [2011](#_bookmark47); [Evans et al](#_bookmark20), [1983](#_bookmark20);

334 [Matenaar et al](#_bookmark35), [2014](#_bookmark35); [Meyer et al](#_bookmark37), [2002](#_bookmark37)), although other drivers, such as

14 *Rangeland grasshoppers and prescribed fire*

335 livestock grazing, likely interact with fire in most grasslands ([McGranahan](#_bookmark36)

336 [and Wonkka](#_bookmark36), [2021](#_bookmark36); [Fuhlendorf et al](#_bookmark22), [2009](#_bookmark22); [Joern](#_bookmark29), [2005](#_bookmark29)). Given these

337 wide-ranging impacts on diversity and mortality, fire could be a sustainable

338 low-cost alternative to conventional control of economically-damaging

339 grasshopper outbreaks —broad-scale chemical applications ([Branson et al](#_bookmark15),

340 [2006](#_bookmark15)), which are expensive, unreliable, and have non-target effects on

341 beneficial arthropods. In addition, ecosystem services provided by non-pest

342 grasshopper species are lost when insecticides are used to control grasshopper

343 outbreaks ([Joern](#_bookmark27), [2000](#_bookmark27)). Longer-term assessment of grasshopper dynamics in

344 burned and unburned areas is needed to determine the potential for fire to

345 reduce outbreaks of economically damaging grasshopper species.

346 Future research should also assess the impacts of fire at larger scales and

347 the interaction of fire with other disturbances such as drought and livestock

348 grazing. Grasshopper responses observed in this study likely reflect

349 movement patterns and attraction to burned plots, which might differ at

350 large scales. Studies of fire-herbivore feedbacks at multiple scales show that

351 small-scale fires result in positive feedbacks, creating grazing hotspots with

352 high crude protein for long durations, similar to our findings here([Cromsigt](#_bookmark18)

353 [and Olff](#_bookmark18), [2008](#_bookmark18)). In contrast, large-scale fires can result in more dispersed

354 herbivore distribution that can homogenize plant nutritional status and

355 structure as grazing pressure is dispersed, resulting in more ungrazed areas

356 within a burn perimeter that do not maintain high nutrient content

357 ([Archibald et al](#_bookmark2), [2005](#_bookmark2)) and lessening the attraction of the burned area to

358 herbivores ([Donaldson et al](#_bookmark19), [2018](#_bookmark19)). However, it is uncertain whether

359 heterogeneity in protein content distribution within a broader fire could

360 result in the creation of similar small-scale nutrient hotspots in the presence

361 of grasshoppers or if the additional grazing pressure from grasshoppers could

*Rangeland grasshoppers and prescribed fire* 15

362 enhance livestock attraction to burned areas at larger scales. Regardless of

363 scale, livestock grazing-fire interactions ([Onsager](#_bookmark43), [2000](#_bookmark43); [O’Neill et al](#_bookmark41), [2003](#_bookmark41))

364 and drought likely play a role in fire-grasshopper dynamics by either

365 enhancing or diminishing contrast in protein content between unburned and

366 burned vegetation ([Augustine and Derner](#_bookmark3), [2014](#_bookmark3); [Yoganand and Owen-Smith](#_bookmark57),

367 [2014](#_bookmark57); [Ozment et al](#_bookmark44), [2021](#_bookmark44)), and our findings suggest that this contrast is an

368 important driver of grasshopper distribution and offtake.

369 **Acknowledgments.** We appreciate the general assistance of D.F. Watson

370 from NPARL in organizing field equipment, the assistance of Cheryl Murphy,

371 with protein analysis at LARRL, and Nicole Davidson, with grasshopper

372 identification at NPARL.

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

374 interest.

375 **Funding.** NGH received salary support from the USDA-ARS Plains Area

376 co-funded internship with matching funds from LARRL and NPARL.

377 **Ethics statement.** This article does not contain any studies with human

378 participants or animals performed by any of the authors.

379 **Availability of data and code.** Data and R script used herein are

380 available under a U.S. Public Domain license at the USDA Ag Data

381 Commons ([doi.org/10.15482/USDA.ADC/1528475](https://doi.org/10.15482/USDA.ADC/1528475)).

382 **References**

383 Allred BW, Fuhlendorf SD, Engle DM, et al (2011) Ungulate preference for

384 burned patches reveals strength of fire–grazing interaction. Ecology and

385 Evolution 1(2):132–144. <https://doi.org/10.1002/ece3.12>

16 *Rangeland grasshoppers and prescribed fire*

|  |  |
| --- | --- |
| 386 | Anderson NL, Wright JC (1952) Grasshopper Investigations on Montana |
| 387 | Range Lands. Bulletin 486. Bulletin 486, Montana State College Agricultural |
| 388 | Experiment Station, Bozeman MT |
| 389 | Archibald S, Bond W, Stock W, et al (2005) Shaping the landscape: |
| 390 | Fire–grazer interactions in an African savanna. Ecological Applications |
| 391 | 15(1):96–109 |
| 392 | Augustine DJ, Derner JD (2014) Controls over the strength and timing of |
| 393 | fire–grazer interactions in a semi-arid rangeland. Journal of Applied Ecology |
| 394 | 51(1):242–250 |
| 395 | Bauer N, Kenyeres Z (2007) Seasonal changes of microclimatic conditions in |
| 396 | grasslands and its influence on orthopteran assemblages. Biologia 62(6):742– |
| 397 | 748 |
| 398 | Behmer ST (2009) Insect Herbivore Nutrient Regulation. Annual Review |
| 399 | of Entomology 54(1):165–187. [https://doi.org/10.1146/annurev.ento.54.](https://doi.org/10.1146/annurev.ento.54.110807.090537) |
| 400 | [110807.090537](https://doi.org/10.1146/annurev.ento.54.110807.090537) |
| 401 | Behmer ST, Joern A (2008) Coexisting generalist herbivores occupy unique |
| 402 | nutritional feeding niches. Proceedings of the National Academy of Sciences |
| 403 | 105(6):1977–1982. <https://doi.org/10.1073/pnas.0711870105> |
| 404 | Belovsky G, Slade J (2000) Insect herbivory accelerates nutrient cycling and |
| 405 | increases plant production. Proceedings of the National Academy of Sciences |
| 406 | 97(26):14,412–14,417 |
| 407 | Belovsky GE, Slade JB (1995) Dynamics of two Montana grasshopper popula- |
| 408 | tions: Relationships among weather, food abundance and intraspecific com- |
| 409 | petition. Oecologia 101(3):383–396. <https://doi.org/10.1007/BF00328826> |

*Rangeland grasshoppers and prescribed fire* 17

410 Bock CE, Bock JH (1991) Response of grasshoppers (Orthoptera: Acrididae)

411 to wildfire in a Southeastern Arizona grassland. The American Midland

412 Naturalist 125(1):162–167. <https://doi.org/10.2307/2426379>

413 Bond WJ (2022) Out of the shadows: Ecology of open ecosystems. Plant Ecol-

414 ogy & Diversity pp 1–18. <https://doi.org/10.1080/17550874.2022.2034065>

415 Branson DH (2003) Reproduction and survival in Melanoplus sanguinipes

416 (Orthoptera: Acrididae) in response to resource availability and population

417 density: The role of exploitative competition. The Canadian Entomologist

418 135(3):415–426

419 Branson DH, Haferkamp MA (2014) Insect herbivory and vertebrate grazing

420 impact food limitation and grasshopper populations during a severe out-

421 break. Ecological Entomology 39(3):371–381. [https://doi.org/10.1111/een.](https://doi.org/10.1111/een.12114)

422 [12114](https://doi.org/10.1111/een.12114)

423 Branson DH, Vermeire LT (2013) Heat Dosage and Oviposition Depth Influ-

424 ence Egg Mortality of Two Common Rangeland Grasshopper Species.

425 Rangeland Ecology & Management 66(1):110–113. [https://doi.org/10.2111/](https://doi.org/10.2111/REM-D-11-00187.1)

426 [REM-D-11-00187.1](https://doi.org/10.2111/REM-D-11-00187.1)

427 Branson DH, Vermeire LT (2016) Grasshopper responses to fire and post-

428 fire grazing in the Northern Great Plains vary among species. Rangeland

429 Ecology & Management 69(2):144–149

430 Branson DH, Joern A, Sword GA (2006) Sustainable Management of Insect

431 Herbivores in Grassland Ecosystems: New Perspectives in Grasshopper Con-

432 trol. BioScience 56(9):743–755. https://doi.org/10.1641/0006-3568(2006)

433 56[743:SMOIHI]2.0.CO;2

18 *Rangeland grasshoppers and prescribed fire*

434 Cappuccino N, Price PW (1995) Population Dynamics: New Approaches and

435 Synthesis. Academic Press, SanDiego, CA, USA

436 Cease AJ, Elser JJ, Fenichel EP, et al (2015) Living With Locusts: Connect-

437 ing Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets.

438 BioScience 65(6):551–558. <https://doi.org/10.1093/biosci/biv048>

439 Cromsigt JP, Olff H (2008) Dynamics of grazing lawn formation: An exper-

440 imental test of the role of scale-dependent processes. Oikos 117(10):1444–

441 1452

442 Donaldson JE, Archibald S, Govender N, et al (2018) Ecological engineering

443 through fire-herbivory feedbacks drives the formation of savanna grazing

444 lawns. Journal of Applied Ecology 55(1):225–235. [https://doi.org/10.1111/](https://doi.org/10.1111/1365-2664.12956)

445 [1365-2664.12956](https://doi.org/10.1111/1365-2664.12956)

446 Evans EW, Rogers RA, Opfermann DJ (1983) Sampling grasshoppers

447 (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: Night

448 trapping vs. sweeping. Environmental Entomology 12(5):1449–1454

449 Fartmann T, Kr¨amer B, Stelzner F, et al (2012) Orthoptera as ecological

450 indicators for succession in steppe grassland. Ecological Indicators 20:337–

451 344. <https://doi.org/10.1016/j.ecolind.2012.03.002>

452 Fuhlendorf SD, Engle DM, Kerby J, et al (2009) Pyric Herbivory: Rewild-

453 ing Landscapes through the Recoupling of Fire and Grazing. Conservation

454 Biology 23(3):588–598. <https://doi.org/10.1111/j.1523-1739.2008.01139.x>

455 Gardiner T, Dover J (2008) Is microclimate important for Orthoptera in open

456 landscapes? Journal of Insect Conservation 12(6):705–709

*Rangeland grasshoppers and prescribed fire* 19

457 Hawlena D, Schmitz OJ (2010) Herbivore physiological response to predation

458 risk and implications for ecosystem nutrient dynamics. Proceedings of the

459 National Academy of Sciences 107(35):15,503–15,507

460 Hewitt GB, Onsager JA (1983) Control of grasshoppers on rangeland in the

461 United States–a perspective. Journal of Range Management 36(2):202–207

462 Ibanez S, Manneville O, Miquel C, et al (2013) Plant functional traits reveal

463 the relative contribution of habitat and food preferences to the diet of

464 grasshoppers. Oecologia 173(4):1459–1470

465 Joern A (2000) What are the consequences of non-linear ecological interac-

466 tions for grasshopper control strategies? In: Lockwood JA, Latchininsky AV,

467 Sergeev MG (eds) Grasshoppers and Grassland Health: Managing Grasshop-

468 per Outbreaks without Risking Environmental Disaster, NATO Science

469 Series, vol 73. Springer, Dordrecht, p 131–144

470 Joern A (2004) Variation in Grasshopper (Acrididae) Densities in Response

471 to Fire Frequency and Bison Grazing in Tallgrass Prairie. Environmen-

472 tal Entomology 33(6):1617–1625. [https://doi.org/10.1603/0046-225X-33.6.](https://doi.org/10.1603/0046-225X-33.6.1617)

473 [1617](https://doi.org/10.1603/0046-225X-33.6.1617)

474 Joern A (2005) Disturbance by fire frequency and bison grazing modulate

475 grasshopper assemblages in tallgrass prairie. Ecology 86(4):861–873. [https:](https://doi.org/10.1890/04-0135)

476 [//doi.org/10.1890/04-0135](https://doi.org/10.1890/04-0135)

477 Joern A, Laws AN (2013) Ecological Mechanisms Underlying Arthropod

478 Species Diversity in Grasslands. Annual Review of Entomology 58(1):19–36.

479 <https://doi.org/10.1146/annurev-ento-120811-153540>

20 *Rangeland grasshoppers and prescribed fire*

480 Joern A, Provin T, Behmer ST (2012) Not just the usual suspects: Insect

481 herbivore populations and communities are associated with multiple plant

482 nutrients. Ecology 93(5):1002–1015

483 Kietzka GJ, Lecoq M, Samways MJ (2021) Ecological and Human Diet Value

484 of Locusts in a Changing World. Agronomy 11(9). [https://doi.org/10.3390/](https://doi.org/10.3390/agronomy11091856)

485 [agronomy11091856](https://doi.org/10.3390/agronomy11091856)

486 Le Gall M, Overson R, Cease A (2019) A Global Review on Locusts

487 (Orthoptera: Acrididae) and Their Interactions With Livestock Grazing

488 Practices. Frontiers in Ecology and Evolution 7

489 Lopes CT, Vasconcelos HL (2011) Fire increases insect herbivory in a

490 Neotropical savanna. Biotropica 43(5):612–618

491 Matenaar D, Br¨oder L, Bazelet CS, et al (2014) Persisting in a windy habitat:

492 Population ecology and behavioral adaptations of two endemic grasshopper

493 species in the Cape region (South Africa). Journal of Insect Conservation

494 18(3):447–456. <https://doi.org/10.1007/s10841-014-9654-4>

495 McGranahan DA, Wonkka CL (2021) Ecology of Fire-Dependent Ecosystems:

496 Wildland Fire Science, Policy, and Management. CRC Press, Boca Raton,

497 FL

498 Meyer CK, Whiles MR, Charlton RE (2002) Life History, Secondary Pro-

499 duction, and Ecosystem Significance of Acridid Grasshoppers in Annually

500 Burned and Unburned Tallgrass Prairie. American Entomologist 48(1):52–

501 61. <https://doi.org/10.1093/ae/48.1.52>

502 Millard SP (2013) EnvStats: An R Package for Environmental Statistics.

503 Springer, New York

*Rangeland grasshoppers and prescribed fire* 21

504 Mulkern GB, Anderson JF, Brusven MA (1962) Biology and Ecology of North

505 Dakota Grasshoppers. 1. Food Habits and Preferences of Grasshoppers Asso-

506 ciated with Alfalfa Fields. North Dakota Agricultural Experiment Station,

507 Fargo ND

508 Olfert O, Weiss RM, Giffen D, et al (2021) Modeling Ecological Dynamics of a

509 Major Agricultural Pest Insect ( *Melanoplus sanguinipes* ; Orthoptera: Acri-

510 didae): A Cohort-Based Approach Incorporating the Effects of Weather on

511 Grasshopper Development and Abundance. Journal of Economic Entomol-

512 ogy 114(1):122–130. <https://doi.org/10.1093/jee/toaa254>

513 O’Neill KM, Olson BE, Rolston MG, et al (2003) Effects of livestock grazing

514 on rangeland grasshopper (Orthoptera: Acrididae) abundance. Agricul-

515 ture, Ecosystems & Environment 97(1):51–64. [https://doi.org/10.1016/](https://doi.org/10.1016/S0167-8809(03)00136-1)

516 [S0167-8809(03)00136-1](https://doi.org/10.1016/S0167-8809(03)00136-1)

517 Onsager JA (1977) Comparison of Five Methods for Estimating Density of

518 Rangeland Grasshoppers. Journal of Economic Entomology 70(2):187–190.

519 <https://doi.org/10.1093/jee/70.2.187>

520 Onsager JA (2000) Suppression of grasshoppers in the Great Plains through

521 grazing management. Journal of Range Management 53(6):592–602

522 Ozment KA, Welti EA, Shaffer M, et al (2021) Tracking nutrients in space and

523 time: Interactions between grazing lawns and drought drive abundances of

524 tallgrass prairie grasshoppers. Ecology and Evolution 11(10):5413–5423

525 Parker MA, Salzman AG (1985) Herbivore Exclosure and Competitor

526 Removal: Effects on Juvenile Survivorship and Growth in the Shrub Gutier-

527 rezia Microcephala. Journal of Ecology 73(3):903–913. [https://doi.org/10.](https://doi.org/10.2307/2260156)

[22 *Rangeland grasshoppers and prescribed fire*](https://doi.org/10.2307/2260156)

528 [2307/2260156](https://doi.org/10.2307/2260156)

529 R Core Team (2020) R: A Language and Environment for Statistical Comput-

530 ing. R Foundation for Statistical Computing, Vienna, Austria

531 Schirmel J, Mantilla-Contreras J, Blindow I, et al (2011) Impacts of succes-

532 sion and grass encroachment on heathland Orthoptera. Journal of Insect

533 Conservation 15(5):633–642

534 Schirmel J, Gerlach R, Buhk C (2019) Disentangling the role of management,

535 vegetation structure, and plant quality for Orthoptera in lowland meadows.

536 Insect Science 26(2):366–378. <https://doi.org/10.1111/1744-7917.12528>

537 Schmitz OJ, Beckerman AP, O’Brien KM (1997) Behaviorally mediated

538 trophic cascades: Effects of predation risk on food web interactions. Ecology

539 78(5):1388–1399

540 Sensenig RL, Demment MW, Laca EA (2010) Allometric scaling predicts

541 preferences for burned patches in a guild of East African grazers. Ecology

542 91(10):2898–2907. <https://doi.org/10.1890/09-1673.1>

543 Spiess JW, McGranahan DA, Geaumont B, et al (2020) Patch-Burning Buffers

544 Forage Resources and Livestock Performance to Mitigate Drought in the

545 Northern Great Plains. Rangeland Ecology & Management 73(4):473–481.

546 <https://doi.org/10.1016/j.rama.2020.03.003>

547 Stein SJ, Price PW, Abrahamson WG, et al (1992) The effect of fire on stim-

548 ulating willow regrowth and subsequent attack by grasshoppers and elk.

549 Oikos pp 190–196

*Rangeland grasshoppers and prescribed fire* 23

550 Van Wingerden W, Musters J, Maaskamp F (1991) The influence of temper-

551 ature on the duration of egg development in West European grasshoppers

552 (Orthoptera: Acrididae). Oecologia 87(3):417–423

553 Vermeire LT, Mitchell RB, Fuhlendorf SD, et al (2004) Selective control of

554 rangeland grasshoppers with prescribed fire. Journal of Range Management

555 57(1):29–33. https://doi.org/10.2111/1551-5028(2004)057[0029:SCORGW]

556 2.0.CO;2

557 Wanchuk MR, McGranahan DA, Sedivec KK, et al (2021) Contrasts in for-

558 age mineral concentration with patch-burn grazing: A preliminary analysis.

559 Translational Animal Science 5(Supplement S1):S75–S79. [https://doi.org/](https://doi.org/10.1093/tas/txab173)

560 [10.1093/tas/txab173](https://doi.org/10.1093/tas/txab173)

561 White TC (2012) The Inadequate Environment: Nitrogen and the Abundance

562 of Animals. Springer Science & Business Media, Berlin, Germany

563 Yoganand K, Owen-Smith N (2014) Restricted habitat use by an African

564 savanna herbivore through the seasonal cycle: Key resources concept

565 expanded. Ecography 37(10):969–982

566 Zhang G, Han X, Elser JJ (2011) Rapid top–down regulation of plant C:N:P

567 stoichiometry by grasshoppers in an Inner Mongolia grassland ecosystem.

568 Oecologia 166(1):253–264. <https://doi.org/10.1007/s00442-011-1904-5>

569 Zhang L, Lecoq M, Latchininsky A, et al (2019) Locust and grasshopper man-

570 agement. Annual Review of Entomology 64(1):15–34. [https://doi.org/10.](https://doi.org/10.1146/annurev-ento-011118-112500)

571 [1146/annurev-ento-011118-112500](https://doi.org/10.1146/annurev-ento-011118-112500)

24 *Rangeland grasshoppers and prescribed fire*

572 **Figure 1** Mean differences in biomass removal rate between grasshopper

573 exclosures and control frames in plots with three different fire treatments.

574 Standing crop was determined by clipping at the end of the four-week study

575 period and differences attributable to grasshopper removal are expressed as

576 mean kg ha-1 day-1.

577 **Figure 2** Mean protein content of western wheatgrass *Pascopyrum*

578 *smithii* sampled from three burn treatments as a percentage of total dry

579 matter. Orange circles indicate the protein content of leaf blades; blue

580 triangles are stems (which include leaf sheaths).

581 **Figure 3** Observed grasshopper counts per square meter. Orange indicates

582 data taken from fall burn treatments, blue from spring burn treatments, and

583 red from unburned (control) plots. *Bottom* shows data from Kendall’s Tau

584 statistic which assessed the observed count trendline consistency over time.

585 Our tau values were compared against the null hypothesis that there was no

586 trend in our data. 95% confidence intervals were calculated to show the

587 possible variance in slope for the data over time. Most grasshoppers observed

588 were the migratory grasshopper *Melanoplus sanguinipes*.

*Rangeland grasshoppers and prescribed fire* 25

1.2



0.9

Daily standing crop removal (mean kg/ha/d ± s.e.)

0.6

0.3

0.0

Fall Spring Unburned

# Season of last burn

**Fig. 1**

26 *Rangeland grasshoppers and prescribed fire*

7



6

Protein content (mean % ± s.e.)

# Organ

5  Leaf

 Stem

4

3

Fall Spring Unburned

# Season of last burn

**Fig. 2**

*Rangeland grasshoppers and prescribed fire* 27

Treatment  Fall  Spring

Unburned

30



Grasshoppers per plot

20

10

Jul 08 Jul 15 Jul 22 Jul 29 Aug 05

# Date

Unburned



Spring

Burn season

Fall

0.0 0.2 0.4 0.6

# Estimated slope and 95% CI

**Fig. 3**