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Source: Journal of the Kansas Entomological Society, 94(3) : 183-198

Published By: Kansas Entomological Society

URL: https://doi.org/10.2317/0022-8567-94.3.183

JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
94(3), 2021, pp. 183-198

Grasshopper Species Composition Differs Between Prairie Dog Colonies and Undisturbed Sites in a Sagebrush Grassland

Ian S. Pearse[1,*], Courtney Duchardt[2], Lillian Legg[3],
and Lauren M. Porensky[4]

Abstract: Grasshoppers are major consumers of plant biomass in grassland and shrubland ecosystems. While often considered generalists, grasshopper species have differing habitat preferences and interactions with other consumers in grasslands. There are conflicting accounts of how prairie dog colonies and differences in vegetation impact grasshopper abundance and composition. We conducted a landscape-scale survey of grasshopper communities, plant communities, and prairie dogs in a grassland/shrubland ecosystem in eastern Wyoming. Over the study landscape, spurthroat grasshoppers (Melanoplinae) were associated with lower sagebrush cover and lower cover of C3 perennial graminoids, bandwing grasshoppers (Oedipodinae) were associated with low-lying areas with a high cover of C4 grasses and a low cover of cheatgrass, and slantface grasshoppers (Gomphocerinae) were associated with low vegetation height. Prairie dogs, presumably because of their effects on vegetation, had different impacts on different groups of grasshoppers. Melanoplinae grasshoppers, the Wyoming toothpick grasshopper (*Paropomala wyomingensis* Thomas), and grasshoppers with early-season phenology were associated with prairie dog colonies. However, because some species of grasshoppers were positively and others negatively associated with prairie dogs, the net effect of prairie dogs on total grasshopper biomass was neutral. Thus, to determine the role of grasshoppers in prairie ecosystems, it will be important to determine whether there is functional equivalence of grasshopper species in consuming plant biomass and as food for vertebrates.

Keywords: Landscape scale analysis, Orthoptera, Acrididae, insect biomass, cheatgrass, Thunder Basin

Prairie dogs, ungulates, and grasshoppers are all herbivores with radically differing foraging strategies and life histories that co-occur in grassland ecosystems throughout the American West (Coppock *et al.,* 1983). Estimates of the total plant biomass consumed by each of these groups can be high. In combination, herbivores in grassland systems can consume over half of all aboveground net primary productivity (Detling, 1988), which suggests a greater role of herbivores in dominating energy flows in grasslands than in other ecosystems (McNaughton *et al.,* 1989). Within prairie dog colonies, consumption and harvesting of plant material can be even higher; up to 80% of annual production of plant material can be harvested by prairie dogs and other herbivores (Whicker and Detling, 1988). The degree to which prairie dog herbivory constrains consumption by other herbivores (e.g., grasshoppers and ungulates) via competition remains an enduring question central to effective management of grasslands (Kotliar *et al.,* 2006).

Each of these groups of herbivores forages in different ways, and the ways they interact remain poorly understood (Coppock *et al.,* 1983). Black-tailed prairie dogs (*Cynomys*

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[1] U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526, U.S.A.
[2] Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, 74078, U.S.A.
[3] Colorado State University, Dept. Agricultural Biology, Fort Collins, CO 80523 U.S.A.
[4] USDA- ARS, Fort Collins, CO 80526 U.S.A.

*Corresponding author email: ipearse@usgs.gov

Received 5 February 2020; Accepted 14 September 2021

ludovicianus Ord) forage on vegetation and clip it to maintain short structure, which increases visibility of potential predators (Hoogland, 1995). These colonies represent discrete islands of short-stature vegetation within a landscape characterized by thicker, denser structure typical of the Great Plains. Prairie dog colonies support unique plant communities (Coppock *et al.,* 1983; Johnson-Nistler *et al.,* 2004), ground-dwelling arthropods (Davidson and Lightfoot, 2007), predators (Dobson and Lyles, 2000; Cook *et al.,* 2003), and birds (Augustine and Baker, 2013; Duchardt *et al.,* 2018). Although alpha (local) diversity of these different guilds may be low inside prairie dog colonies, the colonies often support unique specialists (including the endangered black-footed ferret [*Mustea nigripes* Audubon and Bachman]), and therefore contribute meaningfully to landscape-level beta (difference among sites) and gamma (regional) diversity (Duchardt *et al.,* 2018).

Grasshoppers, while often managed as a single trophic guild, are a speciose group of arthropods with diverse foraging preferences and habitat needs (Chapman and Joern, 1990; Behmer and Joern, 2008). For example, analyses of gut contents revealed that grasshoppers in the Ontario region rely on largely non-overlapping sets of forage plants (McClenaghan *et al.,* 2015). Prairie dogs may compete with grasshoppers by decreasing available plant material. However, their impacts on grasshopper communities may be complex because some grasshoppers prefer habitats that prairie dogs promote, such as more open habitats and those dominated by annual forbs. The interaction between prairie dogs and grasshoppers is particularly important because both herbivores are actively killed with the intention of increasing forage for cattle (Davidson *et al.,* 2012). Our study aims to quantify the impact of prairie dog colonies on grasshopper biomass and community composition.

We conducted a survey of grasshopper species abundance over a large area in a grassland-shrubland ecosystem. We structured our survey to sample inside and outside of prairie dog colonies. At each sampling site, we measured several aspects of the plant community, vegetation structure, and the abiotic environment. We conducted our surveys in the early to mid summer (June-July) when it is thought that grasshoppers, which have not yet reached their peak seasonal abundance, may be especially valuable prey for grassland birds. We found that the abundance of some subfamilies of grasshoppers was strongly correlated with prairie dog colonies, abiotic factors, and plant communities. However, because different grasshopper subfamilies used different habitats, the total abundance or biomass of grasshoppers was relatively consistent among sites within the grassland.

METHODS

Study area and survey design

Our study was conducted within the U. S. Forest Service (USFS)–Thunder Basin National Grassland in Converse, Weston, and Campbell counties, Wyoming (Fig. 1). Mean annual precipitation ranged from 25 – 35 cm, and generally fell during spring and summer (Porensky *et al.,* 2018). The study area included a mosaic of sagebrush grasslands and prairie dog colonies. In uncolonized areas, shrub species included Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britton and Rusby), and other sagebrush species. Common graminoids included blue grama (*Bouteloua gracilis* (Kunth) Lag. ex Griffiths), western wheatgrass (*Pascopyrum smithii* (Rydb.) Barkworth and D.R. Dewey), needle-and-thread (*Hesperostipa comata* (Trin. and Rupr.) Barkworth), and threadleaf sedge (*Carex filifolia* Nutt.).

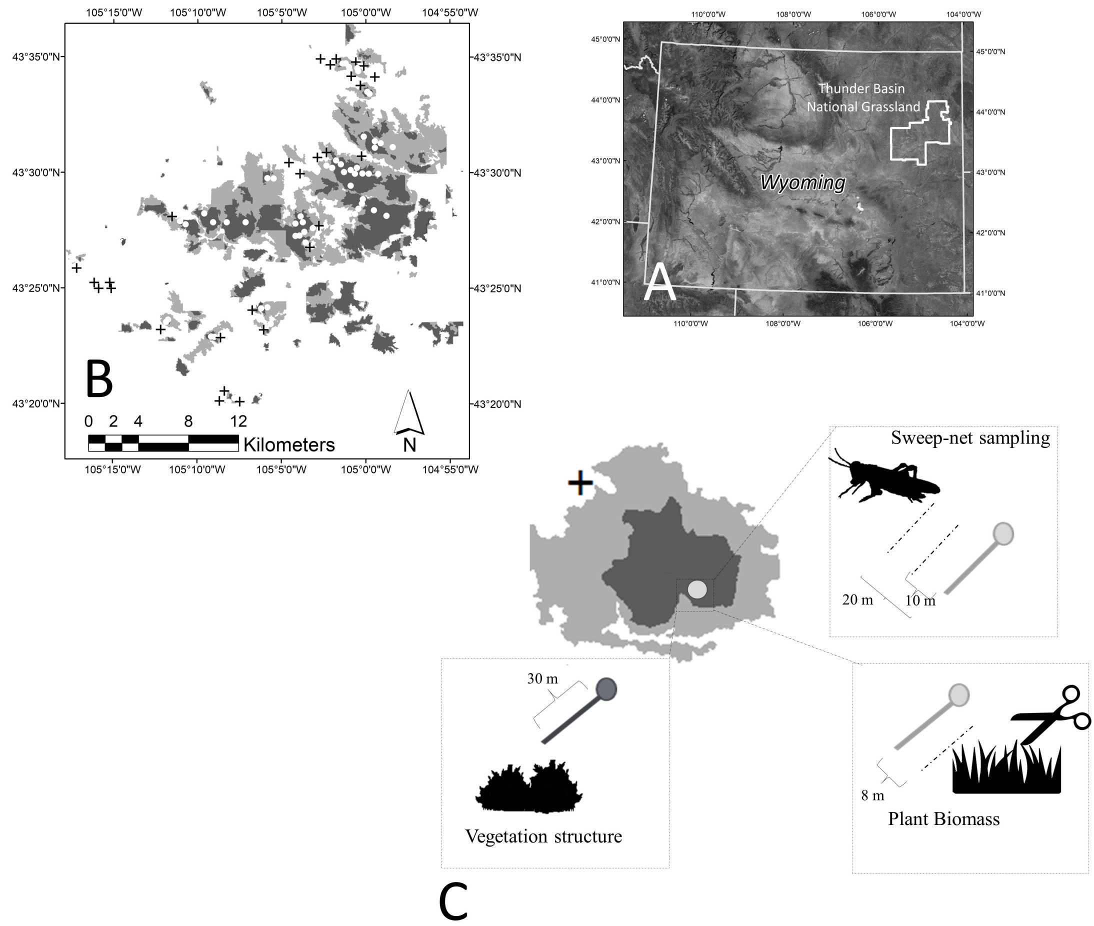

Figure 1. Landscape-scale sampling design. A) Location of Thunder Basin National Grassland within Wyoming, USA. B) Sampled sites (n = 88) in the ca. 400 km^2 study area in Thunder Basin National Grassland. Shading of dots indicates the presence of prairie dog, and grey regions on the map are the outline of mapped prairie dog colonies. C) Sampling design within each site, for estimating plant biomass, plant cover and structure, and arthropod biomass.

Prairie dog colonies were dominated by western wheatgrass, plains prickly pear (*Opuntia polyacantha* Haw.), and short-lived forb species.

To assess plant and insect responses to prairie dog disturbance (e.g., grazing, clipping, and burrowing), we used a point-transect-based sampling design (Fig. 1, Duchardt *et al.,* 2021). We collected data along transects established for a separate, multi-year study of songbird responses to prairie dog disturbance (Duchardt *et al.,* 2018, 2019). Each transect included 5–8 points (depending on colony size) spaced apart by 250 m. To capture landscape variability, transects were stratified into three groups: (1) "colony core" transects, which were randomly placed with the constraint that transects fell entirely within prairie dog colonies; (2) "sagebrush" transects, which were located in 10 known areas of extensive sagebrush habitat; and (3) "colony edge" transects, which were located randomly perpendicular to the edge of a prairie dog colony with the requirement that transects crossed the edge of a prairie dog colony with four points located outside the colony and one to four within the colony, depending on colony size. For this project, we sampled at 35 transects, including 7 colony core transects, 21 edge transects, and 7 sagebrush transects. Along each transect, we sampled at 1-3 points selected from each transect to maximize variability in distance to colony edge. In addition, when selecting points on colony edge transects, we ensured that at least 1 point was located outside of the colony, while 1-2 were within the colony. This resulted in 50 sampling points that were within prairie dog colonies, and 38 points that were outside of prairie dog colonies in 2017. At each site, we established three parallel sub-transects (Figure 1), one to measure vegetation structure, one to measure grasshoppers, and one to measure plant biomass.

Grasshopper sampling

We sampled grasshoppers and other arthropods along 30 m sub-transects that were located parallel to and 10-m away from the vegetation structure sub-transects at each point (Fig 1). Arthropod collection occurred between June 20 and July 5, 2017, and samples were collected between 11:00 AM and 4:00 PM during periods of fair weather with low (< 20 kph) wind speeds. Sampling was conducted such that in a single day, sites both inside and outside of prairie dog colonies were surveyed. All sweep samples were conducted using a 36-cm diameter sweep net and by a single individual (ISP) to avoid biases known from sweep sampling grasshoppers (O'Neill *et al.,* 2002). Arthropods along each transect were collected using sweep samples, completing 60 sweeps per 30-m sub-transect resulting in a sampling of roughly 60 m^2 of vegetation. Each evening following sampling, sweep samples were transferred to a modified Berlese funnel to collect arthropods in alcohol. After this, the bolus of vegetative material with remaining arthropods was treated with permethrin to kill arthropods, and all remaining arthropods were sorted from the sample and added to the ethanol arthropod collection tube. For biomass determination, all arthropods were dried for three days at room temperature, and total dry biomass was weighed separately for grasshoppers and other arthropods.

Grasshoppers in Wyoming can be divided into three major subfamilies: spurthroat (Melanoplinae), bandwing (Oedipodinae), slantface (Gomphocerinae). Members of each subfamily tend to have similar life histories to one another, apart from *Parapomala wyomingensis* (the Wyoming toothpick grasshopper) that has special traits to feed cryptically on tall grasses, in contrast to other members of the Gomphocerinae (Capinera and Sechrist 1982). Based on regional identification field guides and keys, grasshoppers were identified to species, except in cases where degraded grasshopper nymphs were unidentifiable (Capinera and Sechrist 1982; Pfadt 1994; Schell *et al.,* 2005). We also grouped grasshoppers based on their phenology, as identified in the Wyoming Grasshopper Handbook (Schell *et al.,* 2005). The late/overwintering phenological category (Table 1) refers to grasshoppers that overwinter as adults. Grasshopper 'scares', in which grasshoppers were observed jumping away, and not captured, were counted and recorded during sweep net sampling, though not identified to species or subfamily. Wind speed (using a handheld anemometer [Wind Wizard, Davis Instruments, Hayward, CA]) was recorded at each point as the average of the maximum and minimum wind speed measured over one minute just prior to sweep sampling.

Surveys of prairie dogs, vegetation, and abiotic environment

In 2017, the total extent of prairie dog colonies on the public lands within our study area was > 16,000 ha, which at the time represented the largest known colony complex in the world (Duchardt *et al.,* 2019). Individual colonies within the complex ranged from 20 ha to 4,000 ha in size, the latter of which is an order of magnitude larger than the size of prairie dog colonies typically found on National Grasslands in the western Great Plains over the past two decades (Johnson and Collinge 2004; Cully Jr *et al.,* 2010). Prairie dog colony boundaries from 2017 were used in this study. Colony boundaries were operationally defined based on the presence of burrow entrances and clipped vegetation (Duchardt *et al.,* 2019).

We collected vegetation structure, cover, and biomass data at each survey point. Line-point intercept data were collected every meter along 30-m sub-transects radiating from each point, perpendicular to the axis of the survey transect (Fig. 1), (Herrick *et al.,* 2010). We measured visual obstruction, a metric incorporating both vegetation height and density, using a Robel pole (Robel *et al.,* 1970) at 5-m increments along each sub-transect in 2017. We also collected herbaceous cover data by functional group along the same sub-transects using line point intercept (LPI) method in 2017. The major functional groups represented in this measure were percent cover of annual bromes, annual forbs, C4 perennial graminoids, and C3 perennial graminoids. Graminoids (grasses and their relatives) in western grasslands are often divided into C3 and C4 photosynthesis groupings because these grasses have different phenological patterns and respond differently to stresses (Morgan *et al.,* 2011). In 2015, we collected shrub cover data by species along these sub-transects using the line-intercept method (Herrick *et al.,* 2010). Because shrub canopy cover likely varies minimally over 2 years, we used these data to estimate percent cover at each point in 2017 (Duchardt *et al.,* 2021). From July-August 2017, we established additional 30 m sub-transects parallel to and 8m away from the vegetation structure sub-transects (Fig. 2). At 10 m and 20 m along this new sub-transects, we placed a ½ x 1m quadrat on the side

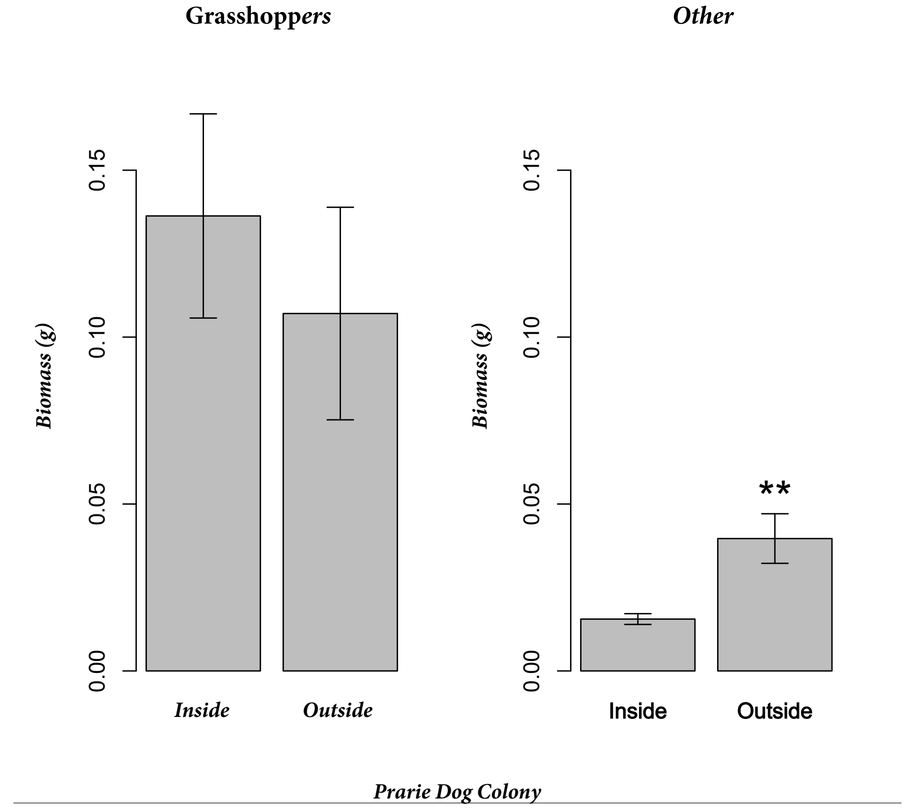

Figure 2: The total biomass of grasshoppers and other arthropods at sites inside and outside of prairie dog colonies. Significance is shown as ** P < 0.01 based on generalized linear models with quasi-Poisson error distributions. Sample size is 50 sites inside and 38 sites outside prairie dog colonies. Bars are mean +/- standard error.

of the tape facing away from the established vegetation structure sub-transects. We clipped all herbaceous biomass rooted inside the quadrat to estimate total vegetation biomass.

We quantified the topography within 100 m of each point. We used a digital elevation model to generate a topographic roughness index (roughness) and topographic wetness index (TWI; Gesch *et al.,* 2002; Porensky *et al.,* 2018). We collected soil cores at 10 and 20 m along each biomass transect. We used a standard soil auger (7 cm diameter) and took a composite sample of soil from 0-10 cm depth. Samples from the two cores per transect were pooled and a subsample of the homogenized material was extracted for texture analysis. Subsamples were air dried and passed through a 2-mm sieve. Soil particle size was determined using the hydrometer method (Bouyoucos 1962). In another work, we quantified bird communities at each site (Duchardt *et al.,* 2018). While birds are major predators of grasshoppers, past work in this system has shown that the abundance of grassland birds was unrelated to grasshopper biomass (Duchardt *et al.,* 2021), so we do not consider effects of birds in the present study.

Statistical analysis

We used generalized linear models (GLMs) with negative binomial error distributions to analyze the association of grasshoppers and other arthropods with prairie dog colonies and characteristics of vegetation and abiotic environment. For grasshopper total biomass and abundance of each subfamily of grasshoppers, we constructed two models: one in which grasshopper abundance or biomass was predicted by the presence of a prairie dog colony, and the second in which grasshopper abundance or biomass was predicted by the following suite of aspects of plant communities, vegetation structure, and abiotic environment: roughness, TWI, percent sand of soil, total plant biomass (g), percent cover of sagebrush, and percent cover of cheatgrass, annual forbs, C4 perennial grasses, and C3 perennial graminoids. To limit this second set of models to the most relevant environmental predictors of grasshopper abundance, we used stepwise AIC model reduction, implemented by the function stepAIC in the R package MASS with a forward and backward stepwise search. Negative binomial GLMs were implemented in the R package MASS (Venables and Ripley 2013; R Core Team 2019). For cases in which prairie dogs affected the abundance of a subfamily of grasshoppers, we tested whether the vegetation or environmental factors that were retained in AIC model reduction as predictors of that subfamily of grasshoppers differed inside and outside of prairie dog colonies. We also analyzed grasshopper biomass and abundance of each of the three grasshopper subfamilies as a function of distance inside the edge of a prairie dog colony (where greater values indicate greater centrality within a colony) to test whether grasshopper biomass and abundance differed between the interior and periphery of prairie dog colonies. To assess sampling efficacy, we conducted two additional tests of pair-wise correlation using Pearson's r: between total grasshopper counts and total number of grasshopper 'scares', and between total grasshopper counts and average wind speed at the time of sampling.

RESULTS

Description of Grasshopper Sampling

We collected 483 grasshopper individuals. Of those, 251 grasshoppers were identifiable to species, and an additional 36 were identifiable only to subfamily (Table 1). The most abundant grasshopper species were *Trachyrhachys kiowa*, *Cordillacris occipitalis*, *Psoloessa delicatula*, and *Melanoplus sanguinipes* (Table 1). The remaining 196 individuals (mostly early instar nymphs) were not identifiable to subfamily. Total grasshopper net captures were strongly and positively correlated with the number of 'scares' of grasshoppers ($r = 0.79$, $P < 0.0001$), with a ratio of 1.65 field scares for every grasshopper caught. The ratio of grasshoppers caught to field scares did not differ on and off prairie dog colonies ($z = -0.37$, $P = 0.72$), indicating that the rate of capture was not substantially affected by major habitat differences. The total number of grasshoppers caught was not related to wind speed during sampling ($r = 0.15$, $P = 0.15$). The total number of grasshoppers caught per sampling unit (60 sweeps along a 30-m transect) was relatively low, an average of 5.5 grasshoppers caught per sampling unit.

Table 1. Grasshopper species collected in 2017 Thunder Basin insect survey.

SPECIES	**SUBFAMILY**	**SEASONALITY**	**SITES PRESENT**	**TOTAL INDIVIDUALS**
Trachyrhachys kiowa Thomas	bandwing (Oedipodinae)	intermediate	24	65
Cordillacris occipitalis Thomas	slantface (Gomphocerinae)	early	21	35
Psoloessa delicatula Scudder	slantface (Gomphocerinae)	Late/overwintering	19	33
Eritettix simplex Scudder	slantface (Gomphocerinae)	Late/overwintering	10	10
Melanoplus sanguinipes Fabricius	spurthroat (Melanoplinae)	early	12	37
Aulocara elliotti Thomas	slantface (Gomphocerinae)	early	9	18
Paropomala wyomingensis Thomas	slantface (Gomphocerinae)	intermediate	8	17
Derotmema haydeni Thomas	bandwing (Oedipodinae)	intermediate	6	6
Cordillacris crenulata Bruner	slantface (Gomphocerinae)	intermediate	5	6
Melanoplus confusus Scudder	spurthroat (Melanoplinae)	very early	3	3
Ageneotettix deorum Scudder	slantface (Gomphocerinae)	early	4	10
Aeropedellus clavatus Thomas	slantface (Gomphocerinae)	very early	2	2
Melanoplus occidentalis Thomas	spurthroat (Melanoplinae)	early	2	3
Metator pardalinus Saussure	bandwing (Oedipodinae)	intermediate	2	2
Arphia conspersa Scudder	bandwing (Oedipodinae)	Late/overwintering	1	1
Melanoplus foedus/packardii Scudder	spurthroat (Melanoplinae)	early	1	1
Opeia obscura Thomas	slantface (Gomphocerinae)	Late/overwintering	1	1
Xanthippus corallipes Haldeman	bandwing (Oedipodinae)	Late/overwintering	1	1

Relationship with Prairie Dog Colonies

Biomass of all grasshoppers was not different between sites inside versus outside of prairie dog colonies (t = -1.14, P = 0.15, Fig. 2); however, the biomass of other arthropods was greater outside prairie dog colonies (t = 3.5, P = 0.001, Fig. 2). Of the subfamilies of grasshoppers, Melanoplinae were more abundant inside than outside prairie dog colonies (t = -2.6, P = 0.01, Fig. 3). The abundance of Gomphocerinae and Oedipodinae grasshoppers was not different between sites inside and outside prairie dog colonies (t = -1.1, P = 0.29; t = -0.90, P = 0.37 respectively, Fig. 3). *Paropomala wyomingensis* (the single tall-grass associated Gomphocerinae grasshopper species) was more abundant at sites outside of prairie dog colonies (t = 2.2, P = 0.03). When grouped by phenology, early season grasshopper species were more abundant inside prairie dog colonies, and grasshoppers with all other phenologies were not affected by prairie dog colonies (Fig. 3). Trends in early-season grasshoppers were largely driven by the abundance of the Mela-

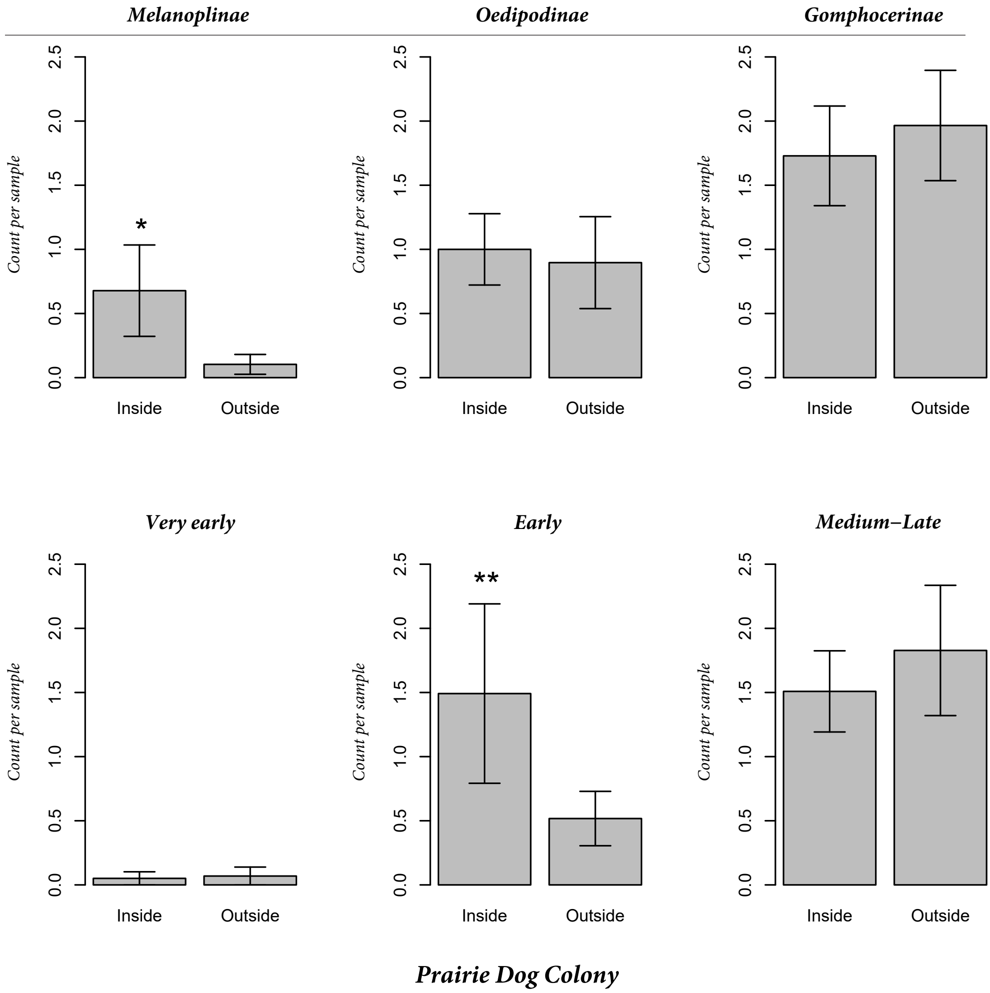

Figure 3. Grasshopper captures inside or outside of prairie dog colonies. Grasshoppers were grouped by subfamily (Melanoplinae, Oedipodinae, or Gomphocerinae [excluding *P. wyomingensis*]), or phenology (very early, early, and intermediate-late). Sample size is 50 sites inside and 38 sites outside prairie dog colonies. Significance is shown as * P < 0.05, ** P < 0.01 based on a negative binomial generalized linear model. Bars are mean +/- standard error.

noplinae grasshopper, *Melanoplus saguinipes*, and the Gomphocerinae grasshopper, *Cordillacris occipitalis*.

Looking only within prairie dog colonies, the biomass of grasshoppers was greater at locations more central within the colony (t = 4.0, P = 0.0002). This trend was largely driven by Melanoplinae and Gomphocerinae grasshoppers, which were more abundant at locations more central to prairie dog colonies (Melanoplinae , z = 3.3, P=0.001, Gomphocerinae : z = 3.4, P = 0.001, Fig. 4). Notably, this trend was heavily influenced by a single sampling location with high abundance of Melanoplinae and Gomphocerinae grasshoppers (Fig. 4), though removal of this sampling point still suggested increasing abundance of these subfamilies at more central sites (Melanoplinae: z = 1.9, P = 0.05; Gomphocerinae : z = 2.5, P = 0.01). The abundance of Oedipodinae grasshoppers did not differ among sites with varying centrality to prairie dog colonies (z = -0.1, P = 0.93, Fig. 4).

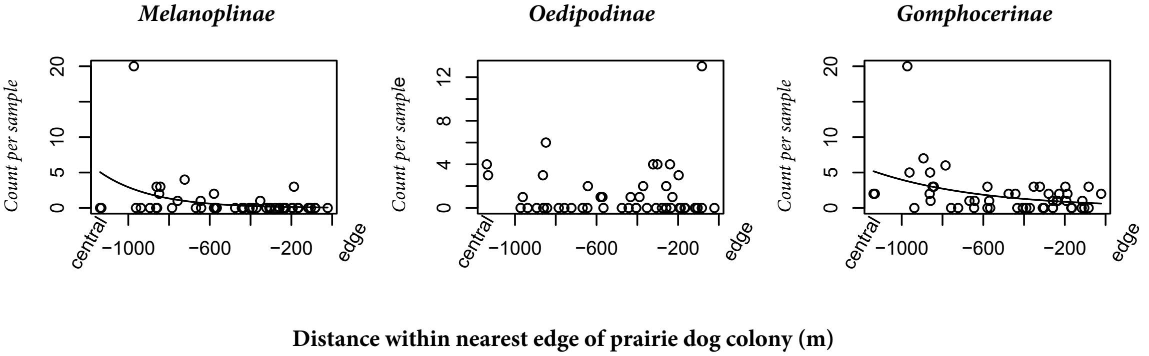

Figure 4. Grasshopper captures within prairie dog colonies based on the distance within the edge of the colony of each site. Grasshoppers were grouped by subfamily (Melanoplinae, Oedipodinae, or Gomphocerinae [excluding *P. wyomingensis*]). Significant trend lines from a negative binomial generalized linear model are shown.

Association with vegetation, plant community, and abiotic environment

Total grasshopper biomass was not associated with any measured aspect of vegetation structure, plant community, or abiotic environment, as a null model best fit the data (Table 2). The abundance of Melanoplinae grasshoppers was lower with increasing sagebrush and C3 graminoid cover (Table 2). The abundance of Oedipodinae grasshoppers was high in low-lying areas (areas with high TWI) and high cover of C4 grasses, but lower in areas with a high abundance of cheatgrass (Table 2). Gomphocerinae grasshoppers (excluding *P. wyomingensis*) were associated with sites with low vegetation structure (Table 2). In all cases, models had low explanatory power (models explained only between 6% and 12% variation in the abundance of a grasshopper subfamily).

Because Melanoplinae grasshoppers were associated with prairie dog colonies, we tested whether this association might be caused by the effect of prairie dogs on vegetation in a way that could increase habitat suitability for Melanoplinae grasshoppers. The two aspects of vegetation associated with Melanoplinae abundance were sagebrush cover and cover of C3 graminoids. The cover of sagebrush was 6 times lower on prairie dog colonies than off (t = 5.05, P = 0.0001), and the cover of C3 perennial graminoids was similar inside and outside of prairie dog colonies (t = 0.49, P = 0.62).

Table 2. Reduced models** of the total biomass of grasshoppers and the abundance of grasshoppers from the three subfamilies (Meloplinae, Oedipodinae, and Gomphocerinae).

Response	Predictor	Scaled Estimate (*P*)	Model R2 (*P*)
Grasshopper biomass	NULL	--	--
Melanoplinae abundance	Sagebrush cover	-0.96 (0.15)	0.06 (0.07)
	C3 grass cover	-0.61 (0.17)	
Oedipodinae abundance	TWI	0.45 (0.06)	0.12 (0.01)
	Cheatgrass cover	-1.04 (0.04)	
	C4 grass cover	0.38 (0.07)	
Gomphocerinae abundance	Vegetation height	-0.61 (0.002)	0.11 (0.002)

** Models reduced using stepwise AIC. Full models included the following predictors: vegetation height, roughness, TWI, percent sand of soil, cover of sagebrush, total plant biomass, cover of cheatgrass, biomass of annual forbs, cover of C4 grasses, and cover of C3 grasses.

DISCUSSION

The composition of grasshopper assemblages at the subfamily level differed inside versus outside of prairie dog colonies, but the total biomass of grasshoppers was not affected by prairie dog colonies. Moreover, when we compared sampling locations with varying centrality within prairie dog colonies, we found, similarly to Russell and Detling (2003), that grasshopper biomass, driven largely by more abundant Melanoplinae grasshoppers, was greater at more central prairie dog locations. This suggests that interactions among prairie dogs and grasshoppers does not solely drive landscape-level patterns in grasshopper biomass in Thunder Basin.

When we compare our results with other studies following the association of grasshoppers and prairie dogs, it is clear that the effect of prairie dogs on grasshopper biomass varies by location (Table 3). In one study in Badlands National Park, USA, total grasshopper abundance tended to be higher inside than outside of prairie dog colonies, a trend that was largely driven by a high abundance of spurthroat (Melanoplinae) and bandwing (Oedipodinae) grasshoppers (Russell and Detling 2003). In contrast, other studies have found that prairie dogs decrease grasshopper biomass or abundance. In New Mexico, grasshopper abundance was lower at sites associated with prairie dog colonies, though this effect reversed when kangaroo rats were also present at a site (Davidson and Lightfoot 2007). A manipulative study in Oklahoma that added prairie dogs to sites found that prairie dog colonies reduced grasshopper biomass by 300% (O'meilia *et al.,* 1982). Likewise, when prairie dogs were removed from sites in Northern Mexico, grasshopper abundance increased (Davidson *et al.,* 2010). Another study in Badlands National Park, USA reported a lower abundance of grasshoppers on prairie dog colonies than off (Agnew *et al.,* 1987). When interpreting our results in light of these past studies, it is important to note that the total density of grasshoppers observed in our study was comparatively low. This is likely due, in part, to our focus on early- to mid-summer grasshopper communities (where our sampling occurred in late June and early July). Later season surveys, and particularly those that take place during grasshopper outbreak years, observe substantially greater grasshopper densities (e.g. Przybyszewski and Capinera 1990).

Despite variable effects of prairie dogs on grasshopper biomass, we found evidence that prairie dog colonies supported different grasshopper composition than non-colony sites. This is consistent with previous work suggesting that prairie dog colonies may support unique birds, mammals, and plant species, thereby enhancing landscape level biotic heterogeneity and beta diversity (Duchardt *et al.,* 2018, 2021). This is also consistent with previous studies focused on grasshoppers. Of the five studies that have looked for shifts in the abundance of grasshopper subfamilies or species in prairie dog colonies, all have found evidence for changes in species composition or relative abundance (Table 3).

To understand why prairie dogs might have variable effects on grasshopper abundance and composition, it is worthwhile considering how prairie dogs impact vegetation at our site and how this effect may differ among sites and years. In the Thunder Basin National Grassland, the dominant long-term effect of prairie dogs on vegetation is a removal of shrubs (predominantly sagebrush), reduction in vegetation structure and grasses, and an increase in short-lived forbs (Duchardt *et al.,* 2021). In Thunder Basin, during average rainfall years, prairie dogs do not substantially reduce total plant biomass (Connell *et al.,* 2019, Duchardt *et al.,* 2021). Notably, the grasshopper subfamily most associated with prairie dog colonies (and also with the sites most central to colonies) at our site (spurthroats, Melanoplinae) includes many generalist grassland species that feed on grasses and forbs. Indeed, because these grasshoppers were associated with areas with low shrub cover, and prairie dogs actively reduce shrub cover (Table 2, Connell *et al.,* 2018), this indirect effect is likely the way in which prairie dogs promoted this subfamily of grasshoppers. Prairie dogs could have numerous plausible impacts on grasshoppers because they affect vegetation that grasshoppers feed on (Duchardt *et al* 2021), they affect birds that prey on grasshoppers (Duchardt *et al.,* 2021), and, while predominantly herbivorous, are even known to occasionally prey on grasshoppers directly. Prairie dogs may have other effects on other grasslands. Because different grasshopper species are associated with different plant communities (Chapman and Joern 1990; Kemp *et al.,* 1990), and the composition of grasshopper communities varies tremendously among years (Capinera 1987; Kemp 1992), it is likely that the effects of prairie dogs on grasshopper abundance may vary widely from year to year and from site to site. Moreover, grasshopper communities differ phenologically, such that the association between grasshoppers and prairie dogs may vary predictably based on the time of year of sampling. Our study was conducted at a single time point (June-July), chosen because of potential importance of grasshoppers as a food source for birds nesting at that time of year. Nevertheless, when we divide grasshopper species by their known phenologies, we find a clear indication that early-season grasshoppers may have a more positive association with prairie dogs than late-season species. The abundance of short-lived forbs, which also have early-season phenology, on prairie dog colonies may be one factor driving this pattern. However, given our short sampling time-frame, it remains to be seen whether this association with species-level phenology translates to actual differences in how prairie dogs affect grasshopper biomass over the season.

Aside from prairie dog impacts, evidence points to grasshopper communities being closely tied to vegetation composition and structure over environmental gradients and management types (Stoner and Joern 2004). As such, processes that affect vegetation often impact grasshopper communities, though sometimes in variable ways. For example, studies have found that grazing has increased grasshopper diversity (Joern 2005), increased grasshopper density

Table 3. A summary of prairie dog effects on grasshoppers in the literature

Study	Abundance or Biomass	Effect on Community Composition	Location	Habitat	Latitude	study type
Russel and Detling 2003	positive	Yes, skewed community toward Oedipodinae grasshoppers	Badlands National Park	mixed-grass prairie	43.86	survey
current study	none	Yes, increased Melanoplinae	Thunder Basin National Grassland	shrub-prairie transition	43.46	survey
Omeilia *et al.,* 1983	negative	unknown	Southern Great Plains Experimental Range, Oklahoma	shortgrass prairie	36.22	experimental addition
Davidson *et al.,* 2010	negative	Yes, loss of dominant *Melanoplus*, shift to bare-ground species	Chihuahua, Mexico, El Uno Ecological Reserve	annual desert grassland	30.9	experimental removal
Agnew *et al.,* 1987	negative	unknown	Badlands National Park	mixed-grass prairie	43.86	survey
Davidson and Lightfoot 2007	negative	Yes	Sevilleta National Wildlife Refuge, New Mexico	Chihuahuan desert	34.4	survey
Davidson and Lightfoot 2007	negative	Yes	Janos-Casas Grandes, Mexico	Chihuahuan desert	30.1	survey

by favoring a very dominant species (Jauregui *et al.,* 2008), and had little effect on grasshopper composition (Joubert *et al.,* 2016). In contrast, despite experimental evidence that avian predation alters grasshopper fitness, population growth, and communities (Bock *et al.,* 1992; Belovsky and Slade 1993) there is little evidence that grasshopper abundance is correlated with avian predator abundance over natural landscapes in the ways predicted by these studies (Greer and Anderson 1989; Hamer *et al.,* 2006; Duchardt *et al.,* 2021). Despite a significant literature on the factors that structure grasshopper communities, much remains to be learned.

The vegetation and abiotic associations of grasshoppers in our study were consistent with what is known about the natural history of grasshopper subfamilies. Melanoplinae grasshoppers were associated with prairie dog colonies and with sites with low shrub and C3 perennial graminoid cover. *al.,* 2005). Oedipodinae grasshoppers were associated with low-lying regions with C4 grasses and less cover of cheatgrass, consistent with the affinity of species within this subfamily (such as *T. kiowa*) for native C4 bunchgrasses like *Bouteloua gracilis* (Craig *et al.,* 1999; Schell *et al.,* 2005). Gomphocerinae grasshoppers, with the exception of *Parapomala wyomingensis*, were associated with lower vegetation structure, consistent with the affinity of many species within this subfamily fr short statured grasses (Craig *et al.,* 1999).

The Thunder Basin system is highly dynamic because prairie dog abundances change cyclically in response to epizootic plague. Additionally, the Thunder Basin Grassland represents a cline from a shrub-dominated system to a grassland system, and prairie dogs affect the patchwork of shrubs and grassland. To understand the dynamics in this system, it will be useful to re-survey biota at intervals along the prairie dog -plague cycle in order to understand the long-term impacts of prairie dogs on other organisms and how those systems recover following prairie dog die-offs. Our study establishes a baseline for grasshopper communities at a high point of prairie dog abundance (total area covered by prairie dog colonies in 2017 exceeded 16,000 hectares, making this the largest known colony complex in the world). We hope that those publicly available data https://doi.org/10.5066/P9ICAONC will help form the foundation for future work to explore these dynamics.

Our study provides a unique look at grasshopper communities and their association with prairie dogs and vegetation in a large grassland-shrubland system. We find that the composition of grasshoppers, but not their total biomass, varied based on prairie dogs and vegetation.

ACKNOWLEDGMENTS

We thank Dave Pellatz and the Thunder Basin Grassland Prairie Ecosystem Association (TBGPEA) for logistical support in sampling arthropods and financial support in processing those samples and mapping prairie dog colonies. This work is part of the Thunder Basin Research Initiative. We thank Tim McNary for identifying grasshoppers. Ana Davidson provided useful advice throughout the study. David Eads provided comments that improved the manuscript. LMP was supported by the USDA ARS Rangeland Resources and Systems Research Unit. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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