

Habitat Relationships among Grasshoppers  
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Habitat Relationships Among Grasshoppers (Orthoptera:Acrididae) at the  
Western Limit of the Great Plains in Colorado

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Abstract. -- We measured grasshopper densities on 66 shortgrass, mixed grass, tallgrass, and hayfield plots on Boulder, Colorado, open space in 1995-1996. Grasshoppers as a group, and most species individually, were more abundant on relatively sparse short and mixed grass prairie plots than on lush hayfields and tallgrass plots - a result consistent with the hypothesis that most species require warm and sunny open ground for survival and reproduction. Bandwinged grasshoppers (Oedipodinae) were particularly associated with open ground in shortgrass prairies, while spur-throated grasshoppers (Melanoplinae) as a group were most abundant in mixed grass prairies with a high percentage of forb versus graminoid cover. Slant-faced grasshoppers (Gomphocerinae) were the most uniformly distributed among habitats, but were generally associated with plots including relatively high proportions of grass versus forb cover.

While 20 of the 25 most common grasshoppers on Boulder Open Space occurred in all four grassland types, each habitat was dominated by a distinctive set of species. However, numerically dominant grasshoppers on Boulder short, mixed, and tallgrass prairies only loosely resembled groups of dominant species in the same habitats elsewhere on the Great Plains. While most Great Plains grasshoppers are widely distributed, they apparently are numerically responsive to combinations of environmental conditions expressed at local scales, rather than characterizing particular grassland types throughout the Great Plains as a whole.

## Introduction

Insects in general, and grasshoppers in particular, are dominant above-ground herbivores in most grassland ecosystems, but much remains to be learned about the structure and function of their communities (Otte, 1981; Curry, 1994; Tscharrntke and Greiler, 1995). Most grasshoppers of the North American Great Plains are widely distributed, with ranges that encompass eastern tallgrass, western shortgrass, and northern mixed grass prairies that comprise the natural vegetation across broad expanses of this region (Daubenmire, 1978; Otte, 1981, 1984; Sims, 1988; Pfadt, 1994). Local and regional studies suggest that many Great Plains grasshoppers have distinct habitat requirements, despite their large ranges (Joern, 1982; Capinera and Thompson, 1987; Evans, 1988; Kemp et al., 1990; Quinn and Walgenbach, 1990; Welch et al., 1991; Kemp, 1992). However, we are not aware of any previous investigation attempting a quantitative comparison of grasshopper densities among short, mixed, and tallgrass prairies. One difficulty is the notorious and apparently climate-related volatility of many grasshopper populations (Capinera and Horton, 1989; Joern and Gaines, 1990; Kemp, 1992). These fluctuations can make it difficult to distinguish fundamental habitat differences from temporal variations in widely-separated sites sampled in different years (but see Joern and Pruess, 1986).

The arid plains of eastern Colorado are, or were, dominated by relatively uniform shortgrass prairie. However, fine-scale mosaics of short, mixed, and tallgrass prairie occur together where the plains meet the eastern edge of the Colorado Rocky Mountains, apparently the result of increased precipitation, topographic heterogeneity, and differences in soils

and land-use history (Livingston, 1952; Branson et al., 1965; Moir, 1969; Bennett, 1997). This circumstance permitted a local comparison of grasshoppers occupying the three fundamentally different sorts of Great Plains grasslands, at a local scale where their regional populations would be experiencing similar patterns of temperature and precipitation, and presumably where individuals could move among the habitats available. That was the objective of the present study.

Grasslands at the base of the Rocky Mountains in Colorado (the so-called Front Range Corridor) are rapidly being fragmented and lost to development (Mutel and Emerick, 1992; Long, 1997). Some of the largest remaining stands are part of municipal open space owned and managed by the City of Boulder, Colorado. In 1995-1996, we quantified densities of grasshoppers on 66 200-m diameter plots on Boulder open space, placed systematically to include stands of short, mixed, and tallgrass prairie, as well as irrigated hayfields that have replaced many native grasslands within the past 150 years. We then compared grasshopper populations among the grassland types, and correlated their densities with vegetative attributes of the plots. Our objectives were (1) to reveal individual species' habitat preferences, (2) to determine if the different grassland plant communities supported distinctive grasshopper assemblages, and (3) to compare our results with those from other studies across the Great Plains.

#### Study Area and Plots

City of Boulder Open Space includes over 10,000 ha of farm and rangeland at about 1,700 m elevation, around the northern, eastern, and southern city limits, all against a Rocky Mountain foothills backdrop of ponderosa pine (*Pinus ponderosa*) savanna. Plains habitats include

riparian corridors along streams, tallgrass prairies and agricultural hayfields in adjacent lowland floodplains, and mixed and shortgrass prairies on upland slopes and benches (Bock et al., 1995). Soils are principally clay or sandy loams (Moreland and Moreland, 1975). Average annual precipitation (47 cm) is sufficient to support mixed grass prairie on all of the uplands, so that shortgrass prairie occurs only in comparatively heavily-grazed areas.

We established 66 200-m diameter circular plots on Boulder open space grasslands in the fall of 1993. Preliminary floristic surveys were conducted in 1994. Each plot was categorized to its predominant grassland type, based on extensive plant frequency data collected in July of 1995 and 1996 (Bennett, 1997). Botanical nomenclature was taken from Great Plains Flora Association (1986), while native versus exotic status of each plant species was determined from Weber (1995). Types and numbers of plots, and their predominant plant species, were as follows:

*Shortgrass prairie* (13 plots). -- These upland plots had a recent or current history of grazing by cattle, horses, and/or black-tailed prairie dogs (*Cynomys ludovicianus*). The most abundant native grasses on shortgrass plots were *Agropyron smithii*, *Bouteloua gracilis*, and *Buchloë dactyloides*. Common native forbs were *Artemisia frigida*, *Plantago patagonica*, and *Sphaeralcea coccinea*. Two common exotic annual grasses were *Bromus tectorum* and *B. japonicus*, while the most abundant exotic forbs were *Alyssum minus* and *Convolvulus arvensis*.

*Mixed grass prairie* (21 plots). -- These upland plots were ungrazed or only lightly-grazed, and were dominated by varying mixtures of mid-height and short grasses and sedges, depending on soils and topography. Common native graminoids included *Agropyron smithii*,

*Andropogon gerardii*, *A. scoparius*, *Aristida purpurea*, *Bouteloua gracilis*, *B. curtipendula*, *Carex heliophila*, *Koeleria pyramidata*, *Panicum virgatum*, *Stipa comata*, and *S. neomexicana*. The most abundant native forbs were *Ambrosia psilostachya*, *Artemisia ludoviciana*, *Aster falcatus*, *Helianthus pumilis*, and *Psoralea tenuiflora*. Common exotics on mixed grass plots included *Alyssum minus*, *Bromus japonicus*, *Poa pratensis*, *P. compressa*, and *Tragopogon dubius*.

**Tallgrass prairie** (11 plots). -- These plots occurred in lowland floodplains or on low benches with cobbly soils and high water tables. Some were winter-grazed by cattle, but all remained undisturbed through the summer growing season. They were dominated by mid-height and tall grasses characteristic of the True Prairie of the eastern Great Plains (Risser et al., 1981): *Andropogon gerardii*, *A. scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, and *Sporobolus asper*. The most abundant native forbs on tallgrass plots were *Ambrosia psilostachya*, *Aster falcatus*, *Dicanthelium oligosanthos*, *Grindelia squarrosa*, and *Prunella vulgaris*. There were many exotic species on tallgrass plots, including the forbs *Cichorium intybus*, *Plantago lanceolata*, *Taraxacum officinale*, and *Trifolium pratense*, and a variety of cool-season meadow grasses planted for pasture improvement (*Agrostis stolonifera*, *Festuca pratensis*, *Phleum pratense*, and *Poa pratensis*).

**Hayfields** (21 plots). -- These lowland plots were flood-irrigated in early summer, and mowed between mid-July and early August. Most also were winter-grazed by cattle. Some included remnants of the tallgrass prairies they replaced, but all were dominated by exotic species such as alfalfa (*Medicago sativa*), and a series of cool-season pasture grasses, including

*Bromus inermis*, *Festuca pratensis*, *Dactylis glomerata*, and *Phleum pratense*.

### Methods

*Vegetation cover.* – Vegetation canopy cover was sampled on each of the 66 plots in June and again in August of 1995 and 1996. During each sampling period, 100-m transects were established running due east and due west from each plot center. An optical point projector was set at 4-m intervals along each transect, and vegetation was sampled at six randomly located points within 1-m of the point projector at each setting. This resulted in 300 points per plot per sampling period ( $n = 1,200$  total points per plot over the two years). Each point was classified as unvegetated, or as covered by one or more of the following four vegetation categories: native graminoids, exotic graminoids, native forbs, and/or exotic forbs. Results from the four sampling periods were averaged to generate a single set of vegetation cover descriptors for each plot.

*Grasshopper densities.* – We collected sweep net samples of grasshoppers off each plot in the summer of 1994, to build a reference collection. Grasshopper densities then were estimated on each plot four times per summer, from late May to early September, in both 1995 and 1996. During each sampling period, 10  $0.5\text{-m}^2$  wire hoops were distributed along each of four 100-m radii following cardinal compass directions out from the center of each plot ( $n = 40$  hoops per plot). Hoops were undisturbed for three days, and then a single observer (always the senior author) approached each hoop and identified adult grasshoppers as they were flushed out, following methods in Thompson (1987). While the hoop method may be best-suited to habitats with low and relatively sparse

vegetation, we found that it was possible to confidently identify grasshoppers in hoops on tallgrass and hayfield plots, and we made a special effort to flush all individuals from the heavier cover in these habitats. It should be noted that none of our plots on Boulder open space were in vegetation as tall as that of the tallgrass prairie in eastern Kansas, where the hoop method proved impractical (Evans et al., 1983).

Results of our eight 40-hoop samples were pooled to generate one estimate of average density per hoop for each species on each plot over the two year sampling period. These estimates were converted to densities/100 m<sup>2</sup>, to facilitate comparisons with certain other studies (e.g., Capinera and Thompson, 1987; Fowler et al., 1991).

*Statistics.* -- Combined densities of three acridid subfamilies, total grasshoppers, and attributes of vegetation cover, were compared among habitats using oneway analysis of variance, with Scheffé a-posteriori pairwise comparisons of means. Because data for most individual grasshopper species failed to meet criteria for parametric analyses, their ranked densities among habitats were compared using the Kruskal-Wallis H statistic, with a-posteriori protected rank-sum tests (Welkowitz et al., 1991) between each pair of habitats. Overall faunal similarities among habitat types were estimated by calculating both Renkonen percentage similarities (Krebs, 1989) and Spearman rank correlations between pairs of habitats, based on their grasshopper population densities. Finally, we computed Spearman rank correlations between grasshopper densities and vegetation cover variables, to examine relationships between individual grasshopper densities and three habitat variables: (1) the amount of unvegetated ground, (2) the relative canopy cover of grasses versus forbs, and (3) the relative canopy cover of native versus exotic species.



## Results

*Grassland faunas.* -- We collected 48 species of Acrididae on Boulder Open Space in 1995-1996 (Appendix). Species richness averaged higher on shortgrass (20.3 species) and mixed grass plots (18.4 species) than in either tallgrass (12.1 species) or hayfields (8.4 species; Fig. 1).

An average 84.1 total adult grasshoppers/100m<sup>2</sup> occurred on shortgrass prairie plots (Fig. 1). Eight species comprised over 70% of these individuals: *Aulocara elliotti*, *Trachyrhachys kiowa*, *Melanoplus sanguinipes*, *Eritettix simplex*, *Opeia obscura*, *Phoetaliotes nebrascensis*, *Ageneotettix deorum*, and *Arphia conspersa*. Of these, only the first two were significantly more abundant in shortgrass than in any other habitat, and no species was restricted to it (Table 1).

Grasshoppers in the subfamily Melanoplinae dominated mixed grass prairie plots (Fig. 1), where seven species (six melanoplines) made up over 70% of the average 122.1 individuals/100m<sup>2</sup>: *Melanoplus keeleri*, *M. packardii*, *M. sanguinipes*, *M. femurrubrum*, *Phoetaliotes nebrascensis*, *Hypochlora alba*, and *Eritettix simplex*. Only the first two *Melanoplus* were uniquely abundant in this habitat (Table 1).

Tallgrass prairies supported an average 54.1 grasshoppers/100m<sup>2</sup>, 70% of which were distributed among five species: *Melanoplus femurrubrum*, *M. bivittatus*, *Phoetaliotes nebrascensis*, *Eritettix simplex*, and *Aulocara elliotti*. No grasshopper species was significantly more abundant in tallgrass than in any other habitat, but counts of *M. bivittatus* and *Chortophaga viridifasciata* were highest in tallgrass (Table 1).

Three species made up nearly 75% of the average 41.7 individuals/100m<sup>2</sup> counted on hayfield plots: *Melanoplus bivittatus*, *M.*

*femurrubrum*, and *Chorthippus curtipennis*. No species was statistically most abundant in hayfields, although we counted highest numbers of the second two of these three species on hayfield plots (Table 1).

In terms of shared species densities, the faunas of shortgrass and mixed grass prairies were most similar to one another (60.1%), and significantly positively correlated (Table 2). Tallgrass prairies and hayfields were 78.1% similar, and also were significantly positively correlated. Faunal similarities and rank correlations consistently declined across the habitat gradient from shortgrass to mixed grass to tallgrass to hayfield (Table 2).

*Habitat associations of species and subfamilies.* – Bandwinged grasshoppers (subfamily Oedipodinae) were most abundant as a group in shortgrass prairie, and very uncommon in tallgrass or hayfield (Fig. 1). *Trachyrhachys kiowa* was the most abundant oedipodine in our study area, and a shortgrass specialist (Table 1). *Chortophaga viridifasciata* was most abundant in tallgrass, but the other five common oedipodines tended to be relatively abundant in short and mixed grass habitats, and rare or absent from tallgrass and hayfields.

Spur-throated grasshoppers (subfamily Melanoplinae) were much more abundant as a group on mixed grass plots than elsewhere in the study area, and least common in hayfields (Fig. 1). Seven of the nine most abundant melanopline species followed this general pattern (Table 1), being more abundant in mixed grass than in any other habitat type (see especially *Melanoplus keeleri*, and *M. packardii*), or more abundant in mixed and shortgrass than in tallgrass or hayfield (especially *Melanoplus sanguinipes*). Conspicuous exceptions to the general pattern among melanoplinae were two species that were most abundant in tallgrass and hayfields: *Melanoplus bivittatus* and *M. femurrubrum*.

Slant-faced grasshoppers (subfamily Gomphocerinae) were the most evenly distributed among habitats, but were more common in shortgrass than in hayfields (Fig. 1). A pattern shared by seven of the nine most abundant gomphocerines was highest densities in shortgrass prairie, usually followed in decreasing order by mixed grass, tallgrass, and then hayfields (e.g., *Eritettix simplex*, *Ageneotettix deorum*, *Aulocara elliotti*), though not all these differences were statistically significant (Table 1). *Chorthippus curtipennis* was the only obvious exception to this pattern, being most abundant in hayfield and tallgrass habitats.

*Correlations with cover variables.* -- In addition to floristic differences, the four grassland habitats differed in terms of three cover attributes (Table 3). First, short and mixed grass plots had significantly more bare ground than either tallgrass or hayfield plots. Second, hayfields had a much higher percentage of exotic vegetation canopy than the other habitats. Hayfield canopy consisted primarily of alfalfa and exotic pasture grasses. Finally, vegetative canopy on short and mixed grass plots consisted of a higher percentage of forbs (versus grasses) than tallgrass, with hayfields intermediate.

Across all 66 plots, total adult grasshopper density was negatively correlated with percentage of vegetative canopy that consisted of exotic species (Spearman  $r = -0.451$ ,  $P < 0.001$ ). However, this relationship was due entirely to low densities on hayfield plots, because the correlation disappeared when hayfield plots were eliminated from the analysis.

We computed Spearman rank correlations between grasshopper densities and the three vegetative cover attributes listed in Table 3, restricting the analysis to the 45 short, mixed, and tallgrass prairie plots. There were no significant correlations between any species or subfamily

and percentage of exotic vegetation. However, there were substantial differences among species in their Spearman rank correlations with amounts of bare ground, and with percentages of vegetative canopy consisting of forbs versus grasses, which we show as an ordination in Figure 2. Oedipodinae as a group, and most of the common species individually, were positively correlated with the percentage of unvegetated ground, a conspicuous exception being the tallgrass species *Chorthopaga viridifasciata* (O3, Fig. 2, Table 1). Total Melanoplineae were strongly positively associated with percent forb cover, and no individual melanoplines were negatively associated with this variable (i. e., positively correlated with grass cover). Most gomphocerine species were centrally positioned in the ordination (Fig. 2), suggesting a lack of strong correlations with either amount of unvegetated ground or forb versus grass cover. The exceptions were *Mermiria bivittata* (G7) and *Aeropedellus clavatus* (G1), whose densities were greatest on plots with relatively high proportions of grass cover, and *Chorthippus curtipennis* (G5), a tallgrass and hayfield species most abundant on plots with little bare ground.

### Discussion

Grasshopper assemblages in eastern Montana, eastern Colorado, and the Nebraska sandhills were dominated by different sets of species, despite having most taxa in common (Kemp, 1992). Kemp attributed these patterns to differences in individual species' resource requirements, rather than to the existence of distinct grasshopper communities predictably associated with different sorts of grasslands. Results of the present study strongly support this conclusion at a local scale, for reasons described below.

Twenty of the 25 most abundant grasshoppers on Boulder Open Space occurred in all four habitats, while an additional three occurred in all grasslands except hayfields (Table 1). This result is consistent with the wide ranges of most Great Plains grasshoppers (Otte, 1981, 1984; Capinera and Sechrist, 1982a; Pfadt, 1994), and it does not support the recognition of habitat-specific grasshopper faunas. Nevertheless, short, mixed and tallgrass prairies were numerically dominated by different sets of species on Boulder open space, and one might argue that these represented characteristic grasshopper communities if those same species dominated similar grasslands elsewhere across the Great Plains. However, that appears not to be the case, as illustrated by the following examples.

Capinera and Sechrist (1982b) sampled grasshoppers in shortgrass prairie at the Central Plains Experimental Range (CPER) in northeastern Colorado in 1980-1981. The five dominant species were *Melanoplus gladstoni*, *Opeia obscura*, *Trachyrhachys aspersa*, *Arphia pseudonietana*, and *Phlibostroma quadrimaculatum*. Welch et al. (1991) sampled shortgrass habitats at CPER in 1989, and found these four species to be most abundant: *Eritettix simplex*, *Phlibostroma quadrimaculatum*, *Psoloessa deliculata*, and *Trachyrhachys aspersa*. On Boulder open space in 1995-1996, the five most abundant species on shortgrass prairie plots were *Melanoplus sanguinipes*, *Eritettix simplex*, *Aulocara elliotti*, *Trachyrhachys kiowa*, and *Opeia obscura* (Table 1), a list that includes only one dominant species each from the two CPER studies, which themselves shared only two dominants.

Evans (1984, 1988, 1989) conducted extensive studies of grasshoppers in tallgrass habitats on the Konza Prairie in eastern Kansas. The most common species was the grass-feeding melanopline, *Phoetaliotes*

*nebrascensis*. While this species was the fourth most abundant species on our tallgrass plots, it was more common on Boulder open space in short and mixed grass prairies (Table 1), and not correlated with grass vs. forb cover across individual plots (Fig. 2). This was an unexpected result, although Mulkern et al. (1964) found *P. nebrascensis* associated with mixed forb-grass and early successional grasslands in North Dakota. Other common grasshoppers in Konza Prairie tallgrass were *Orphulella speciosa*, *Hypochlora alba*, *Melanoplus scudderi*, *M. keeleri*, *M. femurrubrum*, and *M. bivittatus*. Only the last two of these were among the dominant species on Boulder tallgrass plots (Table 1).

As in the preceding two examples, grasshopper assemblages on Boulder mixed grass prairies were only generally similar to those of mixed grass prairies elsewhere on the Great Plains (Joern, 1986; Joern and Pruess, 1986; Kemp et al., 1990; Quinn and Walgenbach, 1990; Fowler et al., 1991; Kemp, 1992). One factor may be the lack of sandy soils on Boulder open space (Moreland and Moreland, 1975). This probably explains the absence of species such as *Melanoplus angustipennis* that are particularly common in sand prairies (Joern, 1986). In other cases, and for whatever reasons, the Boulder Valley is outside or at the extreme margins of the ranges of species that are typical elsewhere in mixed grass prairies across the Great Plains (Otte, 1981, 1984; Pfadt, 1994), such as *Melanoplus infantilis* in North Dakota (Fowler et al., 1991), or *Camnula pellucida* in Montana (Kemp, 1992). There are numerous other cases where we cannot explain the rarity or apparent absence of a grasshopper species from our mixed grass study plots on Boulder Open Space, which were dominated by various species of *Melanoplus* (e.g., *M. sanguinipes*, *M. keeleri*) that are known to prefer forb-rich disturbed ground (Table 1; Pfadt, 1994). One possibility is

that grazing and other aspects of land-use history may have left much of Boulder Valley mixed grass prairie in a disturbed state relative to its condition in other areas across the northern Great Plains.

Alexander and Hilliard (1969) collected grasshoppers in upland grasslands near Boulder between 1949 and 1960. Grasshopper densities were not quantified, but species were categorized as "resident" versus "accidental," apparently based on frequency of collection. Although Alexander and Hilliard found ten species not detected during our study, all were listed as accidental. Furthermore, each of the 25 most common species found in the present study was listed as resident in Boulder grasslands by Alexander and Hilliard. These results suggest that the grasshopper fauna of the Boulder Valley has been relatively stable over the past half-century, so it is unlikely that differences between results of our study and those elsewhere across the plains can be attributed to the two-year limit of our sampling period.

Despite the absence of distinct grasshopper communities associated with shortgrass, mixed grass, and tallgrass prairies, density differences among Boulder habitats, and correlations with grassland characteristics on our individual plots, are generally similar to what is known about habitat preferences of acridid species and subfamilies elsewhere.

Both density and variety of grasshoppers in the Boulder Valley were greater in relatively open and low-stature short and mixed grass prairies than in denser and higher tallgrass prairies or hayfields (Fig. 1). This result supports the hypothesis that most grasshopper species require dry and warm open ground for both survival and reproduction (Capinera and Horton, 1989; Joern and Gaines, 1990; Coxwell and Bock, 1995). In The Netherlands, van Wingerden et al. (1992) found that grasshopper variety

and abundance declined in response to fertilization of hayfields, which they attributed to the resulting increases in dense grassland cover. On Boulder open space, only four of 48 species (*Chortophaga viridifasciata*, *Chorthippus curtipennis*, *Melanoplus bivittatus*, and *M. fermurrubrum*) were clearly associated with tallgrass prairies and hayfields. Each of these species has been characterized generally as preferring relatively lush and moist grasslands and meadows (Otte 1981, 1984; Capinera and Sechrist 1982a; Pfadt, 1994).

Habitat associations of the three major acridid subfamilies in the Boulder Valley conform to results of other studies. Band-winged grasshoppers (Oedipodinae) are well-known to prefer areas of relatively low and sparse vegetation (Capinera and Sechrist, 1982a; Otte, 1984), as they clearly did in our study area (Figs. 1 and 2). Most spur-throated grasshoppers (Melanoplinae) are forb-feeders, frequently associated with sites having relatively high proportions of forb versus graminoid vegetation (Joern and Pruess, 1986; Evans, 1988; see Fig. 2). On Boulder open space, melanoplines were most abundant and the dominant group on mixed grass plots, as they were in ungrazed mixed grass prairies in South Dakota (Quinn and Walgenbach, 1990). Slant-faced grasshoppers (Gomphocerinae) feed mainly on grasses and sedges (Otte, 1981), and they were much less strongly associated with forb-dominated plots than were melanoplines in our study area (Fig. 2).

Ranked relative abundances of grasshopper species were statistically similar over multiple years on two Nebraska prairies, despite wide fluctuations of absolute densities (Joern and Pruess, 1986). If this relationship is generally true, then differences in grasshopper assemblages on similar habitats across the Great Plains cannot be attributed solely to



the years when they happened to be sampled. Various studies suggest that local grasshopper communities have predictable structure, based on diet, microhabitat selection, interspecific competition, and predation (Joern and Lawlor, 1981; Joern, 1982, 1992; Joern and Klucas, 1993; Belovsky and Slade, 1993, 1995). The question remains: over what geographic range do such patterns hold? Results of the present study and others across the Great Plains suggest that, while most species are widely distributed in the region, grasshopper assemblages associated with particular sorts of grasslands are dominated by predictable sets of species only at a local scale.

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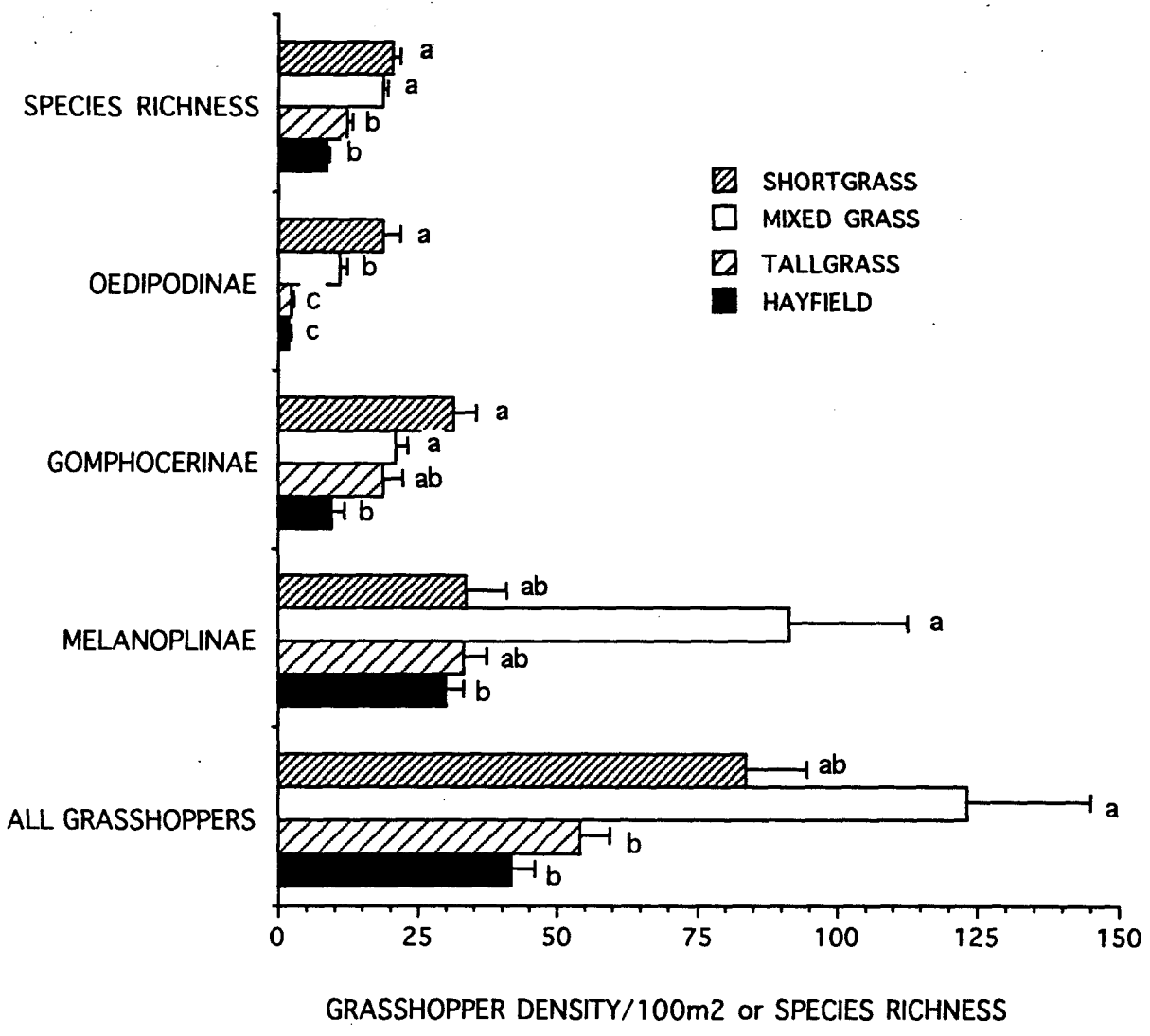
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### Figure Legends

Fig. 1. -- Mean and standard error of species richness and comparative densities of grasshoppers on 66 shortgrass, mixed grass, tallgrass, and hayfield plots on Boulder, Colorado, open space in 1995-1996. Values sharing any letter were not significantly different in Scheffe a-posteriori pairwise comparisons of means. F-scores and P-values for oneway analyses of variance were as follows: species richness,  $F = 26.37$ ,  $P < 0.0001$ ; Oedipodinae,  $F = 22.08$ ,  $P < 0.001$ ; Melanoplineae,  $F = 4.93$ ,  $P = 0.004$ ; Gomphocerinae,  $F = 9.96$ ,  $P < 0.0001$ ; all grasshoppers,  $F = 7.25$ ,  $P = 0.0003$ .

Fig. 2. -- Ordination of the 25 most common grasshoppers counted on 66 Boulder, Colorado, open space grassland plots, and of three subfamilies combined, based on Spearman rank correlations between their densities and 1) percent of the ground that was unvegetated on the plots, and 2) percent of vegetation canopy consisting of forbs versus grasses. Species codes are translated in Table 1. MEL = combined Melanoplineae (solid line enclosing species); OED = combined Oedipodinae (dotted line enclosing species); GOM = combined Gomphocerinae (dashed line enclosing species).

Craig et al. Fig. 1





Craig et al. Fig. 2

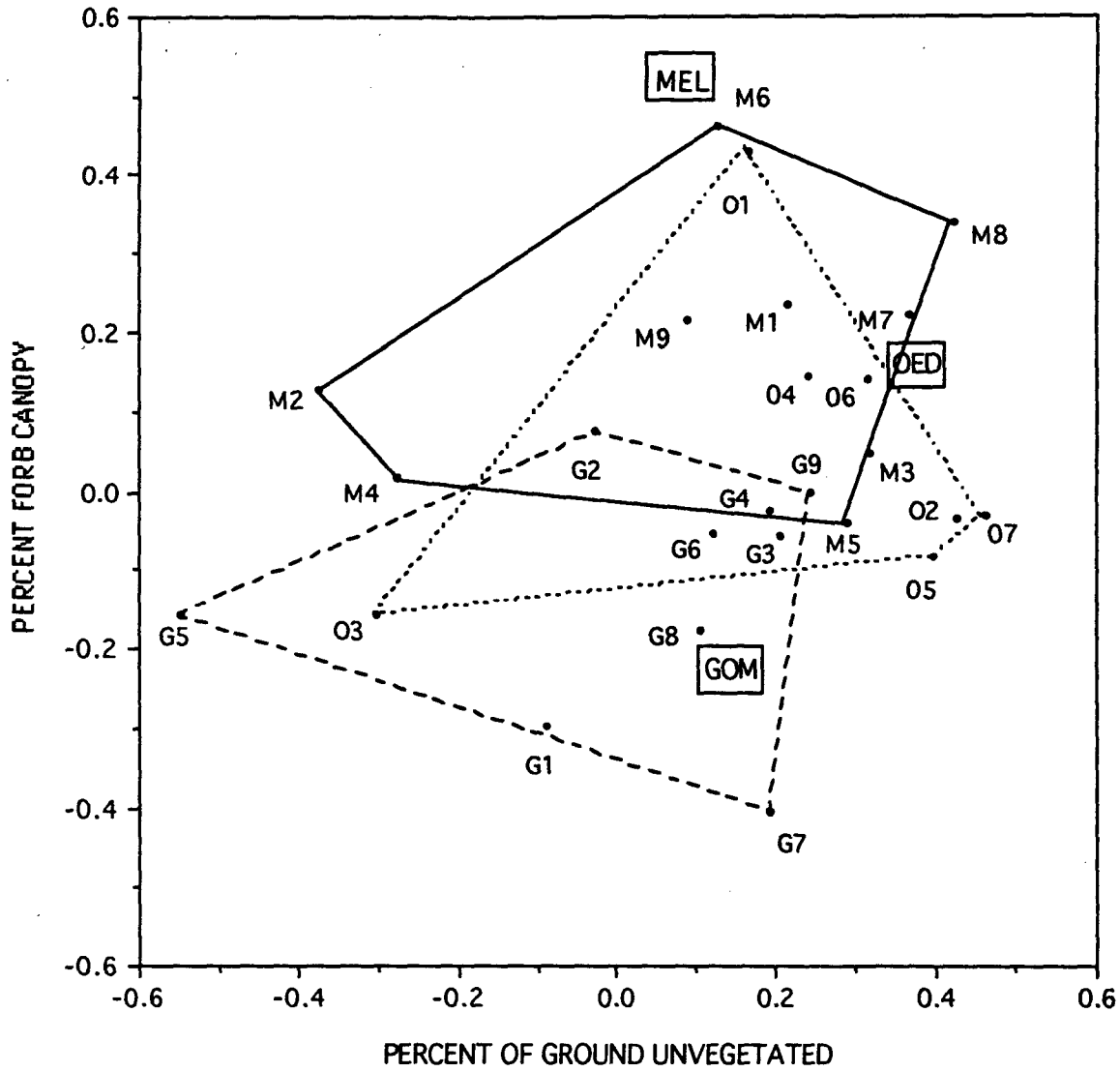


Table 1. -- Densities of the 25 most common grasshoppers on 13 shortgrass, 21 mixed grass, 11 tallgrass, and 21 hayfield plots on Boulder, Colorado, open space in 1995 and 1996.

Species	Mean density/100m <sup>2</sup> (SE)				Kruskal-Wallis H
	Shortgrass	Mixed grass	Tallgrass	Hayfield	
Subfamily Oedipodinae					
O1 <sup>1</sup> <i>Arphia conspersa</i>	3.6 (0.9)a <sup>2</sup>	3.0 (0.4)a	0.5 (0.2)b	0.6 (0.2)b	33.18 ***
O2 <i>Arphia pseudonietana</i>	2.6 (0.6)a	2.4 (0.5)a	0.1 (0.1)b	0.2 (0.1)b	31.33 ***
O3 <i>Chortophaga viridifasciata</i>	0.2 (0.1)ab	0.1 (0.1)a	0.9 (0.4)b	0.4 (0.1)ab	9.26 *
O4 <i>Dissosteira carolina</i>	1.6 (0.4)a	1.6 (0.9)ab	0.1 (0.1)c	0.5 (0.2)bc	12.22 **
O5 <i>Hadrotettix trifasciata</i>	1.0 (0.4)a	0.7 (0.2)a	0.1 (0.1)b	0.1 (0.1)b	17.41 ***
O6 <i>Spharagemon equale</i>	1.4 (0.5)a	0.7 (0.2)a	0.2 (0.2)b	0 b	28.92 ***
O7 <i>Trachyrhachys kiowa</i>	6.8 (1.6)a	1.4 (0.4)b	0.2 (0.1)c	0.2 (0.1)c	29.86 ***

Table 1 (p.2) Mean density/100m<sup>2</sup> (SE)

Species	Shortgrass	Mixed grass	Tallgrass	Hayfield	Kruskal-Wallis H
Subfamily Melanoplineae					
M1 <i>Hypochlora alba</i>	1.8 (1.1)a	9.2 (2.8)a	0.2 (0.2)b	<0.1 (<0.1)b	25.02 ***
M2 <i>Melanoplus bivittatus</i>	0.7 (0.3)a	2.3 (0.7)a	6.4 (1.7)b	4.9 (0.7)b	24.41 ***
M3 <i>Melanoplus confusus</i>	0.6 (0.2)a	3.5 (1.0)a	0.1 (0.1)b	0.3 (0.2)b	19.71 ***
M4 <i>Melanoplus femurrubrum</i>	1.6 (0.6)a	14.6 (4.3)b	20.0 (2.5)c	22.5 (2.7)c	25.84 ***
M5 <i>Melanoplus keeleri</i>	1.5 (0.8)a	17.1 (4.8)b	0.4 (0.3)a	0 c	30.64 ***
M6 <i>Melanoplus lakinus</i>	0.3 (0.1)a	1.1 (0.8)a	0 b	0 b	13.93 **
M7 <i>Melanoplus packardii</i>	2.7 (1.1)a	13.0 (4.0)b	0.3 (0.3)c	0.2 (0.1)c	30.81 ***
M8 <i>Melanoplus sanguinipes</i>	18.4 (3.7)a	19.1 (5.7)a	1.9 (0.9)b	0.6 (0.2)b	46.48 ***
M9 <i>Phoetaliotes nebrascensis</i>	5.1 (1.4)a	9.5 (3.6)a	3.6 (1.2)ab	1.3 (0.6)b	7.84 *

Table 1 (p.3)

Mean density/100m<sup>2</sup> (SE)

Species	Shortgrass	Mixed Grass	Tallgrass	Hayfield	Kruskal-Wallis H
Subfamily Gomphocerinae					
G1 <i>Aeropedellus clavatus</i>	0.3 (0.2)a	1.1 (0.3)bc	0.8 (0.3)ac	0.5 (0.2)ac	6.06 ns
G2 <i>Ageneotettix deorum</i>	3.6 (1.1)a	3.3 (0.7)a	2.6 (0.9)ab	0.9 (0.4)b	12.68 **
G3 <i>Amphitornus coloradus</i>	2.1 (0.5)ab	1.8 (0.4)a	0.8 (0.6)b	0.1 (0.1)c	26.38 ***
G4 <i>Aulocara ellioti</i>	7.4 (1.1)a	3.0 (0.5)b	3.0 (1.6)bc	1.7 (0.7)c	20.49 ***
G5 <i>Chorthippus curtipennis</i>	0 a	0.5 (0.3)a	2.7 (0.5)b	3.7 (1.3)b	25.12 ***
G6 <i>Eritettix simplex</i>	9.6 (1.9)a	6.9 (1.1)a	5.1 (0.8)a	2.2 (0.6)b	18.34 ***
G7 <i>Mermiria bivittata</i>	0.3 (0.2)	1.0 (0.3)	0.7 (0.5)	0.3 (0.2)	1.53 ns
G8 <i>Opeia obscura</i>	5.1 (2.6)a	0.9 (0.3)a	1.7 (0.5)a	0 b	17.52 ***
G9 <i>Orphulella speciosa</i>	1.6 (0.8)	1.0 (0.3)	0.3 (0.2)	0.3 (0.2)	2.32 ns

<sup>1</sup> Species codes relate to ordination in Fig. 2.

<sup>2</sup> Values sharing any letter not significantly different in a-posteriori pairwise rank-sum tests (Welkowitz et al. (1991).

\* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001, ns = not significant, Kruskal-Wallis H tests.

Table 2. Percent similarities (above diagonal) and Spearman rank correlations (below diagonal) between shortgrass, mixed grass, tallgrass, and hayfield habitats on Boulder, Colorado, open space, based on densities of 48 grasshopper species in 1995-1996.

	Shortgrass	Mixed grass	Tallgrass	Hayfield
Shortgrass	----	60.1	36.1	19.9
Mixed grass	0.586*	----	45.8	33.7
Tallgrass	0.253	0.255	----	78.1
Hayfield	0.121	0.224	0.726*	----

\* P < 0.01, Spearman rank correlation.

Table 3. Mean (and standard error) of percent unvegetated ground, percent of total vegetation canopy that was exotic plant species, and percent of total vegetation canopy that was forbs, on 13 shortgrass, 21 mixed grass, 11 tallgrass, and 21 hayfield plots on Boulder, Colorado, open space, in 1995-1996.

Grassland type	% unvegetated	% exotic	% forbs
Shortgrass	54.8 (2.2) a <sup>1</sup>	44.3 (3.6) a	41.6 (3.3) a
Mixed grass	56.6 (1.7) a	29.2 (4.3) a	42.8 (4.5) a
Tallgrass	35.2 (3.3) b	44.7 (4.6) a	24.0 (2.5) b
Hayfield	31.8 (2.8) b	84.9 (3.5) b	30.4 (3.8) ab
F (P)	26.7 (<0.0001)	41.8 (<0.0001)	4.4 (0.007)

<sup>1</sup> Values sharing any letter not significantly different in Scheffé a-posteriori pairwise comparisons.

Appendix. Forty-eight species of grasshoppers\* counted on 66 grassland plots on Boulder, Colorado, open space in 1995-1996, ranked by decreasing densities.

Species	Mean density/100m <sup>2</sup>	No. occupied plots
<i>Melanoplus femurrubrum</i>	15.44	56
<i>Melanoplus sanguinipes</i>	10.22	45
<i>Melanoplus keeleri</i>	5.79	23
<i>Eritettix simplex</i>	5.64	61
<i>Pheotaliotes nebrascensis</i>	5.06	35
<i>Melanoplus packardii</i>	4.80	31
<i>Melanoplus bivittatus</i>	3.50	50
<i>Aulocara elliotti</i>	3.44	44
<i>Hypochora alba</i>	3.33	23
<i>Ageneotettix deorum</i>	2.46	43
<i>Arphia conspersa</i>	1.93	46
<i>Trachyrhachys kiowa</i>	1.90	34
<i>Chorthippus curtipennis</i>	1.78	25
<i>Opeia obscura</i>	1.56	22
<i>Arphia pseudonietana</i>	1.34	39
<i>Melanoplus confusus</i>	1.34	29
<i>Amphitornus coloradus</i>	1.15	35
<i>Dissosteira carolina</i>	1.01	41
<i>Orphulella speciosa</i>	0.79	38
<i>Aeropedellus clavatus</i>	0.68	24
<i>Mermiria bivittata</i>	0.59	19
<i>Spharagemon equale</i>	0.53	24

## Appendix (continued).

Species	Mean density/100m <sup>2</sup>	No. occupied plots
<i>Hadrotettix trifasciatus</i>	0.46	22
<i>Melanoplus lakinus</i>	0.41	11
<i>Chortophaga viridifasciata</i>	0.31	8
<i>Acrolophitus hirtipes</i>	0.30	16
<i>Mermiria picta</i>	0.22	7
<i>Hesperotettix viridis</i>	0.20	7
<i>Spharagemon collare</i>	0.16	9
<i>Xanthippus corallipes</i>	0.16	8
<i>Derotmema haydeni</i>	0.14	6
<i>Hesperotettix speciosus</i>	0.11	2
<i>Aulocara femoratum</i>	0.11	1
<i>Melanoplus gladstoni</i>	0.09	8
<i>Trimerotropis pallidipennis</i>	0.09	8
<i>Melanoplus differentialis</i>	0.09	4
<i>Orphulella pelidna</i>	0.07	8
<i>Cordillacris occipitalis</i>	0.06	6
<i>Brachystola magna</i>	0.04	6
<i>Paropomala wyomingensis</i>	0.04	6
<i>Mestobregma plattei</i>	0.03	4
<i>Metator pardalinus</i>	0.03	4
<i>Hippiscus ocelote</i>	0.02	3
<i>Melanoplus foedus</i>	0.01	4
<i>Aeoloplides turnbulli</i>	0.01	2
<i>Dactylotum bicolor</i>	0.01	2



Appendix (continued).

Species	Mean density/100m <sup>2</sup>	No. occupied plots
<i>Phlibostroma quadrimaculatum</i>	0.01	2
<i>Pardalophora haldemanii</i>	<0.01	1

\* Nomenclature follows Pfadt (1994), then Capinera and Sechrist (1982a) and Otte (1981, 1984).