GRASSHOPPER MONITORING ON PUEBLO CHEMICAL DEPOT (2001-2003)

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John R. Sovell
Colorado Natural Heritage Program
Colorado State University
Warner College of Natural Resources
Campus Mail 8002
Fort Collins, CO 80523-8002
E-mail: jsovell@lamar.colostate.edu
www.cnhp.colostate.edu

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Cover photograph: Sweep netting for grasshoppers on the U.S. Army Pueblo Chemical Depot (*photo by Rebecca Gorneyl*).
Inset: The obscure grasshopper, *Opeia obscura* (*photo by John Sovell*)

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EXECUTIVE SUMMARY

Ecological field surveys conducted from 1995-1998 at the U.S. Army Pueblo Chemical Depot (PCD) documented differences in vegetation and small mammal composition between areas grazed by livestock and areas protected from livestock grazing since 1942. To investigate these floral and faunal differences further, PCD established an invertebrate monitoring program in 1999 in grazed and ungrazed areas. The monitoring effort tested whether grazing affected the diversity of grasshopper species (Othoptera:Acrididae) within three different habitats (greasewood, shortgrass prairie, and sandsage).

The grasshopper species diversity was assessed through intensive sweep net collections at each of 34 monitoring plots surveyed four times a year. Surveys were conducted from May through September in 2001, 2002, and 2003. Fifty-two grasshopper species were documented during three years of sampling. An additional six species were identified, each from a single specimen representing one capture for each. The six specimens, which these species records were based on, were not available for expert verification and they were omitted from analyses. Data were analyzed with a nonparametric multivariate analysis of variance on CY dissimilarities (a coefficient of association) utilizing permutation methods to generate test statistics.

Differences in grasshopper species diversity correlated with species commonness and grazing, grasshopper habitat relationships, grasshopper seasonal phenology, and drought. Grazing did not impact diversity of the **most common** grasshopper species at PCD; however, the diversity of 16 **uncommon species** was affected by past grazing practices. Grazing significantly altered the diversity of uncommon grasshoppers within shortgrass prairie, greasewood, and sandsage. Three of the uncommon species collected (*Encoptolophus costalis, Metator pardalinus*, and *Boopedon nubilum*), were not collected in grazed shortgrass prairie. In addition, *Heliaula rufa* only occurred in ungrazed habitat with seven captures in ungrazed shortgrass prairie and 13 captures in ungrazed sandsage.

Dominant vegetation type (e.g., greasewood, shortgrass prairie, sandsage) influenced grasshopper species diversity. Grasshopper diet preference impacted species associations to habitat. The grass-sedge and obligate grass feeding species prefer shortgrass prairie, and the broad-leaf feeders prefer shrubs of greasewood and sandsage as host plants. In addition, grasshopper species diversity varied among months within each of the three years monitored. This variability can be explained by seasonal phenology of the grasshoppers at PCD. The combined effect of grasshopper habitat relationships and their patterns of seasonal phenology caused species diversity to differ among all habitats, within each month sampled, for all three years of monitoring.

Finally, the drought of the early 2000s impacted grasshopper abundance and the association between habitat and differences in grasshopper species diversity. Grasshoppers are regulated by food abundance and their populations increase under above-average precipitation and above-average forage production. Drought reduced plant production, causing dramatic declines in grasshopper abundance in 2002. Consequently, grasshopper species diversity differed among all habitats, within all months sampled in 2001 and 2003, but only eight of 12 comparisons were significant in 2002 when annual precipitation was 60% below the 43-year mean.

These findings have consequences for management activities at PCD and suggest that 1) appropriate management of grazing to avoid over-grazing is important to sustaining populations of uncommon grasshopper species, 2) moderate grazing may promote grasshopper species diversity if timed appropriately to avoid nymphal development periods, 3) maintaining the existing habitat mosaic at PCD is important for sustaining current grasshopper species diversity, and 4) management reducing grazing intensity during drought will assist in sustaining current grasshopper species diversity. These management suggestions will promote populations of both grasshoppers and their predators, including small mammals and songbirds.

Future research, with grazing on some sample plots, would help clarify whether grazing benefits some grasshopper species at PCD. Relative abundance of some species benefits from grazing, and consequently, grasshopper species diversity is enhanced.

INTRODUCTION

In 1999, PCD established an invertebrate monitoring program on the U. S. Army Pueblo Chemical Depot (PCD) in Pueblo County, Colorado. Grasshoppers were selected as the focus of this research to investigate ecological disturbance on the PCD because they are good indicators of grassland integrity, are key herbivores in grassland biomes constituting a major portion of animal biomass (Shure and Phillips 1991), and some variation in grasshopper species composition is attributable to human induced changes in vegetation structure (Fielding and Brusven 1993).

A 1995 study had detected differences in canopy cover and relative abundance of plant species between grazed and ungrazed areas at PCD (Rust International 1996). Grazed areas experienced an increase in cover and relative abundance of shrubs, forbs, and unpalatable grasses. Because grasshoppers are the major invertebrate herbivores on western grasslands with specific feeding preference types (including obligate grass feeders, obligate forb feeders, and mixed grass and forb feeders) changes in the grass and forb community structure influence grasshopper species diversity. The grasshopper monitoring project investigated the effects of vegetation type and past grazing regime on grasshopper species diversity. Species diversity was determined by measuring the relative abundances and species richness of grasshoppers within designated sample plots. Although PCD is a small portion of the regional grassland prairie environment, it is the southern portion of the Chico Basin and is part of an important landscape-level conservation area. Results from this study are applicable to much of the Chico Basin Conservation Area and are important to the development of an ecosystem management approach at PCD and in the greater Chico Basin area.

Study Area

PCD is a United States military reservation east of the city of Pueblo, Colorado, and occupies nearly 23,000 acres of land approximately 1 mile north of the Arkansas River. There are approximately 11,815 acres of shortgrass prairie, 4,153 acres of sandsage, 2,468 acres of greasewood, and 611 acres of riparian areas at PCD. Buildings and munitions bunkers fill the remaining acreage with remnants of native vegetation interspersed between the rows of bunker.

PCD topography ranges in elevation from 4,550 feet at Chico Creek to 4,814 feet along the northern boundary. Prior to its development as an ammunition storage facility during the 1940s, the area was used to graze cattle. From the early 1900s to 1942, PCD property was a mixture of privately and state-owned parcels. For the past 52 years, PCD has functioned as a storage, maintenance, distribution, and disposal facility for munitions and other military equipment for the U.S. Army (1942-1994).

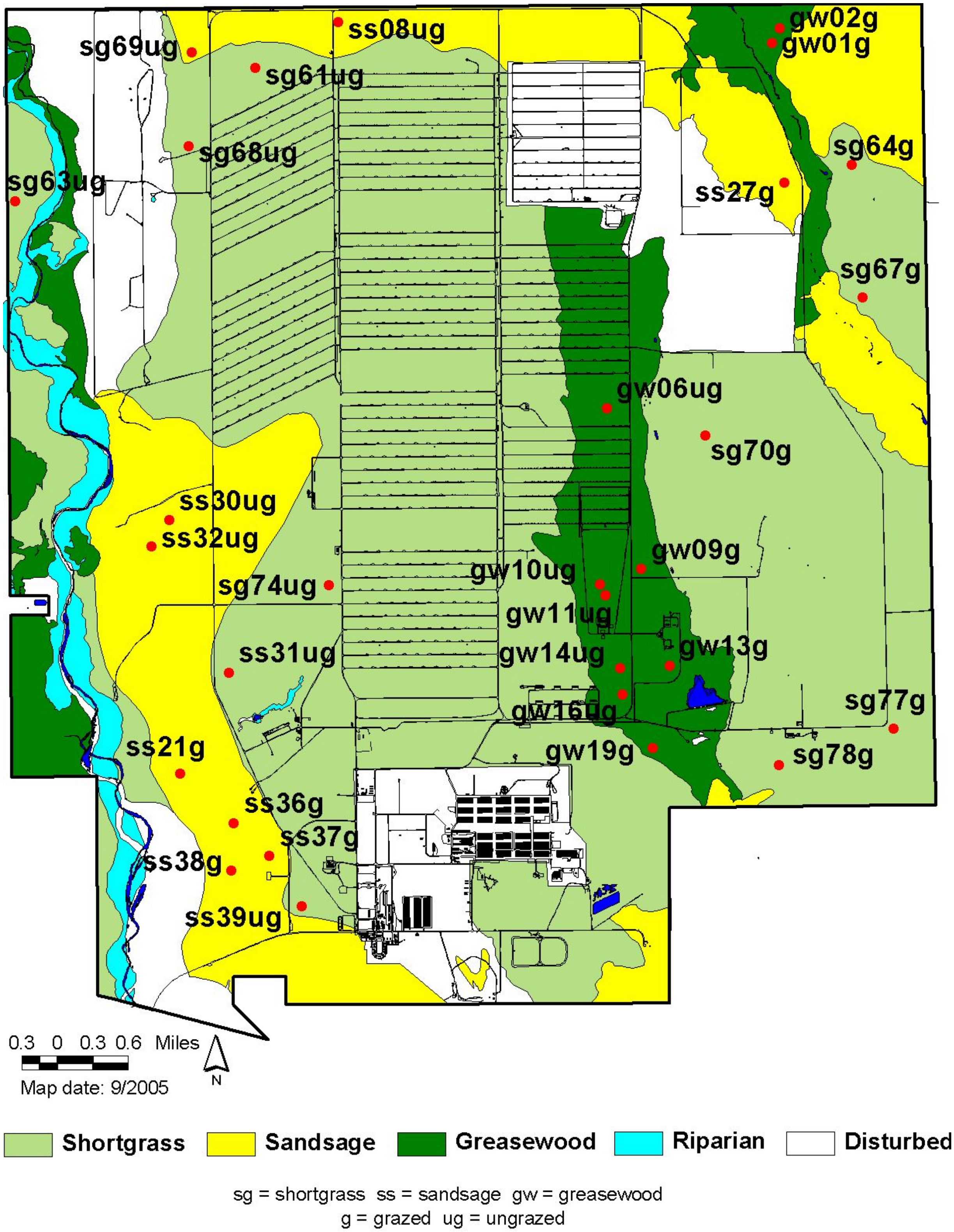
Vegetation: PCD is best characterized as a mosaic of high plains vegetation types, including greasewood, shortgrass prairie, sandsage, wetlands, riparian, and disturbed landscape (Earth Tech 2001). Most of PCD consists of upland habitats that are dominated by grasses and shrubs. Wetland and riparian habitats occupy less than 1% of the area (Figure 1).

Shortgrass prairie occupies approximately 11,815 acres at PCD (Figure 1) and is dominated by low-growing perennial grasses including blue grama (*Chondrosum gracile*) and purple three-awn (*Aristida purpurea*) (Rondeau 2003). Several local areas of shortgrass prairie at PCD are dominated by alkali sacaton (*Sporobolus airoides*) or galleta (*Hilaria jamesii*) (Rondeau 2001).

Sandsage shrub habitats cover approximately 4,153 acres at PCD (Figure 1), and consist of sandy substrates dominated by sandsage (*Oligosporus filifolius*). The ground cover is often sparse with a mix of grasses and forbs, including blue grama, needle-and-thread (*Hesperostipa comata*), and sand dropseed (*Sporobolus cryptandrus*) (Rondeau 2003).

Greasewood scrubland covers approximately 2,468 acres at PCD with the largest stands occurring on the eastern half (Figure 1). At PCD, greasewood scrubland is dominated by greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus nauseosus*) with cholla (*Cylindropuntia imbricata*) (Earth Tech 2001, Rondeau 2001). Dominant grasses in the greasewood scrubland include blue grama, alkali sacaton, and galleta grass. Soils are relatively fine, and much bare ground is present.

Figure 1. Major vegetation types at Pueblo Chemical Depot.
Circles indicate locations of permanent sampling plots for vegetation and grasshoppers.

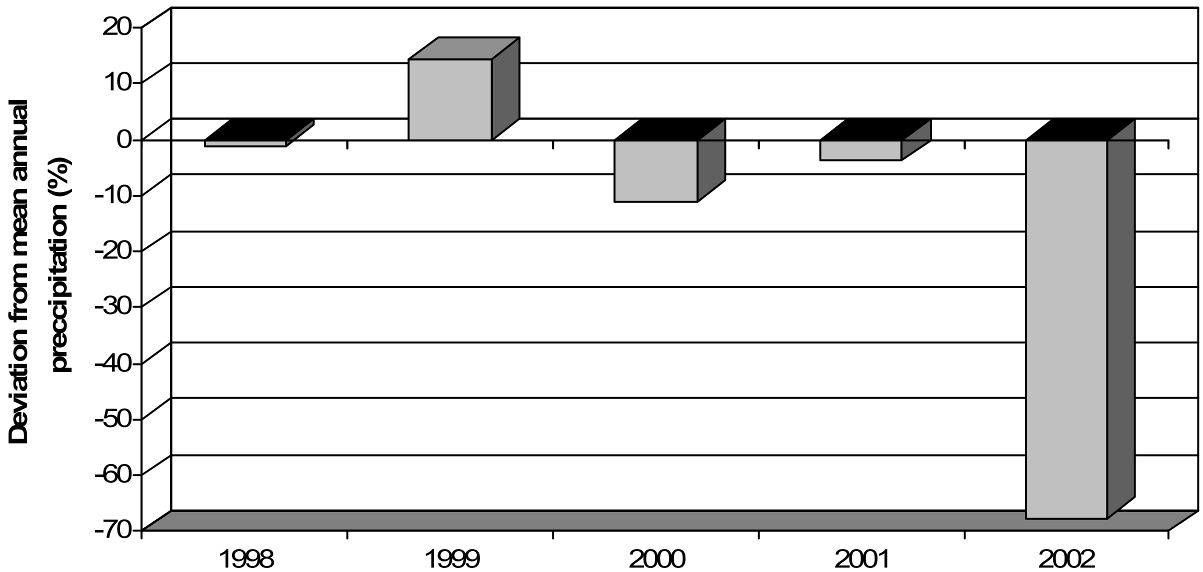


Livestock Grazing History: Prior to PCD's establishment, the entire area was used for cattle grazing. Livestock have not grazed the land within the Munitions Storage Area (the central portion of PCD) for more than 50 years. This area was mechanically disturbed for storage bunker construction and use. From 1942 to 1998, grazing by cattle was permitted on 7,600 of the 23,000 acres at PCD (Rust International 1996), in the eastern portion of the site. Stocking rate was one head of cattle per 35 acres (USFWS 1987), or approximately 220 head total. Although livestock grazing on PCD was terminated in 1998, limited grazing was allowed on portions of the northwestern corner.

Climate: The climate at PCD is characterized by relatively low humidity, abundant sunshine, low rainfall, and moderate to high winds (Western Regional Climate Center 2002). Much of the annual precipitation falls in the summer during heavy thunderstorms. From 1961 to 1990, most (72%) of the mean annual precipitation (24.69 cm) at PCD occurred as rain between May 1 and September 30 (Western Regional Climate Center 2005a). Although an annual mean of 76 cm of snow (approximately 7.6 cm of liquid water) falls in nearby Pueblo, snow cover at PCD generally is not deep or persistent (Western Regional Climate Center 2005b). Over the past 50 years (1954-2005) the warmest months in Pueblo are June, July, and August, with the mean maximum daily temperature near 90º F (87.3º F, 92.7º F, and 89.7º F, respectively) (Western Regional Climate Center 2005c). During the coldest months of the year (December, January), the mean daily high temperature and the mean nightly low temperature are 45.9º F and 13.9º F, respectively (Western Regional Climate Center 2005c).

From 2000 through 2003, PCD experienced a drought with associated effects on vegetation (Rondeau 2003) (Figure 2). Increased, but still below average, rainfall in 2003 ended severe drought conditions.

Figure 2. Deviation from mean annual precipitation at Pueblo Memorial Airport, west of the U.S. Army Pueblo Chemical Depot (1998-2003). Mean is from 1957-2000 (From: Rondeau 2005).



METHODS

Grasshopper sampling

Grasshopper species diversity was assessed through intensive sweep net collections at each of 34 monitored sample plots. Sweep samples provide good estimates of relative abundance and species composition (Evans et al. 1983, Evans 1988). During 2001, 2002, and 2003, grasshopper collections were made in late May, early July, mid-August, and mid-September. All collected grasshoppers were frozen for later identification in the laboratory. To minimize bias in estimates of species composition between sample plots due to interspecific differences in behavior, each grasshopper flushed was captured (Capinera and Sechrist 1982a). Grasshoppers were identified to species using the keys of Capinera and Sechrist (1982b), Otte (1981), Otte (1984), and Pfadt (1994). Nymphs were omitted from the analysis because they are difficult to accurately identify (Pfadt 1994).

Two transects placed perpendicular to one another and crossing at one end, were used on each plot to estimate grasshopper densities. Each transect consisted of twenty 0.1m^2 hoops (Onsager 1977, 1991: Onsager and Henry 1977) placed 5m apart, creating a transect 100m in length, with a sampling area of 2m^2 per transect or 4m^2 per plot. Densities were estimated by approaching each hoop and counting every grasshopper that jumped or flew from within it. Each hoop was then searched for grasshoppers that did not flee. Individual hoops were treated as subsamples; data from all 40 hoops on each plot were pooled and plots were used as replicate samples (13 greasewood, 12 shortgrass and 11 sandsage).

Experimental Design

It was hypothesized that grazing condition (grazed or ungrazed) at PCD would affect grasshopper species diversity (Othoptera: Acrididae), as defined by distribution of species and their abundances within three different habitats (greasewood, shortgrass prairie, and sandsage). Four factors were included in the analysis: Habitat (greasewood, shortgrass prairie, sandsage), Grazing (yes/no), Years (2001, 2002, 2003) and Months (May, June, August, September) (nested in Years) (Table 1). Thirty sample plots (five replicates for each of the six combination of grazing by habitat) were sampled in each of four months, for each of three years, resulting in 360 total samples (30x4x3). Appendix I lists the sample plots at PCD.

Table 1. Number of sampling plots by habitat, grazing regime, year, and month nested within year.

HABITAT	GRAZING	MONTH(YEAR)												
		2001				2002				2003				
		May	July	Aug	Sept	May	July	Aug	Sept	May	July	Aug	Sept	Total
Greasewood	Grazed	5	5	5	5	5	5	5	5	5	5	5	5	60
	Ungrazed	5	5	5	5	5	5	5	5	5	5	5	5	60
Shortgrass	Grazed	5	5	5	5	5	5	5	5	5	5	5	5	60
	Ungrazed	5	5	5	5	5	5	5	5	5	5	5	5	60
Sandsage	Grazed	5	5	5	5	5	5	5	5	5	5	5	5	60
	Ungrazed	5	5	5	5	5	5	5	5	5	5	5	5	60
TOTAL SAMPLES														360

Statistical Analysis

The study simultaneously measured the response of grasshopper species to factors, including grazing, habitat, and time. Grazing and Habitat were analyzed as fixed factors, while Year and Month were random (Ott 1993). Analysis of species abundances requires a multivariate procedure where each species is considered a variable (Legendre and Legendre 1998). Such analyses have traditionally been accomplished using a parametric MANOVA (Multivariate Analysis of Variance). However, parametric analyses are inappropriate for ecological data of species abundances (McArdle and Anderson 2001) because:

- the assumption that counts of species abundance will conform to a multivariate normal distribution (required by MANOVA) is not generally, or even likely, to be true;
- MANOVA implicitly uses Euclidean distances to apportion total variability to individual factors in an experimental design, and it is generally agreed the use of Euclidean distance for species abundance data is inappropriate; and
- there are often more variables (species) in the system than there are sampling units (or degrees of freedom), which makes the traditional MANOVA statistics impossible to calculate.

Therefore, a nonparametric analysis, PERMANOVA (Permutation MANOVA) was used (Anderson 2005).

PERMANOVA is a nonparametric statistical procedure for testing the simultaneous response of one or more variables (e.g. species) to one or more factors (e.g. grazing, habitat, time) in an ANOVA (Analysis of Variance) experimental design on the basis of any similarity or dissimilarity measure (e.g. Euclidean) using permutation methods (McArdle and Anderson 2001, Anderson 2001). Pairwise comparisons among model factors and interaction terms were conducted *a posteriori* in PERMANOVA. A significance level of $P \leq 0.5$ was used for all tests. Setting a level of significance in statistics determines the likelihood of committing a Type I Error, or in our study the probability a difference in grasshopper species diversity between sample plots will be declared significant, when no difference exits. Such errors can occur, because some samples will show a relationship just by chance. When performing many tests comparing differences between multiple sample means (*a posteriori* tests), as in this study, the tendency is to inflate the overall Type I Error rate, and it is advisable to set a lower significance level. Although assignment of significance level is somewhat arbitrary, levels of 0.05 and 0.01 are most commonly used.

Similarity and dissimilarity measures are coefficients of association used to determine the resemblance between study plots as defined by the variables describing them (e.g. species) (Legendre and Legendre 1998). All similarity measures give biased weighting to the different types of variation in species abundance between samples or communities and are subject, to varying extent, to the effects of sampling error or minor community differences. Analyses used the CY dissimilarity measure, one main measure of association. The CY dissimilarity weights different types of variation between samples with minimum bias, greatly improving its ability to discriminate between sampling sites (Cao et al. 1997). Raw data were not transformed because the CY dissimilarity measure accounts for skewed distribution of taxa by incorporating a logarithmic transformation step in calculating the dissimilarity measure (Nicholls and Tudorancea 2001). Because the logarithm of zero is undefined, the use of logarithms requires that a value be chosen to replace zeros in the data set and the published value of 0.1 was used (Coa et al. 1997). A total of 34 plots were sampled, but only 30 are analyzed here. The 34 plots resulted in an unbalanced experimental design and in order to balance the data set, four plots were removed. These four plots were not chosen randomly, but rather represented plots either influenced by grazing during the study, from which sampling events were missing, or for which vegetation data had not been collected during completion of the vegetation monitoring project.

The frequency distribution of hoop sample counts from within each habitat type by grazing disturbance was expected to approximate a Poisson distribution, and so each observed distribution was tested against a Poisson distribution. For all samples a 95% Poisson confidence interval was calculated and samples whose intervals did not overlap were declared different by inspection (*P* unspecified, but <0.05).

RESULTS

Diversity of All Grasshopper Species

Over the three years of sampling (2001-2003), 58 different species of grasshopper were recorded at PCD (Appendix II). Six of these species were observed only once in the three years of sampling (Appendix II, bold font). To avoid spurious results based upon wrongly identified species, these six species were not included in the analyses.

Grasshopper diversity did not differ between grazing and among years, but differed significantly among habitat (P=0.0002), month within year (P=0.0002), and by the habitat-by-month interaction (P=0.0002) (Table 2).

Table 2. Results of the Permutation MANOVA on CY dissimilarity distances for species diversity of Othoptera (Acrididae) subjected to different grazing regimes (grazed, ungrazed), within three habitats (greasewood, shortgrass prairie, sandsage), and sampled in each of four months (May, July, August, September) from 2001 to 2003.

Source	DF[1]	SS	MS	F	P
Grazing	1	0.25	0.25	1.24	0.3280
Habitat	**2**	**7.61**	**3.81**	**4.64**	**0.0002**
Year	2	11.64	5.82	1.00	0.4740
Month(year)	**9**	**52.44**	**5.83**	**32.07**	**0.0002**
Grazing x habitat	2	0.18	0.09	0.44	0.9382
Grazing x year	2	0.40	0.20	1.43	0.2114
Grazing x month(year)	9	1.26	0.14	0.77	0.9210
Habitat x year	4	3.28	0.82	0.90	0.6350
Habitat x month(year)	**18**	**16.48**	**0.92**	**5.04**	**0.0002**
Grazing x habitat x year	4	0.81	0.20	1.25	0.1470
Grazing x habitat x month(year)	18	2.91	0.16	0.89	0.8742
Residual	288	52.33	0.08		
Total	359	149.57			

[1] DF = degrees of freedom, SS = the sum of squares (measure of total variability), MS = mean square (SS divided by degrees of freedom), F = psuedo F statistic (ratio of explained variation to unexplained variation) ($P \leq 0.05$ is significant).

Habitat: There were no significant differences in grasshopper abundance among any of the three habitats studied (Table 3). Comparison of the species present in each habitat indicates that the greasewood-versus-sandsage and shortgrass-versus-sandsage comparisons were most different, with 25% and 31% of the species present differing between them, respectively (Table 4). A subset of grass-sedge and obligate grass feeding grasshoppers is associated with shortgrass prairie, and a subset of broad-leaf feeders is associated with shrub habitats (Figure 3).

Table 3. PERMANOVA *a posteriori* comparison of grasshopper species diversity among habitats using the permutation calculated t-statistic.

Comparison among habitats	t-statistic	P[1]
Greasewood versus Shortgrass	0.878	0.5288
Greasewood versus Sandsage	1.430	0.1484
Shortgrass versus Sandsage	1.361	0.1732

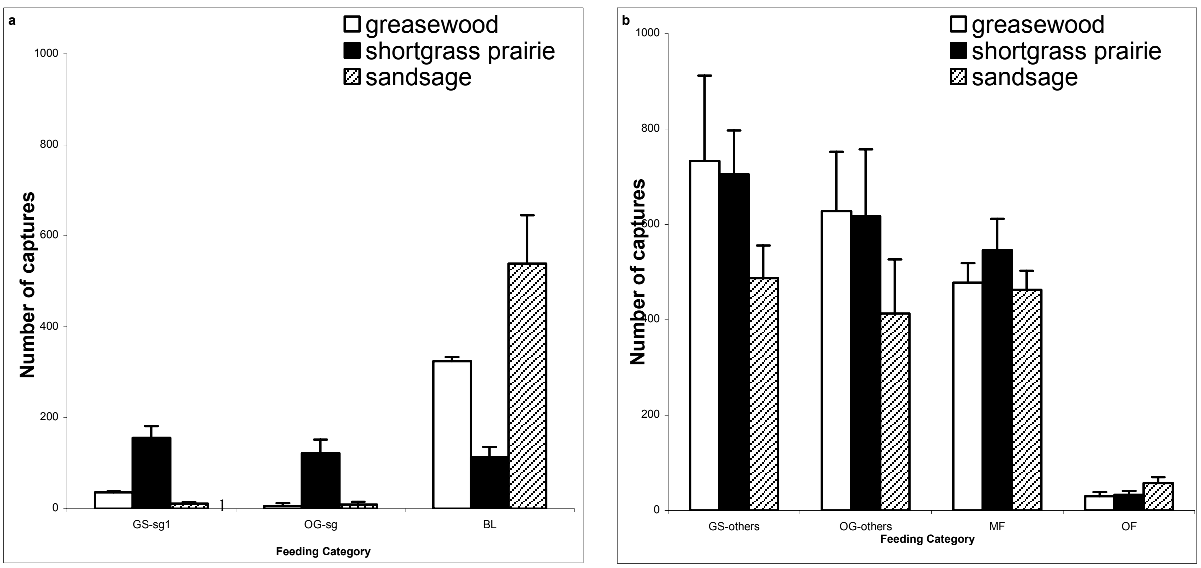
[1] P-values for the permutation calculated t-statistic ($P \leq 0.05$ is significant).

Table 4. Grasshopper species common to both habitats, absent from one habitat, or absent from both habitats in comparisons among greasewood, shortgrass, and sandsage at the U. S. Army Pueblo Chemical Depot.

Status	Habitat Comparison[1]		
	GW/SG	GW/SS	SG/SS
shared species	40 (77%)	37 (71%)	35 (67%)
absent from one habitat	10 (19%)	13 (25%)	16 (31%)
absent from both habitats	2 (4%)	2 (4%)	1 (2%)

[1] GW = greasewood, SG = shortgrass prairie, and SS = sandsage.

Figure 3. Association of grasshoppers, according to absolute abundance (+ 1 Standard Deviation of mean abundance), in each of five feeding guilds with the three habitats at the U.S. Army Pueblo Chemical Depot. a) guilds exhibiting affinity to specific habitats; b) guilds equally distributed across habitats.



[1] GS-sg = grass-sedge shortgrass associates, OG-sg = obligate grass shortgrass associates, OF = obligate forb, GS-other = grass-sedge remaining species, OB = obligate grass remaining species, MF = mixed feeder, and BL = broad-leaf.

Year: Although there was no effect of year on species diversity, trends in the data clearly show a large numerical decline in abundance from 2001 to 2002 with a modest recovery in 2003, in all three habitats (Figure 4).

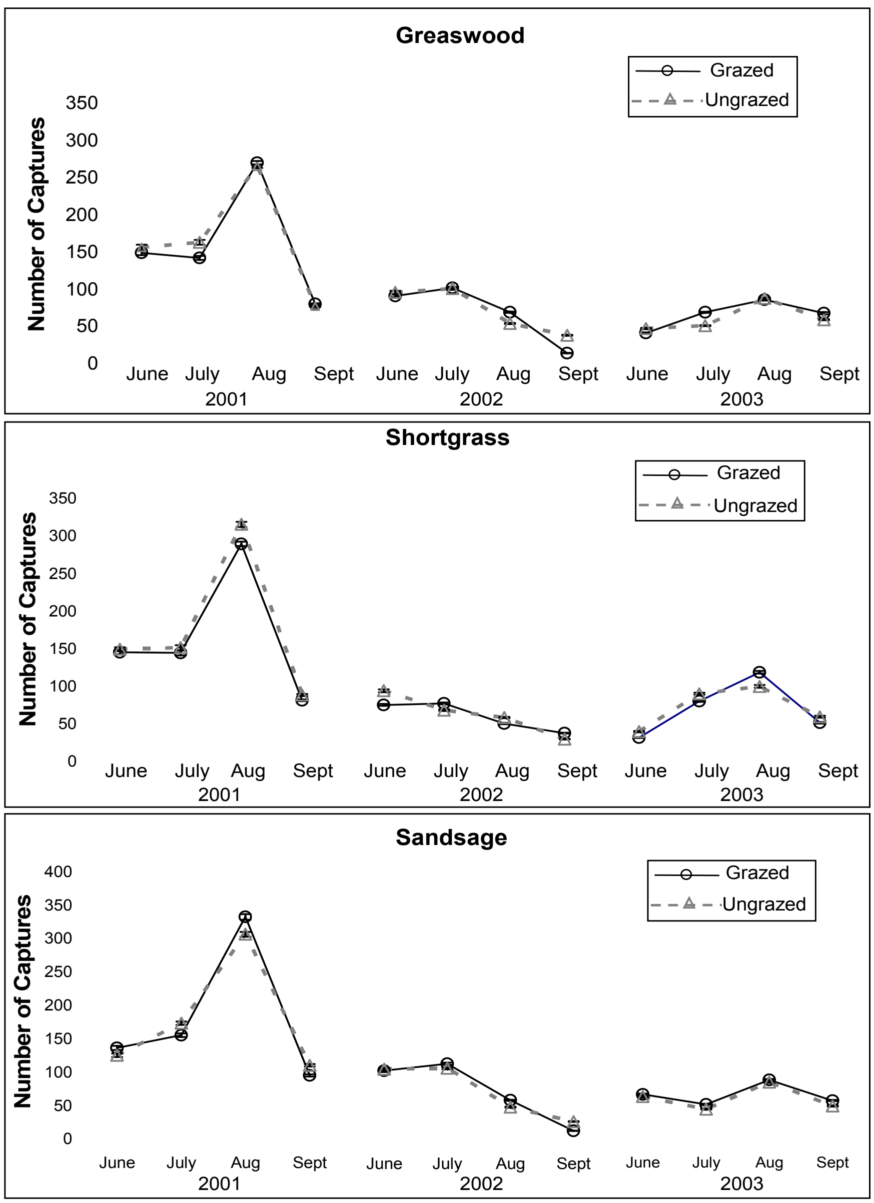
Month Within Year: Grasshopper species diversity differed significantly among all sample months, in every year of the project (Table 5).

Table 5. PERMANOVA *a posteriori* comparison of grasshopper species diversity among months within each year using the permutation calculated t-statistic.

Comparison among months within year	2001	2002	2003
May versus July	0.0002[1]	0.0002	0.0002
May versus August	0.0002	0.0002	0.0002
May versus September	0.0002	0.0002	0.0002
July versus August	0.0002	0.0002	0.0002
July versus September	0.0002	0.0002	0.0002
August versus September	0.0002	0.0014	0.0002

[1] Numbers are P-values for the permutation calculated t-statistic ($P \leq 0.05$ is significant).

Figure 4. Annual variation in grasshopper abundance from 2001 to 2003 within greasewood, shortgrass prairie and sandsage on both grazed and ungrazed plots at the U.S. Army Pueblo Chemical Depot.



Habitat-By-Month Interaction: Grasshopper species diversity differed significantly among habitats by month, nested within year (Table 6). Species diversity differed significantly (or were marginally significant) among all habitats in every month of 2001 and 2003, but only 8 of the 12 monthly habitat comparisons were significant in 2002.

Table 6. PERMANOVA *a posteriori* comparison of grasshopper species diversity among habitats within each month, nested within year, using the permutation calculated t-statistic.

Comparison among habitats by months within year	2001				2002				2003			
	May	July	Aug	Sept	May	July	Aug	Sept	May	July	Aug	Sept
GW[1] versus SG	0.0016[2]	0.0324	0.0004	0.0024	0.0004	0.0004	0.0840	0.6288	0.0502	0.0002	0.0004	0.0558
GW versus SS	0.0002	0.0048	0.0002	0.0002	0.0002	0.0002	0.0002	0.3006	0.0002	0.0096	0.0002	0.0002
SG versus SS	0.0544	0.0004	0.0002	0.0002	0.1330	0.0002	0.0008	0.0064	0.0002	0.0002	0.0002	0.0002

[1] GW = greasewood, SG = shortgrass prairie, and SS = sandsage.
[2] Numbers are P-values for the permutation calculated t-statistic ($P \leq 0.05$ is significant).

Diversity of Uncommon Grasshopper Species

Of the 52 species recorded at PCD, 16 (30%) were uncommon, having been recorded in 4% or fewer samples (14 of 360), and represented in 0.3% or fewer captures (20 out of 7,294) (Table 7). Because captures for these species were few, it was impossible to detect patterns at fine time scales such as months and years with any certainty. Interest in these 16 species was in determining whether they associated among habitats, and whether grazing influenced this association, not if they varied by month and among years. Analyses of these uncommon species using a reduced model, which considered only habitat and grazing as factors, indicate significant differences in grasshopper species diversity between grazing status (P=0.0454) and among habitats (P=0.004) (Table 8).

Grazing: Grazing significantly impacted diversity of the uncommon species (P=0.0454). Within each habitat studied, grazing reduced the number of grasshoppers present for the 16 uncommon species (Figure 5).

Table 7. The 16 uncommon grasshopper species recorded at the U. S. Army Pueblo Chemical Depot.

Species	Feeding Category[1]	Captures by Habitat[2]					
		GW		SG		SS	
		UG	G	UG	G	UG	G
Hippiscus ocelot	GS	2[3]	0	0	0	0	0
Hesperotettix speciosus	OF	1	0	0	0	1	0
Encoptolophus costalis	GS	0	0	16	0	0	0
Metator pardalinus	GS	0	0	2	0	0	0
Boopedon nubilum	OG	0	1	5	0	0	0
Heliaula rufa	OG	0	0	7	0	13	0
Brachystola magna	OF	0	0	1	0	1	0
Melanoplus foedus	OF	0	0	0	0	4	4
Schistocerca alutacea	MF	0	0	0	0	0	2
Arphia simplex	MF	2	3	1	1	2	1
Acrolophitus hirtipes	MF	2	2	3	0	6	6
Derotmema haydeni	MF	2	2	1	1	0	0
Chorthippus curtipennis	MF	8	6	8	6	0	0
Hippopedon capito	MF	5	5	6	5	0	0
Melanoplus confuses	MF	4	2	0	0	2	0
Spharagemon equale	?	0	1	0	1	4	2

[1] GS = grass-sedge, OG = obligate grass, OF = obligate forb, MF = mixed feeder, BL = broadleaf, ? = unknown.

[2] GW = greasewood, SG = shortgrass prairie, SS = sandsage.

[3] Highlighted species are associated with ungrazed habitats.

Table 8. PERMANOVA on CY dissimilarity distances for species diversity of 16 rare Othoptera (Acrididae) with different grazing regimes (grazed, ungrazed), within three habitats (greasewood, shortgrass prairie, sandsage), sampled from 2001-2003.

Source	DF[1]	SS	MS	F	P
Grazing	**1**	**0.44**	**0.44**	**1.86**	**0.0454**
Habitat	**2**	**0.28**	**0.64**	**1.69**	**0.0004**
Grazing x habitat	2	0.38	0.19	0.80	0.6754
Residual	24	5.72	0.24		
Total	29	7.83			

[1] DF = degrees of freedom, SS = the sum of squares (measure of total variability), MS = mean square (SS divided by degrees of freedom), F = psuedo F statistic (ratio of explained variation to unexplained variation) ($P \leq 0.05$ is significant).

Figure 5. The absolute abundance (+ 1 Standard Deviation of mean abundance) of 16 rare species of grasshoppers within grazed and ungrazed plots of greasewood, shortgrass prairie, and sandsage at the U.S. Army Pueblo Chemical Depot. Numbers above bars are the total individuals of all species collected from the combination of habitat and grazing regime (* P < 0.05).

Habitat: The *a posteriori* test for habitat indicated significant differences in grasshopper species diversity among habitats, although this difference was marginal for the shortgrass prairie versus sandsage comparison (Table 8). Comparison of the species present in each habitat indicates that 44% differed between greasewood and shortgrass, 56% between greasewood and sandsage, and 63% between shortgrass and sandsage.

Table 9. PERMANOVA a posteriori comparison of grasshopper species diversity among habitats using the permutation calculated t-statistic.

Comparison among habitats	t	P[1]
Greasewood versus shortgrass	**1.64**	**0.0056**
Greasewood versus sandsage	**1.95**	**0.0006**
Shortgrass versus sandsage	1.29	0.0688

[1] P-values for the permutation calculated t-statistic ($P \leq 0.05$ is significant).

Grasshopper Density Data

The attempt to observe patterns in grasshopper density at the PCD was unsuccessful due to low grasshopper numbers at the site. The frequency data based on abundances more accurately identified changes in patterns of population size among the three years of the study, within the three habitats studied, and by the factor of grazing.

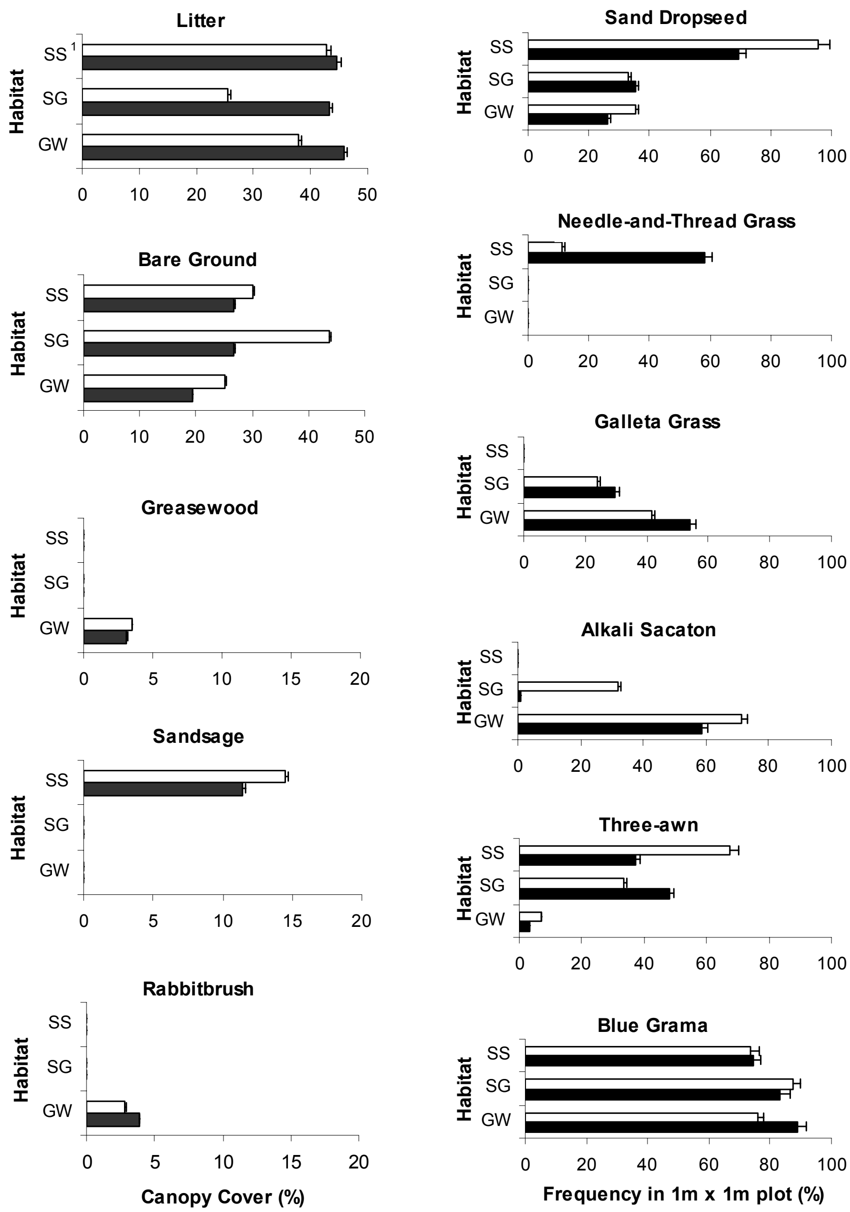
Vegetation

The differences recorded in plant characteristics of ungrazed and grazed habitats are summarized in Figure 6 (Rondeau 2005). These differences, combined with the ecology of uncommon species, might indicate why some uncommon grasshoppers are associated with ungrazed habitats. In ungrazed greasewood there was more litter, galleta grass, and rabbitbrush, but less bare ground, sand dropseed, alkali sacaton, three-awn, and blue grama. In greasewood plots, samples of greasewood did not differ between grazed and ungrazed plots.

Ungrazed shortgrass prairie had more litter, sand dropseed, galleta grass, and three-awn; but less bare ground and alkali sacaton. Samples of blue grama did not differ in grazed and ungrazed shortgrass priaire plots.

Ungrazed sandsage had more needle-and-thread grass, but less bare ground, sand dropseed, three-awn, and sandsage. Samples of blue grama did not differ in grazed and ungrazed sandsage plots. Generally, ungrazed plots in all three habitats (greasewood, shortgrass prairie, sandsage) contained more litter and galleta grass, but less bare ground and alkali sacaton, while blue grama was unaffected by grazing, except for in greasewood plots.

Figure 6. Mean canopy cover or mean frequency (± Standard Error) of plant species observed between grazed and ungrazed habitat at the U.S. Army Pueblo Chemical depot from 1999 to 2003 (summarized from Rondeau 2005).



[1] SS = sandsage, SG = shortgrass prairie, GW = greasewood; absence of data indicates the species was not present in the sampled habitat.

DISCUSSION

PCD harbors a diverse community of grasshopper species. Fifty-two different species were identified at PCD. The biodiversity of grasshoppers at PCD was high compared to recent studies elsewhere (Andersen et al. 2001, Bomar 2001, Bomar and Sechrist 2002, Gebeyehu and Samways 2003, Joern 2005, Samways and Kreuzinger 2001, Torrusio et al. 2002, Wettstein and Schmid 1999). Only one study cited above recorded more species (56), and that study investigated grassland, woodland, and shrubland ecotypes, and included seven distinct plant communities. This study included only three communities (greasewood, shortgrass prairie and sandsage).

Diversity of All Grasshopper Species

Grazing: Grazing can alter vegetation characteristics, including plant species composition, with resulting changes in vegetation structural attributes (Collins et al. 1998, Knapp et al. 1999, Joern 2005, Rondeau 2005). In turn, these changes in habitat characteristics can play important roles in altering animal population size, species richness, and the taxonomic composition of animal communities, like those of grasshoppers (Joern 2005).

Arthropod responses to grazing are not well-understood, but effects on grasshopper communities prove variable, and can be either positive (Gebeyehu and Samways 2003, Joern 2005, Torrusio et al. 2002, Wettstein and Schmid 1999) or negative (Onsager 2000). At PCD, grazing appears not to alter community composition of common grasshopper species. In 1998, three years prior to initiation of this project, grazing was terminated on all of the study's grazed areas. Grasshopper species diversity may have differed on grazed and ungrazed sample plots in 1999, one year after grazing was terminated. Grasshopper monitoring was initiated in 2001, and any changes in species diversity attributable to grazing, if they did occur, might have been short-lived, disappearing prior to commencement of monitoring.

Habitat: Grasshopper species diversity at PCD was significantly influenced by the three habitats (greasewood, shortgrass prairie, and sandsage) that occur there. This was true for both common and uncommon species. Numerous studies document habitat relationships among grasshoppers (Craig et al. 1999, Evans 1988, Fielding and Brusven 1993, Kemp et al. 1990, Parajulee et al. 1997). These relationships exist for numerous reasons, including a preference by some grasshopper species for open structure, use of a wide range of food plants among species, the need for heterogeneous structure that provides enemy-free space and a range of sites to facilitate thermoregulation, and the preference for plant tissue of high nutritional quality (citations above and Joern 2005). At PCD, feeding guild is a primary driver structuring grasshopper diversity across the three available habitats. A subset of species within the grass-sedge and obligate grass feeding categories were predominantly associated with the shortgrass prairie, and all the broad-leaf feeding grasshoppers were associated with the shrub habitats. Although broad-leaf feeders consume a wide variety of forbs, they particularly utilize shrubs as host plants (Pfadt 1994).

The grass-sedge and obligate grass feeding species predominantly associated with shortgrass prairie (excluding species observed once) included *Aulocara elliotti, Aulocara femoratum, Boopedon nubilum, Cordillacris crenulata, Encoptolophus costalis, Heliaula rufa, Metator pardalinus, Phlibostroma quadrimaculatum, Trachyrhachys aspera,* and *Trachyrhachys kiowa,* (Appendix II), which is 50% of the species represented in those two feeding categories. The other 50% of the species appeared equally distributed across habitats (see Figure 3 above and Appendix II). All the broad-leaf feeding species were associated with one or both of the shrub habitats, including *Aeoloplides turnbulli, Hesperotettix viridis, Melanoplus angustipennis, Melanoplus bowditchi, and Mestobregma plattei* (see Figure 3 above and Appendix II). The other two feeding types, including obligate forb (OF) and mixed feeders (MF), appear equally distributed across habitats (see Figure 3 above and Appendix II).

Year: There was no effect of year on species diversity. Although PCD experienced a drought from 2001 to 2003, it did not influence grasshopper species diversity. However, there were dramatic declines in grasshopper abundance from 2001 to 2002. Species present at the onset of drought persisted through the severe drought of 2002, and remained present, but at lower numbers, through the completion of the project in 2003. This factor may be why the analysis detected no difference in grasshopper diversity among years, even though grasshopper abundance declined dramatically from 2001 to 2002, with a minor recovery associated with increased precipitation in 2003.

Month Within Year: Each sample month had distinctly different grasshopper species diversity in all three years of monitoring at PCD. Seasonal phenology of the grasshoppers documented at PCD explains this variabilty (Capinera and Sechrist 1982b, Capinera et al. 2004, Pfadt 1994).

The species at PCD exhibit three distinct seasonal patterns. First, some species occur in either early (May), middle (July), or late (August) summer and persist for a short time; second, some species persist throughout the flight season (May-September); and third, some species appear in either middle or late summer and persist throughout the remaining flight season (Appendix II). One species was associated with early summer (*Arphia simplex*), three with middle summer (*Acrolophitus hirtipes, Brachystola magna, Metator pardalinus*), and four with late summer (*Hippiscus ocelot, Hesperotettix speciosus, Schistocerca alutacea, Spharagemon equale*). Ten species persisted throughout the flight season, while 14 species appeared in middle summer, persisting throughout the remaining flight season, and 11 appeared in late summer and persisted until the flight season's end (Appendix II).

Habitat-By-Month Interaction: The combined effect of grasshopper habitat relationships and their patterns of seasonal phenology caused species diversity to differ among all habitats, within each month sampled, for all three years of monitoring. This well-established pattern faltered slightly in 2002 when only eight of 12 habitat comparisons, within month, were significant. The project area experienced a drought from 2000-2003 with a severe departure from historical precipitation averages during 2002, which caused a decline in plant productivity (Rondeau 2003). Concomitant effects on the grasshopper species diversity at PCD are expected (Kemp and Cigliano 1994) and could explain why grasshopper diversity did not differ between habitats within four of the months sampled in 2002.

Diversity of Uncommon Grasshopper Species

Six species of grasshopper at PCD were each identified from one collected specimen per species. These records are not considered species for these analyses because of the potential for inaccurately identifying a species when based upon one individual. The six specimens, on which these species records were based, were not available for expert verification. If these six specimens were correctly identified, they represent uncommon species at PCD, and it is interesting to note that five of the six were recorded from ungrazed plots.

The least frequently collected species encountered at PCD was *Paropomala virgata*, whose range is limited to southern Colorado (where it is known from six counties), New Mexico, extreme eastern Texas, and extreme north-central Mexico (Capinera and Sechrist 1982b, Capinera et al. 2004). This species is considered globally secure, though it may be rare within parts of its range, especially at the periphery (NatureServe 2005).

Following is a discussion of the impact grazing had on uncommon grasshopper species at PCD, and how the ecology of seven uncommon species might explain their association with ungrazed habitats, given the plant characteristics of sample plots they occupied.

Grazing: Past grazing proved detrimental to eight uncommon grasshopper species, as represented by their association to ungrazed plots, and promoted the occurrence of one uncommon species encountered at the PCD, although this species was only captured twice, each time in grazed sandsage. The changes associated with grazing exhibited by uncommon grasshoppers at PCD were recognizable four years after cessation of grazing, suggesting that uncommon species are more sensitive to grazing disturbance. Grazing by cattle and double rotational grazing by cattle (cattle moved onto pasture twice in one season), timed to occur in tandem with nymphal grasshopper emergence negatively impacts grasshopper abundance, species richness, and diversity (Fay 2003, Onsager 2000). The type of grazing, however, is important. Research examining grazing by cattle and bison indicate that intermediate levels of grazing, grazing by bison alone, and grazing by bison in tandem with fire can all promote insect and, in most cases, grasshopper abundance, richness, and diversity (Fay 2003, Gebeyehu and

Samways 2003, Kruess and Tscharntke 2002, Joern 2005, Welch et al. 1991).

It is not surprising that grazing conducted in the past at PCD has affected diversity of uncommon grasshopper species. Nor is it surprising that grazing's impact was variable, proving both benign and detrimental to grasshoppers, with this variation in effect depending upon how abundant each species was. Historically, in eastern Colorado including the area of PCD, bison grazed some areas intensively, while leaving other areas within the same landscape ungrazed, creating a mosaic of different vegetation structure and composition within a region. It then seems reasonable to expect some grasshoppers to develop a niche for these different patch types, including species that would associate with a changing mosaic of ungrazed areas.

Habitat: The vegetation mosaic created by the distribution of greasewood, shortgrass prairie, and sandsage at PCD significantly influenced how individual species of the uncommon grasshoppers were distributed. Feeding guild was the primary factor structuring grasshopper diversity across the three sampled habitats.

Three out of five (60%) of the grass-sedge and obligate grass feeding uncommon species associated with shortgrass prairie, including *Boopedon nubilum, Encoptolophus costalis*, and *Metator pardalinus* (Table 7). One of the grass-sedge feeding grasshoppers (*Hippiscus ocelot*) was associated with greasewood. Five out of 10 (50%) of the obligate forb and mixed feeding uncommon species associated with one or both of the shrub habitats, including *Acrolophitus hirtipes, Hesperotettix speciosus, Melanoplus confuses, Melanoplus foedus,* and *Schistocerca alutacea* (Table 7). The feeding preference of *Spharagemon equale* is unknown, but it was predominantly associated with sandsage plots (Table 7). Samples of the remaining six uncommon species were equally distributed across the three sampled habitats (Table 7).

1. ***Boopedon nubilum*** Ebony Grasshopper (Grazed gw19 = 1, Ungrazed sg63 = 5 captures) (see Appendix I for a list of sample plots and definitions of the symbols used in their names)
Boopedon nubilum ranges widely in grasslands of the western North America from Montana to central Mexico (Capinera et al. 2004). *Boopedon nubilum* inhabits grasslands including mixed grass, shortgrass, sand and desert prairies, where it occupies luxuriant stands of these habitats

(Pfadt 1994). Feeding trials suggest that this species prefers blue grama, but being a fastidious feeder, it will switch feeding preferences depending upon availability of forage plants. Some other grasses identified from examination of *B. nubilum* crops include buffalograss (*Buchloe dactyloides*), needle-and-thread grass, sand dropseed, and prairie sandreed (*Calamovilfa longifolia*). The ungrazed plots occupied by *B. nubilum* contained ample amounts of litter and bare ground and much galleta grass, and some sand dropseed was present (Rondeau 2005). *Boopedon nubilum* is a mixed grass feeder, and those mixed grasses it exploits all declined in grazed habitats (Rondeau 2005). The shortgrass prairie plot (sg63) from which this species was captured had a particularly luxuriant cover of mixed grasses, which *B. nubilum* prefers, and may be why five of six captures of this species came from this plot. The shortgrass plot sg63 is somewhat of an anomaly at PCD in that its soils have a high content of silt and it virtually has no blue grama and alkali sacaton grass and is instead dominated by galleta grass. The greasewood grazed plot from which *B. nubilum* was captured had a greater amount of galleta grass than other grazed greasewood plots and sand dropseed, blue grama, and alkali sacaton were also all present (Rondeau 2005).

2. ***Brachystola magna*** Plains Lubber Grasshopper (Ungrazed sg63 = 1, Ungrazed ss08 = 1 captures)

Brachystola magna ranges widely throughout the Great Plains region of North America from Montana to north-central Mexico (Capinera et al. 2004). *Brachystola magna* inhabits grasslands including shortgrass, mixed grass, tallgrass, sand, and desert prairies, where it selects for areas within these habitats containing certain forbs (Pfadt 1994). Studies examinating contents of *B. magna* crops included common sunflower (*Helianthus annuus*), hoary vervain (*Verbena stricta*), kochia (*Bassia sieversiana*), prickly lettuce (*Lactuca serriola*), and western wheatgrass (*Pascopyrum smithii*) among other grasses. The reliance of this species on forbs may preclude its occupancy of grazed areas where selective grazing of nutritious and particularly palatable forbs may remove plants necessary to *B. magna*.

3. ***Encoptolophus costalis*** Dusky Grasshopper (sg63ug = 16 captures)

Encoptolophus costalis ranges widely in grasslands of the western North America from central Alberta, Canada, to central Mexico (Capinera et al. 2004). *Encoptolophus costalis* inhabits grasslands including mixed grass, shortgrass, and desert prairies, much like the ebony grasshopper, and it is most dominant on the northern mixed grass prairie where it favors moist areas of rich grass growth interspersed with bare ground (Pfadt 1994). *Encoptolophus costalis* consumes numerous mixed grasses, including western wheatgrass, needle-and-thread grass, blue grama, sand dropseed, prairie junegrass (*Koelaria macrantha*), green needlegrass (*Stipa viridula*), little bluestem (*Schizachyrium scoparium*), and sideoats grama (*Bouteloua curtiendula*), among other grasses (Pfadt 1994). The ungrazed shortgrass plot where *E. costalis* was captured was the same as for *B. nubilim*, and like *B. nubilum*, *E. costalis* seeks luxuriant, rich stands of mixed grasses, but it also prefers ample bare ground, which is present at ungrazed shortgrass plot sg63. Like *B. nubilim*, the mixed grasses that this species prefers were reduced on grazed habitats at PCD (Rondeau 2005).

4. ***Heliaula rufa*** Rufous Grasshopper (Ungrazed sg61 = 3, Ungrazed sg68 = 1, Ungrazed sg69 = 2, Ungrazed sg74 = 1, Ungrazed ss08 = 9, Ungrazed ss30 = 2 captures)
Heliaula rufa ranges from the western edge of the Great Plains into the Rocky Mountains from southeastern Wyoming to the Mexico border (Capinera 2004 et al.). *Heliaula rufa* inhabits deserts and prairies with sparse vegetation, is sometimes found on rocky outcrops and hillsides, and is generally uncommon everywhere it occurs (Capinera et al. 2004). *Heliaula rufa* prefers grama grasses including blue grama, but also feeds on three-awn (Capinera and Sechrist 1982b). This species was only captured from ungrazed shortgrass and sandsage sample plots.

That this species associates with ungrazed shortgrass is not surprising; it prefers blue grama, which dominates the shortgrass prairie at PCD and also selects for three-awn, which had a higher percent of cover in ungrazed, than in grazed, shortgrass prairie at PCD. Captures of *H. rufa* only occurred in ungrazed shortgrass prairie where lack of grazing by cattle resulted in less bare ground in comparison to grazed shortgrass prairie, while *H. rufa* prefers areas of sparse vegetation. However, there was bare ground in all shortgrass prairie sample plots (Rondeau 2005). The interaction between blue grama, three-awn, and the presence of some bare ground may be more important, than solely the amount of bare ground available. Sandsage at PCD had less blue grama than either shortgrass prairie or greasewood, there was less three-awn in ungrazed sandsage than grazed, and like shortgrass prairie less bare ground existed in ungrazed sandsage than in grazed (Rondeau 2005), all of which would negatively impact *H. rufa*. It is difficult to explain why *H. rufa* was captured at ungrazed sandsage plot ss08, because this sample plot exhibited all of the patterns described above (i.e. infrequent blue grama and three-awn, and diminished cover of bare ground). Ungrazed sandsage sample plot 30, however, had more blue grama and three-awn than any other sandsage plot (grazed or ungrazed), and cover of bare ground similar for that in ungrazed shortgrass prairie making occupancy by *H. rufa* understandable. In general, the fact that *H. rufa* was recorded only from ungrazed sample plots at PCD fits, the general patterns of grazing's effect on plant characteristics and the corresponding ecological preferences of this species.

5. ***Hesperotettix specious*** Western Grass-Green Grasshopper (Ungrazed gw06 = 1, Ungrazed ss08 = 1 captures)

The range of *H. specious* includes the Great Plains region of the United States, from the Canadian to the Mexican borders (Capinera et al. 2004). *Hesperotettix specious* particularly likes weedy areas where it feeds on forbs including common sunflower, ragweed (*Ambrosia* spp.), and goldenrod (*Solidago* spp.), among others (Capinera and Sechrist 1982b). Sample plots where *H. specious* was captured contain a rich cover of forbs, making them suitable for *H. specious*, but not particularly more so than other similar sample plots present at PCD. *Hesperotettix specious* association with ungrazed habitats may result from selective grazing of nutritious and particularly palatable forbs by cattle removing plants necessary to *H. speciousus*.

6. ***Hippiscus ocelot*** Wrinkled Grasshopper (gw11ug = 2 captures)

Hippiscus ocelot ranges widely east of the Rocky Mountains in the United States to the east coast and throughout the desert southwest into southern Mexico (Capinera et al. 2004). *Hippiscus ocelot* occupies grassy areas ranging from native prairie to bare areas thinly covered with grasses. It feeds on range grasses almost entirely including blue grama and little bluestem, among other grasses (Capinera and Sechrist 1982b, Otte 1984). The ungrazed greasewood sample plot from which *H. ocelot* was captured contained blue grama, galleta grass, alkali sacaton, and sand dropseed, all of which are potential forage plants. This plot, however, was similar to other ungrazed greasewood sample plots at PCD (Rondeau 2005). *Hippiscus ocelot* does prefer grass areas with thin cover and grass cover in ungrazed greasewood was less than in grazed greasewood, which may account for its association to ungrazed habitats.

7. ***Metator pardalinus*** Bluelegged Grasshopper (Ungrazed sg63ug = 1, Ungrazed sg74 = 1 captures)

Metator pardalinus ranges widely in western North America throughout the Rocky Mountains and Great Plains region from southern Saskatchewan to southern New Mexico. Like *B. nubilum and E. costalis*, *M. pardalinus* inhabitats shortgrass, mixed grass, desert and tallgrass prairies. *Metator pardalinus* feeds on a variety of grasses including blue grama, needle-and-thread grass, sand dropseed, western wheatgrass, green needlegrass, and prairie junegrass. The ungrazed sample plots from which *M. pardalinus* was captured contained a rich cover of mixed grasses, which are this grasshopper's preferred food. Like *B. nubilum* and *E. costalis*, the mixed grasses that this species prefers were reduced on grazed habitats at PCD (Rondeau 2005).

Other Influences on Grasshopper Species Diversity

Drought: In a study spanning a 27-year period, Fielding and Brusven (1993) reported that abundant winter precipitation and warm spring and summer temperatures were associated with high grasshopper populations, presumably through favorable effects on forage production. Similar studies in Colorado and New Mexico (Capinera and Horton 1989) revealed that grasshoppers responded favorably to summer moisture, which also would support abundant forage production. In a study on shortgrass prairie in Arizona, Nerney and Hamilton (1969) reported increased grasshopper populations after seasons with above-average winter and spring precipitation followed by abundant cover of vegetation. These studies suggest grasshoppers are regulated by food abundance and that their populations increase under above-average precipitation and above-average forage production.

The opposite is below average winter and spring precipitation, followed by low vegetation productivity, which cause declines in grasshopper populations. This was certainly the pattern at PCD in 2002, when extreme drought reduced plant production (Rondeau 2005), causing dramatic declines in grasshopper abundance. Abundance of all grasshopper species at the PCD were declining in 2002, and by the end of the year were quite low. The four habitat-within-month comparisons of grasshopper species diversity that were statistically insignificant were from 2002. It is not surprising grasshopper species diversity was more similar among habitats in 2002, because on all sample plots, all species were represented by few individuals leaving little opportunity for variation. The slight recovery in grasshopper numbers occurring in 2003 when precipitation increased, but was still below-average, was enough to again create distinctly different grasshopper communities among all habitats in every month.

CONCLUSIONS

Factors affecting grasshopper species diversity at PCD include grazing; spatially heterogeneous habitat including open structure, a wide range of food plants, and abundant plant biomass; and the negative impacts of drought on plant biomass.

At PCD, persistence of the **most common** grasshopper species is not affected by grazing. The patterns of species occurrence and abundance in ungrazed plots, across all three habitats sampled at PCD, were similar to the patterns observed in grazed plots. In 1998, three years prior to initiation of this project, grazing was terminated on all grazed study plots. Any changes in grasshopper species diversity attributable to grazing, if they did occur, might have been short-lived, disappearing prior to commencement of monitoring. The diversity of 16 **uncommon** species at the PCD, however, was affected by past grazing practices. For seven of these 16 uncommon species, captures were only made within ungrazed habitats. Total numbers of captures within shortgrass and sandsage distinctly favored ungrazed areas, and were slightly higher in ungrazed greasewood for the 16 uncommon grasshoppers. In addition, one species (*Schistocerca alutacea*) was only collected twice in three years of monitoring, both times from grazed sandsage plots.

Habitat (e.g., greasewood, shortgrass prairie, sandsage) had an influence on grasshopper species diversity at PCD, making all three habitats important to grasshoppers. The mosaic of three habitats supports a larger number of grasshopper species than does any individual habitat or any combination of two out of the three habitats. For some species, a single habitat contains the vast majority of observed occurrences making that habitat of ultimate importance in persistence of the species at PCD. For example, some grass-sedge and obligate grass feeding species are dependent upon shortgrass prairie, and some broad-leaf feeding grasshoppers are dependent upon one or both of the shrub habitats, while forb feeding grasshoppers utilized all three habitat types (see Figure 3a). The loss of any habitat would result in the loss of those grasshopper species whose persistence in the landscape is dependent upon the continued presence of that habitat type.

Finally, drought had an impact on grasshopper species diversity at PCD. Grasshoppers are regulated by food abundance, and their populations increase with above-average precipitation and above-average forage production. Extreme drought reduced plant production, causing dramatic declines in grasshopper abundance in 2002. Consequently, grasshopper species diversity associated with the habitat-by-month interaction was weakened.

These findings have consequences for management activities at PCD and suggest that 1) appropriate management of grazing to avoid over-grazing is important to sustaining populations of uncommon grasshopper species, 2) moderate grazing may promote grasshopper species diversity if timed appropriately to avoid nymphal development periods, 3) maintaining the existing habitat mosaic at PCD is important for sustaining current grasshopper species diversity, and 4) reducing grazing intensity during drought will assist in sustaining current grasshopper diversity. Such management practices will also promote current populations at PCD of other animals including small mammals and songbirds at higher trophic levels utilizing arthropods as prey.

Future research on invertebrates would benefit from reintroduction of grazing on some sample plots at PCD. This would allow observation of the impacts current grazing has on species diversity, allowing a more dynamic analysis of grazing’s effects. For some grasshopper species this research might indicate a positive influence of grazing, as has been reported in other recent studies (Fay 2003, Gebeyehu and Samways 2003, Kruess and Tscharntke 2002, Joern 2005).

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APPENDIX I

The plots sampled at U.S. Army Pueblo Chemical Depot, and their grazing conditions and habitat types (G=grazed, UG=ungrazed, GW=greasewood, SG=shortgrass prairie, and SS=sandsage).

Grazing	Habitat	Plot
G	GW	gw01g[1]
G	GW	gw02g
G	GW	gw09g
G	GW	gw13g
G	GW	gw19g
G	SG	sg64g
G	SG	sg67g
G	SG	sg70g
G	SG	sg77g
G	SG	sg78g
G	SS	ss21g
G	SS	ss27g
G	SS	ss36g
G	SS	ss37g
G	SS	ss38g
UG	GW	gw06ug
UG	GW	gw10ug
UG	GW	gw11ug
UG	GW	gw14ug
UG	GW	gw16ug
UG	SG	sg61ug
UG	SG	sg63ug
UG	SG	sg68ug
UG	SG	sg69ug
UG	SG	sg74ug
UG	SS	ss08ug
UG	SS	ss30ug
UG	SS	ss31ug
UG	SS	ss32ug
UG	SS	ss39ug

[1] gw = greasewood, sg = shortgrass, ss = sandsage, g = grazed, ug = ungrazed,

APPENDIX II

Adult flight period and influence of feeding guild on distribution of grasshoppers at the U.S. Army Pueblo Chemical Depot: a) by time (May, July, August, September); b) among habitats (Greasewood, Shortgrass Prairie, Sandsage).

a) Species presented by phenology

Species	Heritage Status	Adult Flight Period at PCD: May	June	July	Aug	Sept
Arphia simplex	G5S?	■				
Hardrotettix magnificus [3]	G4G5S?	■				
Melanoplus confuses	G5S?	■	■	■		
Arphia conspersa	G5S?	■	■	■		
Eritettix simplex	G5S?	■	■	■	■	
Xanthippus corallipes	G5S?	■	■	■	■	
Ageneotettix deorum	G5S?	■	■	■	■	■
Amphitornus coloradus	G5S?	■	■	■	■	■
Cordillacris crenulata	G5S?	■	■	■	■	■
Cordillacris occipitalis	G5S?	■	■	■	■	■
Paropomala virgata	G4?S?	■	■	■	■	■
Paropomala wyomingensis	G5S?	■	■	■	■	■
Psoloessa delicatula	G5S?	■	■	■	■	■
Psoloessa texana	G5S?	■	■	■	■	■
Mestobregma plattei	G5S?	■	■	■	■	■
Melanoplus femurrubrum	G5S?	■	■	■	■	■
Aulocara elliotti	G5S?		■	■	■	■
Aulocara femoratum	G5S?		■	■	■	■
Acrolophitus hirtipes	G5S?			■		
Brachystola magna	G5S?			■		
Dissosteira longipennis	G5S?			■		
Metator pardalinus	G5S?			■		
Boopedon nubilum	G5S?			■	■	
Dactylotum bicolor	G5S?			■	■	
Melanoplus occidentalis	G5S?			■	■	
Aeoloplides turnbulli	G5S?			■	■	■
Chorthippus curtipennis	G5S?			■	■	■
Derotmema haydeni	G5S?			■	■	■
Hadrotettix trifasciatus	G5S?			■	■	■
Heliaula rufa	G5S?			■	■	■
Hesperotettix speciosus	G5S?			■	■	■
Melanoplus bowditchi	G5S?			■	■	■
Melanoplus sanguinipes	G5S?			■	■	■
Mermiria bivittata	G5S?			■	■	■
Paropomala pallida	G5S?			■	■	■
Spharagemon collare	G5S?			■	■	■
Trachyrhachys aspera	G5S?			■	■	■
Trimerotropis pallidipennis	G5S?			■	■	■
Tropidolophus formosus	G5S?			■	■	■
Hippiscus ocelot	G5S?				■	
Hesperotettix viridis	G5S?				■	
Melanoplus lakinus	G5S?				■	
Pardalophora haldemani	G5S?				■	
Schistocerca alutacea	G5S?				■	
Spharagemon equale	G5S?				■	
Arphia pseudonietana	G5S?				■	■
Encoptolophus costalis	G5S?				■	■
Hippopedon capito	G5S?				■	■
Melanoplus angustipennis	G5S?				■	■
Melanoplus arizonae	G5S?				■	■
Melanoplus foedus	G5S?				■	■
Melanoplus gladstoni	G5S?				■	■
Melanoplus packardii	G5S?				■	■
Opeia obscura	G5S?				■	■
Phlibostroma quadrimaculatum	G5S?				■	■
Trachyrhachys kiowa	G5S?				■	■
Trimerotropis latifasciata	G5S?					■
Leprus intermedius	G5S?	No seasonal data for this sp.				

b) Species presented by feeding category

Species	Feeding Category[1]	Abundance by Habitat[2]: GW	SG	SS
Eritettix simplex	GS	487	195	118
Psoloessa delicatula	GS	104	255	198
Ageneotettix deorum	GS	93	102	67
Amphitornus coloradus	GS	59	81	42
Xanthippus corallipes	GS	16	72	60
Chorthippus curtipennis	GS	14	0	2
Aulocara elliotti	GS	2	53	7
Aulocara femoratum	GS	4	51	2
Encoptolophus costalis	GS	0	16	0
Metator pardalinus	GS	0	2	0
Opeia obscura	OG	232	282	34
Cordillacris occipitalis	OG	282	269	275
Paropomala wyomingensis	OG	79	51	93
Mermiria bivittata	OG	35	15	11
Trimerotropis latifasciata	OG	0	0	1
Cordillacris crenulata	OG	18	85	11
Trachyrhachys aspera	OG	9	43	0
Phlibostroma quadrimaculatum	OG	8	22	0
Trachyrhachys kiowa	OG	9	15	0
Heliaula rufa	OG	0	7	13
Boopedon nubilum	OG	1	5	0
Dissosteira longipennis	OG	0	1	0
Dactylotum bicolor	OF	21	19	11
Tropidolophus formosus	OF	4	10	32
Acrolophitus hirtipes	OF	4	4	11
Hesperotettix speciosus	OF	1	0	1
Schistocerca alutacea	OF	0	0	2
Arphia conspersa	MF	105	65	69
Arphia pseudonietana	MF	69	38	0
Arphia simplex	MF	5	2	3
Brachystola magna	MF	0	1	1
Derotmema haydeni	MF	4	2	0
Hadrotettix trifasciatus	MF	0	0	1
Hippiscus ocelot	MF	2	0	0
Melanoplus confuses	MF	6	0	2
Melanoplus femurrubrum	MF	37	0	29
Melanoplus foedus	MF	0	0	8
Melanoplus gladstoni	MF	20	65	6
Melanoplus occidentalis	MF	14	13	44
Melanoplus packardii	MF	20	6	151
Melanoplus sanguinipes	MF	36	23	33
Spharagemon collare	MF	1	0	39
Spharagemon equale	MF	1	1	6
Trimerotropis pallidipennis	MF	143	268	68
Aeoloplides turnbulli	BL	60	21	22
Hesperotettix viridis	BL	31	5	8
Melanoplus angustipennis	BL	14	15	63
Melanoplus bowditchi	BL	119	10	420
Melanoplus lakinus	BL	0	0	1
Mestobregma plattei	BL	100	62	25
Hardrotettix magnificus	?	15	62	4
Hippopedon capito	?	10	10	0
Leprus intermedius	?	0	1	0
Melanoplus arizonae	?	4	12	18
Pardalophora haldemani	?	0	0	1
Paropomala pallida	?	4	2	119
Paropomala virgata	?	7	6	39
Psoloessa texana	?	27	60	271

[1] GS = Grass-sedge, OG = obligate grass, OF = obligate forb, MF = mixed feeder, BL = broadleaf, ? = unknown.
[2] GW = greasewood, SG = shortgrass prairie, SS = sandsage.
[3] Species in bold font were identified from only one individual and were not analyzed.