Journal of Arid Environments

Journal of Arid Environments 60 (2005) 627–646

www.elsevier.com/locate/jnlabr/yjare

Desert grassland canopy arthropod species richness: temporal patterns and effects of intense, short-duration livestock grazing

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Received 22 July 2003; received in revised form 13 July 2004; accepted 26 July 2004

Abstract

Arthropods living in the canopies of two woody shrub species (a sub-shrub (*Gutierrezia sarothrae*) and a large shrub (*Prosopis glandulosa*)) and perennial grasses plus associated herbaceous species, were sampled on 18, 0.5 hectare plots in a Chihuahuan Desert grassland for five consecutive years. Mesquite shrubs were removed from nine plots, six plots were grazed by yearling cattle in August and six plots were grazed in February for the last 3 years of the 5 year study. Arthropod species richness ranged between 154 and 353 on grasses, from 120 to 266 on *G. sarothrae*, and from 69 to 116 on *P. glandulosa*. There was a significant relationship between the number of families of insects on grass and *G. sarothrae* and growing season rainfall but species richness was not a function of growing season rainfall on any of the plants. Several of the arthropod families that were the most species rich in this grassland were found on all of the plants sampled, i.e. Salticid spiders, Bruchid and Curculionid beetles, Cicadellid and Psyllid homopterans, and ants (Formicidae). There were more species rich families that were shared by grasses and the sub-shrub *G. sarothrae* than with mesquite. The absence of a relationship between growing season rainfall and species richness was attributed

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0140-1963/$ - see front matter
doi:10.1016/j.jaridenv.2004.07.004

to variation in life history characteristics of arthropods and to the non-linear responses of annual and perennial desert grassland plants to rainfall.

There were no significant differences in insect family or species richness on any of the plant types as a result of removal of mesquite (*P. glandulosa*) from selected plots. Intense, short duration (24 h) grazing by livestock during in late summer resulted in reduced species richness in the grass-herb vegetation layer but had no effect on insect species richness on snakeweed or mesquite shrubs. Livestock grazing in winter had no effect on insect species richness on any of the vegetation sampled.

Keywords: Arthropods; Desert; Insects; Livestock grazing; Shrub-removal; Species richness

1. Introduction

Desert environments are characterized by low rainfall that is unpredictable in time and space. Desert biota is described by Polis (1991) as dynamic and non-equilibrium, with great variation in species richness and abundance both within and among years. The sporadic availability of moisture, with its effect on primary production, is a major abiotic 'trigger' affecting arthropod abundance and diversity (Wallwork et al., 1986). Because of their dependence on green vegetation, the abundance and diversity of canopy arthropods should vary with rainfall. Experimental studies of grassland insect assemblages found that although increased plant diversity increased arthropod species richness, the diversity of herbivores was also strongly correlated with parasite and predator diversity (Sieman et al., 1998). Arthropod species richness was also related to plant productivity in prairie grasslands (Sieman, 1998). In Chihuahuan Desert grasslands, plant species diversity and production increases with good summer monsoon rains with the emergence of many ephemeral plant species (Gutierrez and Whitford, 1987). In the Chilean arid region, arthropod diversity was related to functional plant characteristics such as water and nitrogen content (Rau et al., 1998). The nutrient status of many Chihuahuan Desert plants is frequently not linked to rainfall (Whitford and Herrick, 1996). Therefore, if arthropod species richness is tied to both water and nitrogen content of plants, species richness may not track annual variation in rainfall.

In Chihuahuan Desert grasslands, honey mesquite (*Prosopis glandulosa*) shrubs produce new foliage, flowers and fruits in late spring independent of the rainfall of the preceeding autumn and winter seasons. Therefore, mesquite shrubs are a reliable source of hydrated foliage during the growing season regardless of the temporal patterns and amounts of rainfall. Mesquite shrubs should serve as a source for generalist herbivores to colonize grasses and herbaceous plants following rains. Grasslands without mesquite shrubs should therefore have lower species richness than grasslands with these shrubs present.

There is a history of continuing vegetation changes in the desert rangelands of the southwestern US beginning in the 1880s coincident with the introduction of the livestock industry and continuing to the present (Buffington and Herbel, 1965;

Hastings and Turner, 1965; Bahre and Shelton, 1993). In the Chihuahauan Desert, grasslands have been replaced by shrub-dominated ecosystems and the remaining grasslands are a mosaic of shrubs and grasses with varying cover of a sub-shrub: snakeweed (*Gutierrezia sarothrae*) and a multistemmed large shrub: mesquite (*P. glandulosa*). There is a paucity of information on the effects of these vegetation changes on faunal diversity (Whitford, 1997). The effects of vegetation changes and grazing on invertebrates is limited to studies of ant communities (Whitford et al., 1999; Kerley and Whitford, 2000). Studies on the effects of grazing on grasshopper communities have documented differences in species composition as a result of livestock grazing (Capinera and Sechrist, 1982). In a review of grassland management, Morris (1978) emphasized the complexity of responses of different arthropod groups with different kinds of grazing management. He called for studies to examine the effects of livestock species, grazing intensities, and temporal patterns of grazing.

We designed a study of Chihuahuan Desert grassland insects to examine the effects of growing season rainfall, the effects of removal of a dominant shrub and the effects of seasonal, short-duration livestock grazing on the species richness of insects in the grass layer, and the canopies of two dominant shrubs. These studies addressed several hypotheses:

(1) desert arthropod species richness and community structure is a function of growing season rainfall and/or annual rainfall,
(2) insect species richness on mesquite exhibits little variation among years,
(3) insect species richness is lower on plots with mesquite removed than on plots with mesquite present,
(4) insect species richness is reduced by summer and winter livestock grazing. Here we report variation in canopy arthropod community structure and arthropod species richness from 1993–1997 in canopies of three types of Chihuahuan Desert grassland plants on plots subjected to shrub removal, seasonal livestock grazing and no manipulations.

2. Study site and methods

Insects were sampled at an experimental site (elev. 1300 m) located 8 km west of the USDA Headquarters, Jornada Experimental Range, Dona Ana Co., New Mexico approximately 58 km NNW of Las Cruces, N. M. The site, on sandy loam soils, is in an ecotone between black grama (*Bouteloua eriopoda*) grassland to the south and encroaching mesquite (*P. glandulosa*) coppice dunes to the north. Rainfall averages *ca.* 230 mm year^{-1}, with more than half usually occurring from July to September. However, in some years winter precipitation contributes a sizeable percentage of the annual total. Kunkel et al. (1990) indicate an average pan evaporation rate of 1727 mm annually for the study region.

Eighteen, 0.5 ha plots were enclosed with three strand barbed wire fencing in 1993. Six of the plots were assigned to winter grazing by livestock and six plots were assigned to summer grazing by livestock. All mesquite shrubs were removed by cutting from nine of the plots in January 1994 and resprouts were treated with Roundup™ in subsequent years. Plots were winter-grazed in February and summer-grazed in August of 1995–1997 (1994 was judged too dry to initiate grazing). Stocking rate was adjusted for the estimated forage available in the plots. Plots were stocked with between 20 and 40 yearling cows per plot for 24–36 h in order to remove between 65% and 80% of the estimated available forage.

The temporal patterns of arthropod species richness in relation to rainfall was examined by combining the data from all plots regardless of treatment. Canopy arthropods were sampled in late August coincident with the peak in primary production.

Three plant types were sampled in each plot: mesquite (in shrub intact plots), snakeweed (*G. sarothrae*), and perennial grasses (most frequently mixes of black grama, *B. eriopoda*, spider grass, *Aristida ternipes*, and mesa dropseed, *Sporobolous flexuosus*). Mesquite (*P. glandulosa*) is a large, winter deciduous, long-lived, multi-stemmed shrub. Snakeweed is a small, short-lived, evergreen subshrub. Arthropods were sampled with a 38 cm diameter insect sweep net. Sweeps of one type of vegetation were made in all plots before the next plant type was sampled. Each plant type required a different sampling protocol. Each plot was subdivided into 102 cells or subplots. Fifteen cells were selected at random in each plot for sampling of each plant type. Cells within a plot were selected at random for sampling of canopy arthropods. For mesquite, one plant (usually the largest) was beat-sampled per cell. The net was placed below the canopy (once on each side) and the foliage beaten three times with a rod. For snakeweed, five plants were sampled per cell, one sweep per plant. For grass, ten sweeps were made while walking across the cell. Care was taken to avoid shrubs in the grass sweeps. Samples were placed in plastic ziplock bags and stored in a freezer.

Arthropods were identified and counted using an Olympus zoom stereomicroscope. The arthropods were initially sorted to family using the keys in Borrer and DeLong (1971). Identifications were made to species when possible, using reference collections at the Biology and Entomology—Plant Pathology Departments, New Mexico State University and some groups were sent to specialists (see acknowledgements). Voucher specimens were prepared for each species or morphospecies. The voucher collection is stored in the Entomology—Plant Pathology insect museum at New Mexico State University. Certain specimens could only be determined to genus and others, particularly in the parasitic Hymenoptera and the Hemiptera, were numbered as morphospecies. Pik et al. (1999) discuss and support use of morphospecies in estimating species richness in terrestrial invertebrates.

Comparisons of mean species richness among years and treatments were made using a three-way factorial analysis of variance, with the Bonferroni/Dunn test used for multiple (pairwise) comparisons of treatment effects. Plot means for the baseline year (1993) were also compared with ANOVA to test for intrinsic richness differences in untreated plots. Normality of data sets was checked with the Kolmogorov–Smirnov test. StatView˙˙ was the statistical package in all analyses.

3. Results

Nearly 1000 species and morphospecies of arthropods were identified with the species richness on individual plots ranging from 11 to 102 species. Both numbers of families and numbers of species/morphospecies exhibited decreases on all plant types during years with below average growing season rainfall (Tables 1–3). Mesquite shrubs supported fewer families and species/morphospecies of canopy arthropods than grass or snakeweed. Family richness and species/morphospecies richness of canopy arthropods on snakeweed, a woody sub-shrub, were more similar to that of grasses than of the large shrub, mesquite (Tables 1–3).

Relatively, few taxa accounted for a high percentage of all arthropods sampled within each vegetation type (Tables 1–3). Only 13 species/morphodspecies accounted for an average of 49% of the total arthropod sample. On mequite, only three species accounted for 76% of the arthropods sampled. Only one species, the ant, *Dorymyrmex* (= *Conomyrma*) *insana*, constituted 1% or more of the richness for all vegetation types in all periods. Some taxa, including *Empoasca mexicana* (Cicadellidae) on snakeweed and the psyllid, *Aphalaroida* spp. on mesquite, were dominant on their host plants. Other groups, such as parasitic Hymenoptera, were common in aggregate but individual morphospecies (or even families) were not.

The relationship of species/morphospecies and family richness to growing season rainfall was statistically significant only for family richness on grass and snakeweed canopies (Table 4). Species and family richness of grass canopy arthropods were considerably higher in 1996 than the preceding 2 years. The species/morphospecies richness in 1996 was equal to that of 1997, the second successive year of average growing season rainfall. This pattern was recorded for families but not for species/morphospecies on snakeweed. Canopy arthropod species richness was higher on grasses than on either a dense canopy sub-shrub (*G. sarothrae*) or a large woody shrub (*P. glandulosa*) (Table 4).

The species rich families of grass and snakeweed canopy arthropods were essentially identical on these two types of vegetation (Tables 1 and 2). In each of the species rich families there was considerable variation in the numbers of species recorded, e.g. 2–7 species and 3–6 species of Bruchidae recorded from grass and snakeweed, respectively. The species rich families were distributed among several orders, i.e. Aranea: Salticidae, Coleoptera: Buprestidae and Coccinellidae, Diptera: Bombyliidae, Chloropidae and Empididae, Heteroptera: Lygaeidae and Miridae, Homoptera: Cicadellidae and Psyliidae, Hymenoptera: Formicidae, and Orthoptera: Acrididae (Tables 1 and 2). There were only four species rich families of arthropods on mesquite and those species rich families were also species rich on grasses and snakeweed: Bruchidae, Cicadellidae, Psyliidae, and Formicidae (Table 3).

There were no treatment differences in the arthropod species richness during the two baseline years (1993 and 1994). There were significant reductions ($t = 5.4$, $p < 0.03$) in species richness of perennial grass canopy arthropods on both winter and summer grazed, shrubs intact plots compared to the ungrazed control during the first year of the grazing treatment (Table 5). There were no significant differences in species richness of perennial grass canopy arthropods on the summer-grazed,

Table 1
Comparison of the number of species/morphospecies of arthropods sampled from grasses on all study plots at the Chihuahuan Desert grassland study site on the Jornada Experimental Range, New Mexico among the years of the study

Taxon	1993	1994	1995	1996	1997
Arachnida. Acari: Ixodidae	1	1	1	1	1
Oribatidae	1	1	1	1	1
Tetranychidae	1	1	1	1	1
Araneae: Araneidae	1	1	1	5	2
Dictyinidae				1	2
Linyphilidae				1	1
Mimetidae				1	
Oxypodidae	1	1	1		1
Philodromidae				3	3
Pisauridae	1				
Salticidae	1	4	4	5	5
Tetragnathidae		1			3
Theridiidae				2	1
Thomisidae	1	1	1	4	2
Insecta, Coleoptera: Anobiidae					1
Anthribidae	1	1			
Bruchidae	5	2	4	7	7
Buprestidae					2
Cantharidae					1
Carabidae	1			2	2
Chrysomelidae	6	2	3	8	11
Clambidae	1	1	1	1	2
Cleridae	2	2	1		1
Coccinellidae	4	2	2	9	7
Curculionidae	5	4	3	8	4
Melandryidae					1
Meloidae	5		2	1	1
Melyridae		3	2	1	1
Mordellidae	1	1	1	1	1
Phalacridae	1				
Scarabaeidae					1
Staphylinidae					1
Tenebrionidae			1		2
Collembola: Sminthruidae	1	2	2	2	2
Diptera: Agromyzidae	1				
Anthomyiidae	1	1	1		1
Asilidae	2	2	1	2	2
Bombyliidae	1	4	1	13	10
Calliphoridae				1	1
Cecidomyiidae	3		1	3	2
Ceratopogonidae	1			1	
Chloropidae	12	8	8	20	17
Conopidae					1
Culicidae	1			1	1
Dolichopodidae	1			2	1
Drosophilidae	1	1	1		
Empididae	1	2	1	12	10
Lonchaeidae	1	1			

Table 1 (*continued*)

Taxon	1993	1994	1995	1996	1997
Muscidae	1	2	1		1
Opomyzidae	1	1			
Phoridae	1	1			1
Pipunculidae	2	1	1	2	2
Sarcophagidae			1	5	5
Scatopsidae	1	1			1
Scenopinidae	1	2	1	3	1
Sciaridae	1	1	1	1	1
Sepsidae	1			1	1
Syrphidae	2		1	2	1
Tachinidae				1	4
Tephritidae	7	2	2	4	7
Tipulidae	1				1
Heteroptera: Alydidae	1				
Anthocoridae	1	1		1	1
Berytidae		1	1	1	3
Coreidae	1				
Cydnidae			1		
Lygaeidae	6	4	5	4	12
Miridae	15	4	6	11	25
Nabidae	2	1	1	1	1
Pentatomidae	1		1	5	5
Phymatidae			1		
Reduviidae	1				1
Rhopalidae	1	1	2	2	5
Scutellaridae	1			2	1
Thyreocoridae		1		1	2
Tingidae	1	1	2	6	6
Homoptera: Acanaloniidae	2			2	1
Aleyrodidae	1		1	1	1
Aphididae	1		1	1	1
Cercopidae	1		1		
Cicadellidae	17	12	32	32	30
Cixiidae	1				
Coccidae	1	1		1	1
Dephacidae	1	1		1	4
Dictyopharidae	1		1	1	1
Flatidae	2	2	1	1	2
Issidae	1	1	1		1
Keriidae			1		
Membracidae	2				2
Pseudococcidae	1	1	1	1	1
Psyliidae	6	4	2	5	3
Hymenoptera: Andrenidae			1		1
Anthophoridae	1		1	2	
Argidae				1	
Bethylidae	1			1	1
Braconidae	1		1	5	6
Ceraphhronidae				1	
Chalcididae	1	1	1	1	2
Chrysididae				1	1

Table 1 (*continued*)

Taxon	1993	1994	1995	1996	1997
Colletidae	1		1	1	2
Cynipidae	1				
Dryinidae	1		1	4	3
Encyrtidae	1	4	1	12	1
Eucharitidae	1		1	7	1
Eulophidae	1		1	9	1
Eupelmidae	1	3	1	13	1
Eurytomidae	7	5	2	10	1
Formicidae	9	12	8	10	10
Halictidae	2		1	2	9
Ichneumonidae		1	1	5	2
Megachilidae	1		1	1	
Melittidae				1	
Mymaridae	1	1	1	5	1
Perilampidae		1	1	1	1
Platygasteridae	1			2	1
Pteromalidae	1	4	1	6	1
Scelionidae	1			7	1
Sphecidae	1	1	1	2	7
Tiphiidae	2		1	3	2
Torymidae		1	1		
Trichogrammatidae	1			6	1
Vespidae	1				
Isoptera: Termitidae				1	
Lepidoptera: Coleophoridae	1	1	1	1	
Gelechiidae	1	1		1	
Geometridae	1		1	5	4
Gracillaridae	1				
Lycaenidae			1		1
Lyonetidae	1				
Noctluidae	1	1	1	1	4
Plutellidae			1		
Pyralidae	1	1	1		
Tortricidae				1	
Neuroptera: Chrysopidae	1	1	1	1	1
Coniopterygidae	1			3	1
Hemerobiidae	1	1	1	1	
Myrmeleontidae	1	1	1	1	3
Odonata: Coenagrionidae					1
Orthoptera: Acrididae	8	9	10	6	12
Gryllidae	2	1	1	1	1
Mantidae	2	1	1		
Tettigoniidae	1			1	2
Phasmatodea: Phasamatidae	4	3	3	2	4
Psocoptera: Liposcelidae			1		
Thysanoptera: Phlaeothripidae	2	3	2	4	2
Thripidae	2	1	3	4	5

Table 2
Numbers of species/morphospecies in the families of arthropods collected on snakeweed (*Gutierrezia sarothrae*) on all plots in the Chihuahuan Desert grassland study site on the Jornada Experimental Range, New Mexico each year of the study

Taxon	1993	1994	1995	1996	1997
Arachnida. Acari: Ixodidae		1	1	1	1
Oribatidae	1	1	1	1	1
Tetranychidae	1	1	1	1	1
Araneae: Araneidae	1	2	1	2	2
Dictyinidae		1		1	2
Linyphilidae		1		1	1
Oxypodidae	1	1		1	
Philodromidae		1		2	2
Pisauridae	1				
Salticidae	1	5	4	6	5
Tetragnathidae		1		1	3
Theridiidae	1	1		1	2
Thomisidae	1	2	1	3	1
Solfugae: Eremobaetidae				1	
Uropygii: Thelphonidae	1				
Insecta, Coleoptera: Anthribidae	1				
Bruchidae	3	3	3	6	4
Buprestidae	1				
Carabidae				1	
Cerambycidae					1
Chrysomelidae	4	3	4	6	10
Clambidae		2	1	2	1
Cleridae			1	1	
Coccinellidae	4	2	2	7	4
Curculionidae	4	1	3	3	5
Meloidae	2		2	1	1
Melyridae			1	1	2
Mordellidae	1				2
Scarabaeidae		1	1		
Tenebrionidae	2		1	1	2
Collembola: Sminthruidae	1	2	2	2	2
Diptera: Asilidae	1	1	2	1	1
Bombyliidae	1		1	8	13
Cecidomyiidae	3	1	1	3	4
Ceratopogonidae	1				
Chloropidae	6	6	5	13	11
Dolichopodidae	1				
Empididae	2	6	2	5	6
Opomyzidae	1	1			
Otitidae					1
Phoridae	1		1	1	
Pipunculidae	1	1			1
Sarcophagidae				1	2

Table 2 (*continued*)

Taxon	1993	1994	1995	1996	1997
Scatopsidae	1	1			
Scenopinidae	1	1			
Sciaridae	1	1		1	1
Sepsidae	1			1	1
Syrphidae	2		1		
Tachinidae				1	4
Tephritidae	5	2	1	3	4
Heteroptera: Alydidae	1				
Anthocoridae	1		1	1	1
Aradidae				1	
Berytidae					3
Coreidae	1				1
Lygaeidae	4	3	5	3	8
Miridae	12	6	10	24	25
Nabidae	1			2	2
Pentatomidae	1		1	1	7
Reduviidae	1			1	1
Rhopalidae	2		1	4	4
Scutellaridae					1
Thyreocoridae				1	
Tingidae	2		2	3	4
Homoptera: Acanaloniidae	4	1	1	1	1
Aleyrodidae	1		1	1	1
Aphididae	1	1		1	1
Cercopidae	1				
Cicadellidae	16	8	10	26	23
Coccidae		1		1	1
Dephacidae	2			1	3
Dictyopharidae	1	1	1	1	
Flatidae	3	2	2	1	1
Fulgoroidea	1	1			
Issidae	1	1	1		1
Keriidae	1	1			
Membracidae	2				1
Pseudococcidae	1	1	1	1	1
Psyliidae	6	4	4	6	5
Hymenoptera: Andrenidae	3			2	
Anthophoridae	1				
Argidae				1	
Bethylidae				2	
Braconidae	1	1		2	4
Ceraphhronidae		1			1
Chalcididae	1	1			1
Colletidae			1	1	
Dryinidae	1		1		1
Encyrtidae	1	3	1	1	1
Eucharitidae	1	1	1	3	1
Eulophidae	1	2	1	1	1

Table 2 (*continued*)

Taxon	1993	1994	1995	1996	1997
Eurytomidae	3	3	2	1	1
Formicidae	7	5	6	9	7
Halictidae	2				5
Ichneumonidae	1			2	
Megachilidae	1		1	1	
Mymaridae	1	1	1	1	1
Perilampidae		1	1	1	1
Platygasteridae	1			1	1
Pteromalidae	1	2	1	1	
Scelionidae				1	1
Sphecidae	1		1		2
Tiphiidae	1		1	1	3
Torymidae		1			
Trichogrammatidae	1		1	1	1
Vespidae			1		
Lepidoptera: Coleophoridae	1	1		1	1
Gelechiidae		1			
Geometridae	1	1	1	6	2
Noctluidae	1		2	1	1
Pyralidae	1		1		
Tortricidae	1	1	2	1	1
Neuroptera: Chrysopidae	1		1	1	1
Coniopterygidae			1	1	
Hemerobiidae			1		
Myrmeleontidae				2	1
Orthoptera: Acrididae	6	7	6	7	8
Gryllidae	1	1	1	1	1
Mantidae			1		1
Tettigoniidae	1		1	1	2
Phasmatodea: Phasamatidae	3	1	2	1	2
Thysanoptera: Phlaeothripidae	1		2	2	2
Thripidae	1	1	3	6	8

shrub-removed and winter grazed, shrub-removed plots but the species richness on these plots were significantly lower than ungrazed-shrub removed plots ($t = 6.9$ and 5.3, respectively; $p < 0.03$) (Table 5). Following the second year of grazing, there were significant reductions in species richness of grass canopy arthropods in the summer-grazed, shrub-intact plots in comparison to the winter-grazed shrub-intact plots and the ungrazed, shrub-intact plots ($t = 12.2$, $p < 0.01$). There were no significant differences in species richness of grass canopy arthropods among the shrub-removed treatments following the second year of grazing. There were no significant differences in species richness of grass canopy arthropods among the treatments following the third year of grazing (Table 5).

Table 3
Numbers of species/morphospecies in the families of arthropods collected in the samples from mesquite (*P. glandulosa*) on plots in the Chihuahuan Desert grassland study site on the Jornada Experimental Range, New Mexico

Taxon	1993	1994	1995	1996	1997
			1		
Arachnida. Acari: Ixodidae	1		1	1	1
Oribatidae	1		1	1	1
Tetranychidae	1		1	1	1
Araneae: Araneidae	1		1	2	2
Dictyinidae				1	2
Mimetidae			1		1
Philodromidae				1	1
Salticidae	1		3	1	3
Thomisidae	1		1	2	1
Insecta, Coleoptera: Bostrichidae	1			1	2
Bruchidae	2		6	3	4
Buprestidae			2	1	1
Carabidae					1
Chrysomelidae	1		1		1
Clambidae			2	1	
Cleridae					1
Coccinellidae	2				2
Curculionidae	2		1	3	5
Dermestidae					1
Elateridae				1	
Tenebrionidae	1		2	1	1
Collembola: Sminthruidae	1		1	2	2
Diptera: Bombyliidae				1	
Cecidomyiidae	1		1	1	1
Conopidae					
Chloropidae	4		1	1	3
Otitidae					1
Sciaridae	1		1		
Tachinidae					1
Tephritidae					1
Heteroptera: Anthocoridae	1			1	1
Coreidae	2				1
Lygaeidae	3		1		1
Miridae	2		1	2	3
Nabidae					1
Pentatomidae	1			1	1
Rhopalidae	1				2
Tingidae				1	1
Homoptera: Acanaloniidae	2		1	1	1
Aleyrodidae	1		1	1	1
Aphididae	1		1	1	
Cicadellidae	8		1	4	10

Table 3 (*continued*)

Taxon	1993	1994	1995	1996	1997
Coccidae	2		2	1	
Dephacidae	1			1	1
Flatidae	2		2	1	1
Issidae	1				
Membracidae	5			2	6
Pseudococcidae	1		1	1	1
Psyliidae	6		4	7	5
Hymenoptera: Bethylidae	1			1	
Braconidae	1				1
Ceraphhronidae					1
Encyrtidae	1		1	1	1
Eucharitidae	1				
Eulophidae			1	1	1
Eupelmidae			1	1	
Eurytomidae	1				
Formicidae	6		6	7	4
Halictidae					2
Mymaridae	1		1		1
Perilampidae				1	1
Pteromalidae	1		1	1	1
Scelionidae			1		1
Tiphiidae	1				1
Trichogrammatidae					1
Lepidoptera: Gelechiidae	1		1	3	1
Geometridae	1		1		1
Gracillaridae			1		
Noctluidae	1		1		
Pyralidae	1			2	1
Tortricidae					1
Neuroptera: Chrysopidae	1		1		1
Hemerobiidae				1	1
Myrmeleontidae			1		
Orthoptera: Acrididae	1			1	1
Gryllidae	1		1	1	1
Mantidae	1			1	3
Tettigoniidae	2		1	1	4
Phasmatodea: Phasamatidae	1		1		1
Thysanoptera: Phlaeothripidae	1		2	1	3
Thripidae	1		2	1	2

There were no significant differences in insect species richness on snakeweed canopies as a result of mesquite removal (Table 6). Summer grazing resulted in a significant reduction in insect species richness only in the shrub intact plots during the second year of grazing (1966). Species richness was higher on snakeweed in winter-grazed, shrub-intact plots and shrub-removed plots compared to controls in

Table 4
Comparison of total number of arthropod families and species/morphospecies on plant functional groups in each year of the study in Chihuahuan Desert grassland with the results of regression analysis of richness and growing season rainfall

	1993	1994	1995	1996	1997	r^2	p
Grass—families	109	72	88	101	112	0.75	0.05*
Grass—species/morphospecies	226	154	175	368	353	0.21	0.57
Snakeweed—families	91	62	69	69	87	0.90	0.01*
Snakeweed—species/morphospecies	177	120	132	235	266	0.26	0.38
Mesquite—families	57	ND	46	46	68	0.67	0.19
Mesquite—species/morphospecies	93	ND	69	75	116	0.64	0.20
Growing season rainfall (June–August)(mm)	178.3	47.5	75.7	77.5	155.9		

ND—no data.
*Regression that is statistically significant.

Table 5
Mean ±standard deviation of species richness of arthropods on perennial grasses on seasonally grazed (summer, winter) and shrub removed (rem) plots compared with shrubs intact (int) and ungrazed (control) plots on the desert grassland study area on the Jornada Experimental Range during the 5 years of the study

Year	Summer-int	Winter-int	Control-int	Summer-rem	Winter-rem	Control-rem
1993	67.7±5.1	60.3±4.6	69.7±7.0	73.3±10.4	63.7±3.1	58.7±7.8
1994	30.3±3.1	37.3±4.5	34.3±3.8	31.7±8.1	33.3±3.2	26.7±1.5
1995	27.3±2.6*b	33.3±9.9*b	44.0±11.0*a	26.7±11.0*d	40.3±6.0*d	57.7±5.0*c
1996	48.3±4.0*a	75.7±15.0*ab	80.0±4.6*b	71.3±11.4	80.3±14.7	85.3±0.6
1997	66.0±10.6	81.0±9.5	91.7±4.9	75.0±3.0	88.3±15.2	83.0±4.6

Grazing was initiated in 1995, shrubs were removed in winter 1994. Means with * and letter are significantly different at $p<0.05$ from plots with * different letters within a year.

Table 6
Mean ±standard deviation of species/morphospecies richness of arthropods on broom snakeweed (*G. sarothrae*) on seasonally grazed (summer and winter) and shrub removed (rem), shrubs intact (int) and control plots in the desert grassland grazing and shrub removal experimental plots on the Jornada Experimental Range

Year	Summer-int	Winter-int	Control-int	Summer-rem	Winter-rem	Control-rem
1993	48.0±10.4	46.3±4.1	49.7±5.7	44.7±1.4	46.7±18.5	46.7±14.7
1994	20.0±2.7	16.3±2.1	17.7±1.5	21.3±7.2	22.3±4.0	19.7±4.0
1995	29.3±3.8	31.3±8.1	33.0±2.0	28.7±5.0	36.0±9.8	32.0±7.0
1996	47.0±3.6*a	65.3±4.0*b	58.0±4.4*ab	61.3±9.1*cd	72.7±2.5*c	60.0±3.0*abd
1997	54.0±12.3	64.3±3.5	67.0±9.2	70.0±13.5	77.0±8.2	65.3±5.5

*Statistically significant differences ($p<0.05$) among treatments.

Table 7
Means ± one standard deviation of the number of species of arthropods in samples taken on mesquite (*P. glandulosa*) on seasonally grazed plots and ungrazed control plots. None of the plot means were significantly different

Year	Summer grazed	Winter grazed	Ungrazed control
1993	24.8±3.8	26.3±2.5	28.7±4.5
1995	15.3±4.0	16.3±2.6	17.7±4.7
1996	22.7±2.5	27.7±3.1	29.0±2.0
1997	29.7±5.9	39.3±9.3	38.3±7.2

No data were available for 1994.

1996 (Table 6). There were no significant differences in insect species richness on mesquite among treatments in any of the years of the study (Table 7).

4. Discussion

The insect faunas of desert grasslands are poorly known (Whitford et al., 1995). In a survey of black-grama (*B. eriopoda*) desert grassland insects done at irregular intervals during a single year, Watts (1963) reported 120 species of insects representing nine orders and 55 families. In this study, we recorded 109 families and 368 species and morphospecies of insects in the grass layer of the black-grama grassland. Ellstrom (1973) reported between year differences in arthropod community structure in a black-grama grassland with differences in rainfall. Acarina, Homoptera and Hemiptera were the most abundant orders during a year with below-average growing season rainfall and Homoptera, Collembola and Hymenoptera as the three most abundant orders during a year with above average rainfall. In our study, Homoptera and Hymenoptera increased in aboundance and species richness in years with average or above average growing season rainfall.

Although analyses demonstrated treatment and year differences in species numbers, our understanding of the basis for such differences is incomplete. Regressions certainly did not support a simple linear relationship between richness and rainfall. A study of insects on an evergreen shrub, creosotebush (*Larrea tridentata*) that used irrigation to supplement natural rainfall and “rain-out” shelters to simulate drought found that some taxa exhibited positive response to irrigation while other taxa exhibited positive responses to drought. Several taxa responded to neither treatment (Schowalter et al., 1999). This kind of species specific variation in response to rainfall probably contributed to the lack of relationship between species richness and growing season rainfall. Obviously, a complex interaction of biotic and abiotic factors effects arthropod richness.

Many of these factors are embodied in the differences among years. Part of the complexity involves comparisons of arthropods with very different life history strategies. Polis and Yamashita (1991) note that r-selected (opportunistic) species, such as many Homoptera, are more strongly impacted by abiotic factors than are

K-selected (equilibrium) species. Such species with a short life history will respond differently to rainfall than predators, such as asilid flies, which minimally have a 1–2 year life cycle (Musso, 1981). Holometabolous insects may respond differently to moisture at different stages of their life cycle. Each species has characteristic lag times in responding to abiotic events, and in the case of predators/parasitoids, to the buildup of prey or host numbers. Relationships of herbivores with food plants also affects how herbivores respond to moisture, and these relationships are complex and varied (Jolivet, 1998).

An intuitive assumption is that desert arthropod species numbers will be higher in wet years, and such is often the case. Some desert Lepidoptera, including *Papilio polyxenes* and *P. indra* in the southwestern US, may be virtually absent as adults in years of deficient rainfall, and are capable of extended pupal diapause (Crawford, 1986).

Lightfoot and Whitford (1991) examined foliage arthropod populations in creosote bush (*L. tridentata*) in southern New Mexico, where plants along a road edge supported greater arthropod densities and species richness, in part because of the greater moisture availability from run-off and soil retention. Crawford (1986) cautioned that responses of long-lived desert insects to rainfall may be secondary to other life history strategies, citing the meloid beetle *Pyrota*, which synchronizes its emergence with the flowering of mesquite. Another Chihuahuan Desert meloid, *Eupompha fissiceps*, displays a similar relationship with creosote bush during the summer rainfall season.

Insects exhibit a number of food plant selection strategies. For example, phytophagous insects that feed on plants of a number of different families are classified as polyphagous, insects that feed on plants of a single family are considered oligophagous and insects that feed on plants of a single genus or species are considered monophagous. Of the phytophagous insect species on arid rangeland shrubs (*Baccharis* spp.), 25% were polyphagous, 13% were oligophagous, and 2% were monophagous (Boldt et al., 1988; Boldt and Robbins, 1994). Feeding patterns of polyphagous, oligophagous and monophagous insect herbivores are affected by the nutrient content and/or concentration of toxins and feeding deterrants (Cates, 1980). The chemistry of plant foliage varies considerably over time in arid ecosystems because of the pulse nature of rainfall and the effect of that rainfall on soil moisture and nutrients (Whitford, 2002). Schowalter et al. (1999) reported a diversity of responses to rainfall and drought in foliage chewers and sap-sucking insects. Therefore, departures from a linear relationship between annual or seasonal rainfall and species richness of the insect fauna may in part be the result of differences in the physiological responses of the plant species. In this study, the species richness of the insect communities was measured on plants with very different phenologies, foliage chemistries, and nutritional characteristics. These phenlological and physiological differences account in part for the failure of insect species richness to respond in a predictable and positive way to rainfall.

Just as insect–plant relationships are complex, responses of plants to increased moisture are highly variable and may be species-specific (Gutierrez and Whitford, 1989). Whitson (1975) found that in artificially watered plots in the Chihuahuan desert, summer annuals established early (June) and maintained continuous growth, in contrast to no establishment of annual plants on unwatered plots. One factor that affects both the productivity and species richness of Chihuahuan Desert herbaceous annual plants is available soil nitrogen (Gutierrez and Whitford, 1987; Gutierrez et al., 1988; Mun and Whitford, 1989). The relationship between rainfall pulses and soil nitrogen availability is complex and non-linear (Fisher and Whitford, 1995). Grassland insect species richness was reported to increase in response to increases in both plant species richness and plant productivity (Sieman, 1998; Sieman et al., 1998). Because herbaceous annual plants are such an important component of diversity and productivity in Chihuahuan Desert grasslands, the non-linear relationships between herbaceous annual plant species richness and productivity and annual or seasonal rainfall are probably most responsible for the variability in insect species richness and rainfall in Chihuahuan Desert grasslands.

Even among years with similar rainfall totals, species richness patterns are influenced by timing of rainfall events. Early rains, such as noted for June 1997, may allow arthropod populations to increase during what is usually a drought period, an effect that can carry over into the rainy season. In certain years most of the summer rainfall comes in one month or even in one event, with consequent effects on arthropod populations. Our data for 1994 show that in an extreme drought year, richness actually declined in late summer (the usual rainy season) from spring levels.

In comparisons of grazing treatments, winter-grazed and control plots had higher richness means than summer plots, with few significant differences between winter-grazed and non-grazed controls. Summer grazing, occurring just prior to sweep sampling, often appeared to have a deleterious effect on the number of arthropod species, as host plants, nectar sources, and plant species richness were damaged by trampling or grazing. The grass-herbaceous plant vegetation layer had no opportunity to recover from foliage removal by the cattle. The negative impact of summer grazing on snakeweed canopy insects was probably the result of trampling. The differences resulting from seasonal grazing supports the contention of Morris (1978) that temporal patterns of grazing can affect insect abundance and species richness. Whatever damage was inflicted by winter grazing did not significantly lower invertebrate richness totals when compared to summer-grazed plots. Vegetation on winter grazed plots had an opportunity to recover from canopy removal and trampling by the late August sampling period. The negative effects of summer grazing on snakeweed canopy arthropods were probably the result of trampling by livestock. Since the stocking rates were dramatically reduced (approximately 20 yearlings per plot for 24 h) during the last year of the study, there would have been less trampling effect. The positive effect of winter grazing on snakeweed arthropod richness may be the result of modified water redistribution on the grazed plots (Nash et al., 2004). Nash et al. (1999) examined the impact of cattle on annuals along a disturbance gradient on the Jornada Experimental range, finding that species richness of annuals was impacted much less by direct effects (trampling or grazing) than by the role of cattle in altering soil nutrient composition.

As mesquite has a large associated insect fauna (Ward et al., 1977), the lack of significant mesquite-removal effects was unexpected. Much of the mesquite insect fauna was also present on grass and snakeweed. Also, the small number of taxa that are mesquite specialists were swamped by the overall species totals and were not statistically important. Despite the fairly large size of the plots, there is also the possibility of immigration of insects from adjacent mesquite-intact plots.

In summary, our data show major fluctuations in species richness in arthropods over a 5 year period. Although years with wetter summers tended to have higher species totals, we were unable to attribute the increased richness to rainfall alone. Among the year differences encompassed a number of biotic and abiotic interactions. Removal of a dominant shrub (mesquite) from the system did not have the anticipated result of lowering species richness. Summer grazing of plots did, in several instances, lower richness in comparison to plots that were ungrazed or winter-grazed.

Acknowledgements

We thank David Richman (spiders), William MacKay (Hymenoptera) and Charles O'Brien (Coleoptera: Curculionidae) for providing identification to genus and species. This research was funded through an interagency agreement with the US Environmental Protection Agency's Office of Research and Development, Las Vegas Laboratory. This paper has not been subjected to the EPA's administrative and peer-review.

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