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Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona

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Abstract. Despite the importance of invertebrates in grassland ecosystems, few studies have examined how grassland invertebrates have been impacted by disturbances in the southwestern United States. These grasslands may be particularly sensitive to one common disturbance, livestock grazing, because they have not recently evolved in the presence of large herds of bison, an important mammalian herbivore. This study examined how livestock grazing influenced vegetation-associated insect communities in southeastern Arizona. Insect abundance, richness, diversity, community composition, and key environmental variables were compared between sites on active cattle ranches and sites on a 3160 ha sanctuary that has not been grazed by cattle for over 25 years. Vegetation-associated insect communities were found to be sensitive to livestock grazing. Overall abundance of these insects was lower on grazed grasslands, and certain insect orders appeared to be negatively affected by livestock grazing; beetles were less rich, flies were less diverse, and Hymenoptera were less rich and diverse on grazed sites. Conversely, Hemiptera were more diverse on grazed sites. Species composition of vegetation-associated insect communities also differed and was significantly correlated with percent vegetation cover and number of shrubs. Insect species responsible for these differences were taxonomically diverse, and included herbivores and predators/parasites. When compared to other studies conducted in areas of the United States that fall within the historic range of bison, this study suggests that invertebrates in areas outside this range may be more sensitive to grazing pressure.

Abbreviations: ANOVA – analysis of variance; CCA – canonical correspondence analysis; MDA – multigroup discriminant analysis; NMDS – nonmetric multidimensional scaling; PCoA – principal coordinate analysis; PCA – principal component analysis

Introduction

Livestock grazing is only one of several human activities that threaten the world's grasslands, yet in certain areas, such as in the western United States, its widespread prevalence has generated great interest among conservation biologists and managers in understanding its ecological effects (e.g., Brussard et al. 1994; Fleischner 1994; Noss 1994). In response to this interest, numerous studies have examined the effects of livestock grazing on grassland plants, birds, reptiles, and mammals (see Fleischner 1994; Jones 2000 for reviews). In contrast, far fewer studies have examined the effects of livestock grazing on invertebrates, despite the fact that grassland invertebrates comprise an overwhelming proportion of animal biomass and biodiversity, form a major component of terrestrial food webs, and play pivotal roles in ecosystem functions, including decomposition, pollination, seed dispersal, pest control, soil conditioning, and nutrient cycling (Wilson 1987; Kellert 1993; Whitford et al. 1995; Coleman and Hendrix 2000). Livestock grazing alters various environmental factors that should impact invertebrates, including vegetation characteristics, soil compactness, and microhabitat temperature and humidity (Whitford et al. 1995; Loftin et al. 2000). Studies examining the responses of invertebrates to disturbance suggest that they can be as sensitive to changes in these environmental factors as vertebrates and plants, but that patterns in invertebrate diversity are not necessarily correlated with patterns in vertebrate or flowering plant diversity (Majer 1983; Yen 1987; Burbidge et al. 1992; Milchunas et al. 1998), Thus, as Wilson (1987) pointed out over a decade ago, studies on how human disturbance affects invertebrate communities are vital for pursuing the goals of conservation biology.

The most extensive research on the effects of livestock grazing on grassland invertebrate communities has taken place in Europe. Early studies in England were motivated by a concern for preserving the biodiversity of grassland invertebrates *per se*, and a wide variety of invertebrate taxa were examined (Morris 1967, 1968, 1969a, b). European researchers have continued to expand on this work over the last decade (Gibson et al. 1992a, b; Dennis et al. 1997; Bonte et al. 2000; Bell et al. 2001; Kruess and Tscharntke 2002a, b). These studies indicate that (1) livestock grazing can affect grassland invertebrate communities, primarily through their effect on the composition, quality, and architecture of vegetation, and (2) certain invertebrate groups are more sensitive to livestock grazing than others.

In contrast to European work, most studies of livestock grazing of grassland invertebrates in the United States have had a more narrow focus. Numerous studies have examined the effect of livestock grazing on grasshopper communities (e.g., Capinera and Sechrist 1982; Jepson-Innes and Bock 1989; Quinn and Walgenbach 1990; Miller and Onsager 1991; Welch et al. 1991). This research has been motivated both by the fact that some grasshopper species are considered to be serious rangeland and crop pests and by the fact that grasshoppers are dominant herbivores in many grassland systems in the United States (Otte 1981). Of the relatively few studies that have expanded our knowledge of livestock grazing on grassland invertebrates in the United States, most have examined belowground non-insect invertebrates (e.g., Leetham and Milchunas 1985; Wall-Freckman and Huang 1998; Kay et al. 1999).

Although these studies have provided valuable insights on livestock grazing effects on grassland invertebrates and added much to our knowledge of specific geographic regions, several important gaps in our knowledge remain. First, in contrast to European work, the relatively narrow focus of studies in the United States limits our knowledge about the effects of livestock grazing on grassland invertebrate communities in general, and how particular groups may be differentially affected. Second, we know very little about how livestock grazing affects invertebrate communities in grasslands whose recent evolutionary history does not include herds of large herbivores. Grasslands and their associated fauna that have evolved in the presence of large herbivores are expected to be relatively insensitive to, or even dependent upon, grazing by domestic livestock compared to grasslands with no recent evolutionary history of large herbivores (Mack and Thompson 1982; Fielding and Brusven 1996; Pykala 2000). Most European grasslands have been subjected to grazing for millennia, both by native grazers and domestic livestock (Pykala 2000), and almost all studies in the United States have been conducted in areas that fall within the historic range of the American bison (*Bison bison*). Yet a large portion of the far western and southwestern United States has not been exposed to large herds of native herbivores since the Pleistocene (McDonald 1981). Thus, there is a pressing need for studies that examine how invertebrate communities associated with these potentially more sensitive grasslands are affected by livestock grazing (Loftin et al. 2000).

This study seeks to address these gaps in our knowledge by examining how livestock grazing affects a variety of invertebrates in grasslands of southeastern Arizona. The Audubon Appleton-Whittell Research Ranch, a 3160 ha sanctuary in southeastern Arizona that has not been grazed by cattle since 1967, provides an excellent opportunity to examine long term effects of grazing cessation. Surrounded by active cattle ranches, the Ranch is one of the largest sanctuaries of ungrazed grassland in the southwestern United States. Most other sites used in comparative studies of grazing involve enclosures of ungrazed grasslands less than 50 acres (Fleischner 1994). In addition, the Ranch has been the site of numerous studies of other taxa, including vegetation, mammals, and birds (e.g., Bock et al. 1984; Brady et al. 1989; Bock and Bock 1993). Studies at the Ranch have shown strong vegetative responses to the cessation of livestock grazing (Brady et al. 1989; Bock and Bock 1993) and support the hypothesis that plants in these grasslands are more sensitive to livestock grazing than plants of the Central Plains of the United States.

The study described here focuses on a diverse group of invertebrates, insects, and addresses four objectives by comparing insect communities at multiple ungrazed sites on the Ranch with paired grazed sites on adjacent cattle ranches. These objectives are to: (1) determine if insect community structure differs between grazed and ungrazed lands, (2) identify insect groups that may be sensitive to livestock grazing, (3) compare the effect of two types of grazing regimes (traditional and holistic approaches) on insect communities, and (4) determine whether any observed differences in insect community structure between grazed and ungrazed sites are related to key environmental variables (percent plant cover, number of shrubs, vegetation structure, and microhabitat temperature and relative humidity).

Study area

The study was conducted at Audubon's Appleton-Whittell Research Ranch located on the Sonoita Plain in Santa Cruz County, Arizona. Operated by the National Audubon Society, the Ranch is a 3160 ha sanctuary of private and public land, which is surrounded by active cattle ranches. Although the Ranch was grazed by livestock until 1967, I use "ungrazed" to describe the grasslands within the Research Ranch boundary. By "ungrazed" I mean that it is no longer disturbed by active livestock grazing; I do not suggest that the area has returned to its "pregrazed" condition, whatever that may have been.

Four 30 × 30 m ungrazed sites on the Research Ranch were paired with four 30 × 30 m grazed sites on adjacent active cattle ranches. Sites were paired based on similarities in elevation, topography, soil type, and general vegetation and sites within a pair were separated by between 1.0 and 1.8 km. Distance between pairs of sites varied between 1.8 and 6 km, with an average distance of 4.3 km. Two of the grazed sites (Sites 2-D and 4-D) were managed using holistic resource management practices (Savory 1999) that involve using high density stocking rates (one animal unit per 6 ha) with short duration rotation. The other two grazed sites (Sites 1-D and 3-D) were managed with traditional grazing practices that involve using lower stocking rates (approximately one animal unit per 39 ha) with season-long grazing.

Because of its size and the length of time it has been ungrazed, the Research Ranch provides one of the greatest contrasts between grazed and ungrazed grasslands in the southwestern United States, and as such represents the logical point to start investigations into the effects of livestock grazing in the area. Although the four ungrazed sites are all located on the Research Ranch, there is no reason to believe that their location on the Research Ranch reflects any commonality other than the cessation of livestock grazing in 1967 for the following reasons: (1) the sites are widely separated, and (2) the only management practice conducted on the Research Ranch sites between 1967 and the time the study was conducted was the removal of livestock. In other words, no specific management practices, other than the removal of livestock, have taken place on the Research Ranch that would make it different from any other area in the region where livestock had been removed. However, the results of this study are generalized only to the grasslands of the Research Ranch and the surrounding cattle ranches to avoid pseudoreplication (Hurlbert 1984).

Sampling methods

Environmental sampling

Several environmental characteristics were measured at each site. Relative humidity and temperature were measured 2.5 cm above the soil surface with a Fisherbrand® Printing Hygrometer/Thermometer at 9 regularly spaced locations within each site. All pairs of sites were sampled, in varying order, on 11 days in the late summer and early fall of 1993 between 1000 and 1600. In August 1994, percent vegetative cover was measured at each site by visually estimating the percent vegetative cover to the nearest 5% in each of 54, 1 m^2, wire rings used to delineate subsample boundaries (Onsager and Henry 1978). In addition, the total number of the most common shrub found in the study area, *Baccharis pteroniodes*, was counted, and the maximum height of each was measured to give an estimate of habitat structure.

Insect sampling

I employed a repetitive sampling regime of the eight sites because repetitive sampling over more limited areas has been found to be a more efficient strategy for collecting cryptic, covert, or rare species than non-repetitive sampling efforts spread over larger areas (Dobyns 1997). Vegetation-associated insects were sampled in the same location with sweep net (Martin 1977) three times in 1993 (September–November) and four times in 1994 (June–August). At each site, sweep net sampling was conducted once a day for four days per sampling bout, so that each pair of sites could be sampled once during four time periods throughout the day: mid-morning, late-morning, early afternoon, and late afternoon. Thus, during each bout, each site was sampled once during each of the four sampling periods. Each sampling effort consisted of 100 arc-shaped sweeps.

Insects were identified to the lowest taxonomic level possible. Specimens that could not be identified to species were separated into recognizable taxonomic units (i.e., taxa based on morphological similarity) (Rees 1983). Estimates of richness and diversity obtained by using recognizable taxonomic units have been found to be comparable to those obtained by specialists who identify to known species (Oliver and Beattie 1993). Data from both years were combined because of the non-overlapping temporal distribution of sampling (i.e., different parts of the season were sampled each year).

Data analysis

Environmental data

Data used in parametric analyses were tested for normal distribution using Lillefors test (SYSTAT 1997) and transformed before analyses, if necessary. If data could not be transformed to meet the assumption of normality, nonparameteric statistics were used. Differences in average relative humidity and temperature for each pair of sites (ungrazed site – grazed site) were calculated and average differences were compared to zero using a one sample *t*-test. Shrub abundance at ungrazed and grazed sites was compared using a

Mann–Whitney *U* test. Data on percent vegetation cover and structure (as estimated by the height of *B. pteroniodes*) were analyzed for differences associated with grazing history using an ANOVA blocked by paired sites. Means are reported ± one standard error.

Insect data

Total abundance, species richness, and species diversity of insects in grazed and ungrazed sites were conducted at two taxonomic resolutions: for all insects combined and for each of the six most common insect orders. Abundance was simply the absolute number of individuals found at each site and richness was the total number of species present at each site. Diversity was calculated using the Shannon-Wiener Index, which not only reflects richness but also takes the evenness of species abundances into account (Smith 1986). Abundance, richness, and diversity were analyzed with ANOVA, blocked by paired sites.

To determine whether species composition of insect communities differed between grazed and ungrazed sites, patterns in insect community composition were examined using multivariate statistical techniques. Specifically, ordination methods were used to examine whether sites showed any patterns in species space relative to grazing history. Data sets were first reduced by eliminating rare species. Rare species were considered to be any species whose average abundance was less than 0.15% of the total insects captured. Rare species are typically removed from data analyzed with multivariate techniques because their presence may be due more to chance than to any underlying ecological condition, and their inclusion in analyses may increase the statistical "noise" and mask underlying patterns (Gaston 1994).

After reduction, a similarity index was calculated for each combination of sites. Percentage similarity (also known as Renkonen's index) was used because it performs well over a diverse set of ecological data sets, and sample size and diversity have only small effects on the performance of the index in measuring actual similarity between sampling units (Gauch 1982; Ludwig and Reynolds 1988; Krebs 1989). Similarity indices were used in a principal coordinate analysis (PCoA), which in combination with principal component analysis (PCA), was employed to detect general ordination patterns of the sites in species space. PCoA was used because it is an ordination method which is robust against non-linear relationships between sampling units (Gauch 1982; Pimentel 1993) and PCA was used to assign species loadings to ordination axes. The resulting configurations were rescaled using nonmetric multidimensional scaling (NMDS).

The significance of patterns found in species space with relationship to grazing types was determined using multigroup discriminant analysis (MDA), a technique that evaluates the within and between variation of *a priori* groups (Digby and Kempton 1987) and calculates generalized distances and 95% confidence radii about group centroids. I conducted two MDAs: one comparing ungrazed sites vs. grazed sites, and one comparing ungrazed sites vs. holistically managed grazed sites vs. traditionally grazed sites.

Finally, to determine whether any of the environmental variables measured explained patterns observed in the ordination, Spearman rank correlations were calculated for each environmental variable and the site scores of the first two NMDS ordination axes (Jongman et al. 1995; Quinn and Keough 2002). Performing an ordination and secondarily relating the ordination to environmental variables are preferred when the primary purpose of a study is to detect patterns in community structure *per se* and of secondary interest is whether any of the environmental variables measured explain those patterns (Jongman et al. 1995; McCune and Grace 2002). In this study, the major goal was to detect patterns in insect communities that might be associated with livestock grazing, with a secondary goal of determining whether any of the abiotic and vegetative variables measured might be associated with observed differences. Alternative methods, such as canonical correspondence analysis (CCA), are not appropriate under these circumstances. CCA ignores community structure that is unrelated to measured environmental variables and, as such, is best suited for studies designed to determine whether specific environmental variables play any role in structuring communities, not to determine whether the strongest community patterns are related to environmental variables (Jongman et al. 1995; McCune and Grace 2002).

Results

Environmental variables

The average difference in temperature between ungrazed and grazed sites (0.04 ± 0.65 °C) was not significantly different from zero ($T = 0.05, p = 0.96$). Similarly, the average difference in relative humidity between ungrazed and grazed sites (2.1 ± 1.51%) did not differ significantly from zero ($T = 1.4$, $p = 0.26$). In contrast, several characteristics of vegetation differed between ungrazed and grazed sites. Total percent vegetation cover was significantly greater on ungrazed sites (57.7 ± 1.80%) than grazed sites (30.8 ± 3.31%) ($F = 9.5, p = 0.03$). The abundance of the common shrub, *B. pteroniodes*, was also significantly greater on ungrazed sites (120 ± 44.9) than grazed sites (11 ± 3.3) ($U = 0$, $p = 0.02$). However, vegetation structure, as measured by the average height of *B. pteroniodes* (40.9 ± 1.56 cm for ungrazed sites, 31.1 ± 6.9 cm for grazed sites), did not differ significantly between grazed and ungrazed sites ($F = 1.8, p = 0.24$).

Insects associated with vegetation

A total of 6058 adult individuals collected in 1993 and 1994 were sorted into 229 species in 10 orders: Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera, Orthoptera, and Phasmida. Insects were more abundant on ungrazed sites, although species richness and diversity did not differ significantly between ungrazed and grazed sites (Table 1). Six of the most common insect orders were examined for differences in abundance, richness, and diversity (Table 1). On ungrazed sites, Coleoptera were more rich, Diptera were more diverse, and Hymenoptera were both more rich and diverse. In contrast, Hemiptera were less diverse on ungrazed sites.

The data set was reduced prior to multivariate analysis by eliminating rare species, resulting in 5661 individuals of 41 species being used in all multivariate analyses. Eigenvalues and percent variance explained for the first six principal coordinate axes are reported in Table 2. Because axes 3–6 explained relatively little variation compared to axes 1–2, they are not considered further. Rescaled ordination of the data revealed an obvious pattern in insect species space between grazed and ungrazed sites along axis 1 (Figure 1), which explained 52.6% of the variation. MDA was used to analyze the magnitude of these differences. A test of overall discrimination based on equality of centroids showed that groups differed significantly ($\lambda = 0.03$, $F = 23.1$, $p = 0.01$) and

Table 1. Differences in abundance, richness, and diversity for all insects combined and for the six most common insect orders collected by sweep net.

Group	Ungrazed	Grazed	*F*-value
All Insects			
Abundance	957.8 ± 159.54	561.5 ± 110.32	**$F = 12.1, p = 0.04$**
Richness	77.0 ± 5.79	68.0 ± 2.38	$F = 1.3, p = 0.39$
Diversity	3.7 ± 0.22	3.8 ± 0.27	$F = 0.1, p = 0.79$
Coleoptera			
Abundance	109.0 ± 39.89	101.8 ± 44.00	$F = 0.01, p = 0.92$
Richness	18.5 ± 1.32	14.5 ± 0.87	**$F = 19.2, p = 0.02$**
Diversity	2.9 ± 0.39	2.1 ± 0.42	$F = 2.6, p = 0.21$
Diptera			
Abundance	21.0 ± 5.61	25.3 ± 2.32	$F = 0.7, p = 0.47$
Richness	14.0 ± 2.61	11.5 ± 0.87	$F = 2.0, p = 0.25$
Diversity	3.6 ± 0.24	2.9 ± 0.08	**$F = 9.6, p = 0.05$**
Hemiptera			
Abundance	254.8 ± 97.28	21.5 ± 3.62	$F = 5.9, p = 0.09$
Richness	7.3 ± 0.95	6.5 ± 0.87	$F = 0.3, p = 0.64$
Diversity	0.4 ± 0.09	1.8 ± 0.45	**$F = 9.4, p = 0.05$**
Homoptera			
Abundance	431.8 ± 95.27	322.0 ± 83.86	$F = 1.0, p = 0.40$
Richness	12.0 ± 0.71	11.8 ± 0.85	$F = 0.1, p = 0.71$
Diversity	2.01 ± 0.11	1.66 ± 0.23	$F = 1.9, p = 0.27$
Hymenoptera			
Abundance	8.3 ± 1.60	3.0 ± 0.71	$F = 7.4, p = 0.07$
Richness	7.0 ± 1.23	2.7 ± 0.48	**$F = 10.5, p = 0.05$**
Diversity	2.7 ± 0.27	1.4 ± 0.23	**$F = 16.2, p = 0.03$**
Orthoptera			
Abundance	128.8 ± 29.57	83.3 ± 21.83	$F = 2.6, p = 0.20$
Richness	14.5 ± 2.02	17.8 ± 1.18	$F = 1.0, p = 0.38$
Diversity	3.3 ± 0.15	3.6 ± 0.13	$F = 1.4, p = 0.32$

Means are reported ± one standard error. F values with a $p \leq 0.05$ are in bold face font.

Table 2. Eigenvalues, percent variance, and cumulative variance for principal coordinate axes associated with insect data.

Axes	1	2	3	4	5	6
Eigenvalue	7050.33	2761.40	1551.78	1066.88	724.53	545.87
Percent variance	52.60	20.60	11.58	7.96	5.41	1.86
Cumulative percent	52.60	73.20	84.78	92.73	98.14	100.00

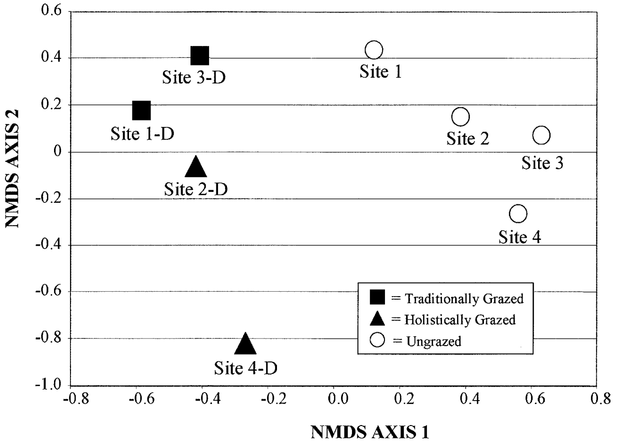

Figure 1. Nonmetric multidimensional scaling (NMDS) ordination of species collected at grazed and ungrazed sites.

univariate testing along the first two principal coordinate axes showed that ungrazed and grazed sites separated significantly along axis 1 (Table 3). The generalized distance, or the distance between grazed and ungrazed centroids in discriminant space expressed in units of standard deviations, was 9.6 and the 95% confidence radii for both groups were 1.59.

Table 3. Insect Species MDA Manova Table: Univariate testing for group differences along the first two principal coordinate axes between (A) ungrazed and grazed sites and (B) ungrazed, holistically grazed, and traditionally grazed sites.

Coordinate axis	Among mean square	Within mean square	*F*-Ratio	Probability	Adjusted probability
A. Between ungrazed and grazed sites along the first two principal coordinate axes					
1	0.880	0.020	43.69	< 0.001	0.003
2	0.052	0.158	0.33	0.879	0.972
B. Among ungrazed, holistically grazed, and traditionally grazed sites along the first two principal coordinate axes					
1	0.447	0.021	20.85	0.005	0.018
2	0.262	0.095	2.75	0.156	0.493

The particular insect species correlated with principal component axis 1, and the strength and direction of the relationship, are shown in Table 4. Thirteen species showed a positive correlation with axis 1, meaning that they are associated with ungrazed sites, while three species showed a negative correlation with axis 1, indicating that they are associated with grazed sites.

Rescaled ordination of the data also suggests a pattern in insect species space between traditionally and holistically grazed sites along axes 1 and 2 (Figure 1). A test of overall discrimination based on equality of centroids of ungrazed, holistically grazed, and traditionally grazed sites was suggestive of differences ($\lambda = 0.01$, $F = 4.1$, $p = 0.10$) and univariate testing along principal coordinate axes 1 and 2 showed group differences along axis 1 (Table 3). However, generalized distances between groups show that the centroids of both types of grazed groups were much closer to each other than either was to the ungrazed group; the generalized distance between ungrazed sites and traditionally and holistically grazed sites was 8.95 and 10.43, respectively, and the distance between holistically and traditionally grazed sites was 2.89. The confidence radius for the ungrazed centroid was 1.59 and confidence radii for both grazed centroids were 8.98.

Relationship of insect community composition and environmental variables

Rank correlations for sweep net data showed that both percent vegetative cover and shrub number were significantly positively correlated with NMDS ordination scores for axis 1 (Table 5).

Table 4. Principal component correlations for 16 species or morphospecies with common names of lowest taxonomic unit to which identified.

Order	Species, Genus, or Family – Common Name	Correlation
Orthoptera	*Opeia obscura* (Thomas) – Obscure Grasshopper	0.265
Coleoptera	Melyridae – Soft-Winged Flower Beetle	0.255
Homoptera	Cercopidae – Froghopper/Spittlebug	0.251
Homoptera	*Acanalonia conica* (Say) – Acanalonid Planthopper	0.250
Orthoptera	*Eritettix simplex* (Scudder) – Velvetstriped Grasshopper	0.246
Orthoptera	*Dactylotum variegatum* (Scudder) – Rainbow Grasshopper	0.241
Diptera	Bombyliidae – Bee Fly	−0.228
Orthoptera	*Poecilotettix pantherinus* (F. Walker) – Panther Spotted Grasshopper	0.221
Coleoptera	Curculionidae – Snout Beetle	0.220
Orthoptera	*Amphitornus coloradus* (Thomas) – Striped Grasshopper	0.220
Homoptera	Cicadellidae – Leafhopper	0.217
Orthoptera	*Oecanthus* sp. – Tree Cricket	0.211
Orthoptera	*Cordillacris crenulata* (Bruner) – Crenulatewinged Grasshopper	−0.209
Hemiptera	*Extarademus macer* (Van Duzee) – Lygaeid Bug	0.195
Homoptera	*Cuerna arida* (Oman and Beamer) – Cicadellid Leafhopper	0.190
Orthoptera	*Trachyrhachis mexicana* Saussure – Bandwinged Grasshopper	−0.155

Correlations of species with principal component axis 1 (only those greater than 0.15 are reported).

Table 5. Spearman rank correlations of values of environmental variables at each site with the NMDS ordination scores at the same site.

Environmental Variable	Axis 1	Axis 2
Relative humidity	0.45	−0.17
Temperature	0.41	−0.24
Percent vegetative cover	0.74*	0.21
Shrub number	0.83*	−0.17
Shrub height	0.31	0.48

*$p < 0.05$.

Discussion

Responses of vegetation-associated insects

This study found that vegetation-associated insect communities of grazed and ungrazed grassland sites in southeastern Arizona differed strongly. Overall, insects were significantly more abundant in ungrazed areas than in grazed areas, a result also found in European studies involving several insect orders associated with vegetation (Morris 1967, 1968, 1969a; Kruess and Tscharntke 2002a). In addition, several insect groups in this study showed differences between grazed and ungrazed sites at the order level. On ungrazed sites, beetle communities were more rich, flies were more diverse, and Hymenoptera were more rich and diverse compared to grazed sites. Some of these results are similar to those found by Kruess and Tscharntke (2002a, b), who found that species richness of Hymenoptera and Coleoptera was higher on ungrazed grasslands than on grazed pastures in Germany.

Differences in total abundance of all vegetation-associated insects, and specific differences in richness and diversity of particular orders may be related to differences in vegetative characteristics between ungrazed and grazed sites. Average percent vegetative cover on ungrazed grasslands was almost double of that on grazed grasslands, and average shrub abundance was over 10-times greater on ungrazed grasslands. Thus, the abundance of resources available for phytophagous insects is much higher on ungrazed sites, and may translate to bottom up effects on higher trophic levels, leading to a greater overall abundance of all insects. In addition, although species composition of vegetation was not measured in this study, previous studies on the Research Ranch have found that ungrazed sites have a greater diversity of plants than grazed sites (Bock et al. 1984; Brady et al. 1989), and this increased complexity of vegetation may account for greater richness and/or diversity of certain insect groups. This may be particularly true of beetles, flies, and Hymenoptera, many of which have close associations with particular plants.

In contrast to these groups, Hemiptera in this study were more diverse on grazed sites than on ungrazed sites. This pattern is undoubtedly due to one sap-feeding species of lygaeid bug, *Blissus omani*, which was much more abundant in ungrazed sites and accounted for 94% of all Hemiptera captured. Thus, the overwhelming abundance of this one species in ungrazed sites is responsible for the decreased diversity observed in Hemiptera in ungrazed sites.

This study also showed that species composition of vegetation-associated insect communities between grazed and ungrazed areas was quite different, and that these differences were significantly correlated with two vegetation characteristics, percent vegetation cover and shrub abundance (Table 5). While most of the work in the United States on the effects of livestock grazing on invertebrates has focused on grasshoppers, this study found that species affected by grazing were taxonomically diverse, falling into five different orders (Orthoptera, Coleoptera, Homoptera, Diptera, and Hemiptera) (Table 4). Less than half of the most heavily affected species were grasshoppers. The majority of affected species in the five orders were positively correlated with ungrazed sites, with only two grasshopper species strongly associated with grazed sites. The results concerning grasshoppers in this study are similar to those obtained by Jepson-Innes and Bock (1989) in their study of an ungrazed site on the Ranch and a grazed site on an adjacent cattle ranch. Although analyzed at a coarser scale (grasshopper subfamily), their results are comparable to this study. They found that grasshopper community composition differed between the two sites, with patterns in grasshopper subfamilies in the summer consistent with the pattern displayed by six out of the seven grasshopper species found to be responsive to grazing in this study. In this study, other plant feeders besides grasshoppers were also found to load significantly on the first principal component axis, including a snout beetle, a tree cricket, a true bug, and four Homopteran hopper species (Table 4).

Not all species sensitive to livestock grazing were herbivores, however. A species of soft winged flower beetles (Melyridae), whose adults and larvae are predaceous and common on flowers (Borror et al. 1992) was found to be positively associated with ungrazed grasslands. A strong association with flowers has been found to be important in determining invertebrate community composition in European studies; Morris (1967) found that species associated with flowers had higher abundances in ungrazed plots in English chalklands. In contrast, a bee fly (Bombyliidae), whose larvae are either parasitic on immature stages of other insects or predaceous on grasshopper eggs (Borror et al. 1992), was positively associated with grazed grasslands. This is in contrast to a study by Kruess and Tscharntke (2002b), who found that parasitism rates of digger wasps were higher on ungrazed grasslands.

Unlike the clear differences between community composition of vegetation-associated insects in grazed and ungrazed areas, differences between traditional and holistic grazing practices in this community were not obvious. Although multivariate techniques tended to separate out insect communities according to these two grazing practices, the generalized distances between traditional and holistic groups was small compared to the distances separating each from ungrazed communities. Because of the small sample size in this study, more study of the effects of holistic management techniques on grassland insects is necessary to determine its influence on insect community composition. However, this study, like others conducted on vegetation on the Ranch (Brady et al. 1989; Bock and Bock 1993), does not support Savory's theory that the removal of grazing animals will have long term deleterious effects on the grassland, or the specific prediction that, after an initial improvement, grasslands on the Research Ranch would deteriorate, leading to a loss of diversity (Savory 1986). No overall differences in diversity or richness in insects between grazed and ungrazed sites were found in this study.

Evolutionary history of grasslands and sensitivity of invertebrates to grazing

When contrasted with other studies of insect community responses in grasslands of the United States, this study provides evidence that insects in grasslands without a recent evolutionary history with large herds of mammalian herbivores may be more sensitive to grazing pressure than grasslands that have evolved in their presence. Although a few studies of grasshopper communities in regions within the historic range of bison have found decreased abundance or changes in community composition associated with grazing (Capinera and Sechrist 1982; Quinn and Walgenbach 1990; Fielding and Brusven 1995), numerous other studies have shown that grasshoppers and other insects are either positively influenced or not affected by livestock grazing in these areas. For example, several early studies (Coyner 1939; Weese 1939; Smith 1940) from the tall-grass prairie region of central Oklahoma documented greater total abundances of a variety of insect taxa, including grasshoppers, in response to increased grazing intensity. This pattern has also been found in Kansas and Nebraska, where greater grazing intensity was associated with higher abundances of grasshoppers (Campbell et al. 1974; Joern 1982). Milchunas et al. (1998) report data from Lavigne et al. (1972) that show that aboveground macroarthropod abundance was higher in lightly grazed grasslands than in ungrazed grasslands in the Central Plains Experimental Range of Colorado. In addition, arthropod diversity in that area also showed a bell shaped pattern, with the highest diversity associated with moderately and lightly grazed lands, and the lowest diversity with ungrazed grasslands, indicating that diversity was actually increased by low to moderate levels of livestock grazing. Other studies conducted within the historic range of bison (e.g., Holmes et al. 1979; Miller and Onsager 1991; Welch et al. 1991) have found little response of insect communities to livestock grazing. In contrast to these studies, the results reported here show that livestock grazing in an area outside that range is associated with decreased total abundance and differing community composition, and not with increased insect diversity. However, this conclusion must be interpreted with caution given the difficulty of comparing grazing intensity across studies. Although the level of grazing intensity at these sites were judged to be moderate, based on the stocking levels and the condition of the grassland, the possibility exists that the grazing intensity in this study corresponds to high intensity grazing reported in other studies. If so, then additional studies examining a range of grazing intensities needs to be conducted in the area to establish if low to moderate levels of grazing result in similar patterns.

Implications for conservation

The results of this study highlight the need for examining a variety of taxa in order to obtain a more complete picture of how human impacts affect invertebrate communities. While studies of dominant groups, such as grasshoppers, provide information useful to conservationists, patterns seen in these taxa may not be reflective of trends in other important invertebrates. As in European studies, this study showed that livestock grazing was found to affect multiple functional groups and a wide variety of taxa. In addition, some taxa as a whole appear to be sensitive to grazing, and may warrant particular management attention. In this study, Hymenoptera, many of which are important pollinators, appeared to be particularly sensitive to livestock grazing, and further studies are needed to examine the extent of this effect and its ramifications for ecosystem function.

This study suggests that several characteristics associated with vegetation may be important in driving many of the differences observed in vegetation-associated insect communities. However, multiple abiotic and biotic factors are undoubtedly responsible for community differences, and the relative importance of these variables surely varies species by species. While determining specific mechanistic reasons of how particular environmental variables associated with livestock grazing affect insects is interesting ecologically, it is less important for directing conservation efforts. In other words, even if one or two specific effects of livestock grazing (e.g., soil compaction, vegetative cover) could be identified as the most important environmental variables driving patterns in most insect species, it is unlikely this knowledge would change options available for land managers. There is no obvious way to change grazing practices so that only one variable (e.g., soil compaction) is affected without also affecting other variables associated with grazing. Because of this, priority should be placed on understanding how grazing as a whole, through its multiple effects on numerous environmental factors, affects insect species and communities and the important ecological functions associated with them.

The importance of considering invertebrates in grassland management cannot be overstated. Because invertebrates comprise the major component of animal diversity and fulfill important ecosystem functions, an understanding of how this diversity can be protected must be a high priority for conservation biologists. This study shows that the composition of vegetation-associated insect communities differs between grazed and ungrazed areas in a southwestern United States grassland, indicating that overall diversity should theoretically be higher in a landscape which includes a mosaic of both types of environments. This is a management strategy suggested by several scientists working with invertebrates in Europe (Dennis et al. 1997; Bell et al. 2001; Kruess and Tscharntke 2002b), where livestock grazing has the added benefit of suppressing exotic plant invasions (Dennis et al. 1997). However, given the prevalence of livestock grazing in grasslands in the southwestern and western United States, overall diversity of invertebrate communities can potentially be maximized by emphasizing the protection of grasslands from livestock grazing.

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