Pol # 00-010

Impact of Grazing and Desertification in the Chihuahuan Desert: Plant Communities, Granivores and Granivory

GRAHAM I. H. KERLEY[1] AND WALTER G. WHITFORD[2]

Department of Biology, New Mexico State University, Las Cruces, 88003

ABSTRACT.—Livestock effects on plant communities through overgrazing (desertification) should affect the structure and functioning of semarid rangeland communities. We measured plant, granivorous ant and rodent communities and rates of seed removal by rodents and ants in grazed (by livestock) and ungrazed desert grasslands as well as mesquite and creosotebush shrublands to test hypotheses on the effects of grazing and desertification on ecosystem structure and functioning. In desert grasslands grazing reduced the cover of perennial grasses, particularly the dominant *Bouteloua eriopoda*, but the cover of forbs and shrubs did not differ between treatments. One species of perennial grass, *Dasyochloa pulchellum*, increased in grazed grasslands compared with grassland exclosures. Detrended correspondence analysis showed that grazing caused desert grasslands to shift in community structure towards the shrublands. There were more seed harvesting ant and rodent species in the creosotebush shrublands than in the grasslands and mesquite shrublands. Grazing had no effect on the diversity of ants or rodents within grasslands, and detrended correspondence analysis revealed no clear trends in granivorous ant community structure in the grazed and ungrazed grasslands or the mesquite and creosotebush shrublands. Ants removed more seeds than did rodents in the grassland sites but rodents removed more seeds than did ants in the creosotebush sites and seed removal rates by rodents and ants were the same in the mesquite sites. Our data support the hypothesis that livestock grazing leads to a shift from grassland to shrubland in the Chihuahuan Desert, with associated changes in the structure and functioning of faunal communities. Because grasslands support few species and low densities of rodents, seed harvesting ants are the most important granivores in these desert grasslands. On a larger scale, we therefore hypothesize that the observed dominance of rodents as seed harvesters in the Chihuahuan desert is a function of the desertification of desert grasslands to shrublands by livestock, and that associated feedback effects may complicate the regeneration of degraded communities.

INTRODUCTION

Degradation of desert grasslands to less productive shrublands (desertification) has encompassed a large portion of the landscape in the Chihuahuan Desert over the past 150 y and has been correlated with the introduction of domestic herbivores, chiefly cattle (Buffington and Herbel, 1965; Bahre, 1995). While the rate of vegetation change has slowed considerably, the shift from grassland to shrubland continues. Shrub dominated ecosystems are very resistant to climate stress (drought) and to attempts to restore the shrublands to grassland (Whitford *et al.*, 1995; Roundy and Beidenbinder, 1995).

Documentation of desertification of Chihuahuan Desert grasslands has focused on changes in the composition and cover of the vegetation and on soil movement (Hennessy *et al.*, 1983; Gibbens *et al.*, 1983; 1992; Gibbens and Beck, 1988; Bahr, 1995). The consequences

---

[1] Present address and corresponding author: Terrestrial Ecology Research Unit, Department of Zoology, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth 6000, South Africa. e-mail: zlagik@zoo.upe.ac.za; FAX + 27-41-504 2317

[2] Present address: U.S. Environmental Protection Agency, National Exposure Research Laboratory, Characterization Research Division, P.O. Box 93478, Las Vegas, Nevada 89196

of the changes in vegetation and soils on other components and processes within the desertified ecosystems have received little attention. The few studies that have examined changes in the fauna attributable to livestock grazing have described changes in species composition and abundances of rodents, ants or birds (Grant *et al.*, 1982; Bock *et al.*, 1984; Heske and Campbell, 1991) with few attempts to investigate changes in ecological processes. In addition, many of these studies suffer from either a lack of replication or pseudoreplication, making interpretation of often contradictory findings difficult.

Granivory has been intensively studied in desert ecosystems as a range of taxa rely on seeds as resources, and the consequences of granivory have been shown to affect both plant communities and the coexistence of the granivorous taxa (Brown *et al.*, 1979). Studies of granivory have focused on competition among rodents and ants and the importance of body size differences in structuring the granivorous ant and rodent communities (Brown *et al.*, 1979). In North American desert shrublands, seed removal experiments have shown that rodents take more seeds than ants (Brown *et al.*, 1975; Mares and Rosenzweig, 1978). Long-term studies manipulating granivorous ants and rodents have shown that the exclusion of these taxa results in changes in plant communities (Brown and Munger, 1985; Heske *et al.*, 1993), indicating that granivory is important in structuring desert plant communities. Despite the large literature on granivory, few studies have examined the relative impacts of seed-eating ants and rodents in desert grassland habitats or the implications of desertification for this ecologically important process.

We investigated the effects of vegetation changes due to livestock grazing and effects of historical changes in vegetation on the granivorous rodent and ant communities and on the process of granivory. Our study focused on a set of grazed and ungrazed sites in an area that is a desert grassland with relatively low cover of shrubs. We compared the data from these sites to two different sets of shrubland sites which have been in the shrub-dominated state for more than 50 y, but were historically grasslands (Buffington and Herbel, 1965). These shrub-dominated sites are considered to be alternate stable endpoints of desertification of Chihuahuan Desert rangelands (Whitford, 1995).

We hypothesized that vegetation cover and composition changes would result in changes in abundance and species composition of the granivorous rodent and ant communities. We tested our prediction that this would change the rates of seed removal by ants and rodents in the different habitats.

STUDY SITE

Study sites were located on the Chihuahuan Desert Rangeland Research Center and the adjacent U.S. Department of Agriculture Jornada Experimental Range, 40 km north-west of Las Cruces, NM. This region is part of the northern Chihuahuan Desert. Annual precipitation averages 210 ± 77 mm, mainly as summer convective storms (Houghton, 1972).

A total of 20 sites (each approximately 40×50 m) were sampled, representing ungrazed (n = 5 exclosures) and grazed (n = 5) grasslands, creosotebush-dominated shrublands (n = 5) and mesquite-dominated shrublands (n = 5). One of the exclosures in desert grassland was fenced to exclude livestock in 1939 and the remaining four were fenced in 1954 (R. E. Beck, pers. comm.). Each exclosure was paired with a randomly selected site at least 200 m away in the grazed grasslands to investigate the effects of grazing. These grassland sites represent replicates as each exclosure is located within independent pastures, which have been managed as such since at least 1954. Five sites were selected at random in both typical creosotebush shrubland and mesquite shrubland habitats within 10 km of the grassland sites. The creosotebush shrubland sites were within an ungrazed pasture that was

established in 1971 to accommodate studies of the International Biological Program's Desert Biome effort. The mesquite shrubland sites had not been grazed since 1934.

METHODS
PLANT COMMUNITIES

At each site canopy cover of perennial shrubs and basal cover of perennial grasses was recorded over three 30 m randomly located line transects during October 1991. For each plant encountered the species and cover (to the nearest 1 cm) was recorded (Mueller-Dombois and Ellenberg, 1974). Cover of annual plants was similarly recorded on three 10 m transects (the middle 10 m of the perennial transects) at each site.

We calculated the cover and numbers of perennial grasses, forbs and shrubs as well as annuals. Species richness was expressed as the number of species encountered on the transect separately for annuals and for perennials. Species diversity was calculated as the *ln* form of the Shannon-Wiener index H' (Zar, 1984). For statistical analysis, the original data expressed as cm cover on the transects was used, but results are expressed as percentage cover for ease of interpretation. Differences between the matched grazed and exclosure grassland sites were tested using Student's-*t* for paired samples. All sites were compared using ANOVA (Zar, 1984). Perennial plant communities were analyzed using Detrended Canonical Analysis (DCA) with the program CANOCO for perennial cover data, in order to test whether grazed grasslands were intermediate in plant species composition between ungrazed grasslands and shrublands.

GRANIVOROUS ANT COMMUNITIES

Ant species harvesting seed from each of 20 seed trays at each site (*see* 'Granivory' below) were recorded after the trays had been available for at least 24 h during October 1991 (''ants'' therefore refers to ''granivorous ants'' throughout). Ants were recorded to species, with identifications confirmed from preserved specimens. We measured head width at the mandibles for a sample (n = 7) of *Pogonomyrmex desertorum* and *Solenopsis xyloni,* collected on the Jornada, to represent sizes of large and small ants, respectively. We calculated the mean number of ant species per tray, the total number of species and the Shannon-Wiener diversity (H') of granivorous ants (using species frequencies at the 20 trays as an index of the abundance of that species) at each site. Variation in these parameters was investigated using ANOVA. DCA was applied to the ant communities to test whether ant community responses reflected those of the plant communities.

RODENT COMMUNITIES

We sampled rodent communities within one grassland exclosure and at one of the mesquite and one of the creosotebush shrubland sites for three consecutive nights with 50 traps per site. Rodents were trapped in Longworth live traps baited with cracked milo (*Sorghum bicolor*) set in 10 × 5 trap grids with 15 m trap spacing. Captured rodents were identified, temporarily marked and released at the capture site, and the community taken as the total number of individuals captured. We were unable to replicate this sampling, hence can only use these data to illustrate the observed communities within the different habitats.

GRANIVORY

Seed harvesting by nocturnal vertebrates (rodents) and invertebrates (largely ants) was measured (at each site) at 20 stations in a 4 × 5 grid, with stations set out 10 m apart, during October 1991. Stations comprised two experimental seed trays differentially available to each group. The ant trays were placed on the ground and covered with an inverted

TABLE 1.—Summary (mean ± SE, n = 5) of plant cover, diversity (H') and species richness (S) for the grazed and ungrazed grassland sites and the shrubland (creosotebush and mesquite) sites

	Grasslands		Shrublands	
	Grazed	Ungrazed	Creosote	Mesquite
Perennial cover %	34.6 ± 5.3	49.2 ± 8.2	64.4 ± 4.5	36.3 ± 7.5
Perennial grass cover %	15.9 ± 4.6	35.1 ± 7.8	9.0 ± 2.8	4.8 ± 2.1
Perennial shrub cover %	10.3 ± 2.7	7.5 ± 2.7	52.9 ± 6.3	31.3 ± 6.8
Perennial forb cover %	8.4 ± 3.1	6.6 ± 2.2	2.5 ± 0.6	0.2 ± 0.1
Annual cover %	6.0 ± 1.4	7.6 ± 2.2	2.4 ± 0.6	9.4 ± 3.7
Perennial H'	1.8 ± 0.2	1.3 ± 0.2	0.9 ± 0.2	0.7 ± 0.2
Perennial S	14.2 ± 1.0	12.8 ± 0.4	10.6 ± 2.3	6.0 ± 0.8
Annual H'	1.4 ± 0.2	1.7 ± 0.2	0.9 ± 10.3	1.2 ± 0.2
Annual S	7.4 ± 1.5	7.8 ± 1.6	3.2 ± 0.7	4.8 ± 0.9

plastic dish with 5 mm slits cut in the rim to allow access by ants but exclude rodents. Rodent trays were covered during the day and open at night and were elevated 3 cm off the ground on small platforms supported by large nails. The top cm of the nail was coated with Tanglefoot℗ to prevent access by ants. The seed trays were plastic petri dishes provisioned with 20 g of commercial millet *Panicum miliaceum* with an additional 20 g of couch grass *Cynodon dactylon* in the ant trays. Seed removal was measured over 3 d and trays were checked at dawn and dusk and additional weighed amounts of seed added when necessary to maintain seed resources. At the end of the sampling session the remaining seeds were collected and weighed in the laboratory and the amount of seed removed calculated (Kerley, 1991). For each treatment samples comprised the five sites, each being represented by a mean (for the 20 stations) seed removal rate. Differences between matched grazed and ungrazed grassland sites were investigated using a paired Student's-t test.

For the shrubland (creosotebush and mesquite) sites, the location of stations in relation to perennial shrubs (in the open or beneath shrubs) was recorded. Differences in seed removal beneath shrubs and in the open were investigated for both taxa with ANOVA, using the 100 stations in each shrubland type.

RESULTS

PLANT COMMUNITY STRUCTURE

Effects of grazing in grasslands.—Total (grasses, shrubs and forbs, Table 1) perennial cover in grazed (34.6 ± 5.3 %, mean ± SE) and ungrazed grasslands (49.2 ± 8.2 %) was not significantly different (Student's-t = 2.13, df = 4, P > 0.05). Perennial grass cover was significantly lower in the grazed grasslands (15.8 ± 4.6 %) than the ungrazed grasslands (35.0 ± 7.8 %, Student's-t = 2.29, df = 4, P < 0.05), but cover of forbs or shrubs did not differ between treatments (Student's-t < 0.65, df = 4, P > 0.05). The major perennial grass to respond to grazing was black grama *Bouteloua eriopoda* which decreased significantly from 31.4 ± 8.5 % in the ungrazed grasslands to 8.2 ± 5.7 % in the grazed grasslands (Student's-t = 2.35, df = 4, P < 0.05). Not all perennial grasses responded similarly to grazing. Fluffgrass *Dasyochloa pulchella* increased from 0.1 ± 0.1 % in the ungrazed grasslands to 0.4 ± 0.1 % in the grazed grasslands (Student's-t = 2.59, df = 4, P < 0.05). Fluffgrass cover increased as the cover of other perennial grasses decreased, although this was not significant (r = −0.595, n = 10, P = 0.0753).

There was no significant difference in annual plant cover between grazed (18.0 ± 4.2 %)

TABLE 2.—Mean percentage cover (n = 5) of dominant perennial species (four most abundant species for each habitat, indicated in bold) for the grazed and ungrazed grassland sites and the shrubland (creosotebush and mesquite) sites

	Grasslands		Shrublands	
	Grazed	Ungrazed	Creosote	Mesquite
Bouteloua eriopoda	**8.2**	**31.4**	0.1	0
Aristida purpurea	**3.8**	1	0.5	0.3
Croton potsii	**4.7**	**5.4**	0.2	0
Gutierrezia sarothrae	**5.6**	1.4	0.9	**3.2**
Sporobolus flexuosus	2.9	2.2	0	0.4
Larrea tridentata	0	0	**48.6**	0
Muhlenbergia porteri	0	0	**7.2**	0.2
Bahia absinthifolia	0	0	**1.7**	0
Prosopis glandulosa	2.3	4	**1.7**	**28.1**
Atriplex canescens	0	0	0	**1.9**
Dasyochloa pulchella	0.4	0.1	1.1	**2.0**

and ungrazed grasslands (22.9 ± 6.6 %, Student's-t = 1.2, df = 4, P > 0.05). There was no correlation between annual plant cover and perennial plant cover (or the cover of any of the perennial growth forms) in the grasslands (r < 0.2, n = 10, P > 0.05). Correlation analysis indicated no relationship between the cover of perennial forbs, shrubs or grasses (r < 0.2, n = 10, P > 0.05) for the grassland sites. The cover of *Bouteloua eriopoda* was negatively correlated with that of mesa dropseed *Sporobolus flexuosus* (r = −0.673, n = 10, P = 0.0331). The diversity and richness of perennials (Table 1, Student's-t < 1.4, df = 4, P > 0.05) and annuals (Table 1, Student's-t < 0.4, df = 4, P > 0.05) were not significantly different between ungrazed and grazed grasslands.

Grasslands vs shrublands.—Total (grasses, shrubs and forbs) perennial cover differed significantly among habitats, being higher in shrubland habitats, particularly in the creosotebush habitat, than the other habitats (Table 1, F = 4.61, df = 3,16, P = 0.017). Perennial shrubs showed the biggest differences between treatments (F = 17.65, df = 3,16, P < 0.0001), and were significantly lower in the grassland habitats than either the mesquite or creosotebush habitats, which also differed from each other according to Tukey's range test. In contrast, perennial grasses were significantly higher in the grassland habitats than the shrublands (F = 7.63, df = 3,16, P = 0.0022), and the perennial forbs showed similar differences (F = 3.95, df = 3,16, P = 0.0276, Table 1). Annual plant cover did not differ significantly among habitats (Table 1, F = 1.69, df = 3,16, P = 0.21).

Perennial plant species richness and diversity differed significantly among habitats, being lower in the shrubland habitats than the grasslands (Table 1, F = 7.42, df = 3,16, P = 0.0025 for richness, and F = 6.22, df = 3,16, P = 0.053 for *H'*). However, annual plant richness and diversity did not differ between habitats (Table 1, F < 3.1, df = 3,16, P > 0.05). Grassland sites shared three of the four most dominant plant species between the grazed and ungrazed sites, but only one (*Gutierrezia sarothrae*) of the dominant species was shared between the grasslands and a shrubland site (Table 2).

Detrended Canonical Analysis separated the ungrazed grassland, creosotebush and mesquite shrublands sites, particulalrly along Axis 1 (Fig. 1). It also indicates a clear shift along Axis 1 in the perennial plant community structure of all except one of the grazed grasslands towards that of the shrublands compared to the ungrazed grasslands (Fig. 1).
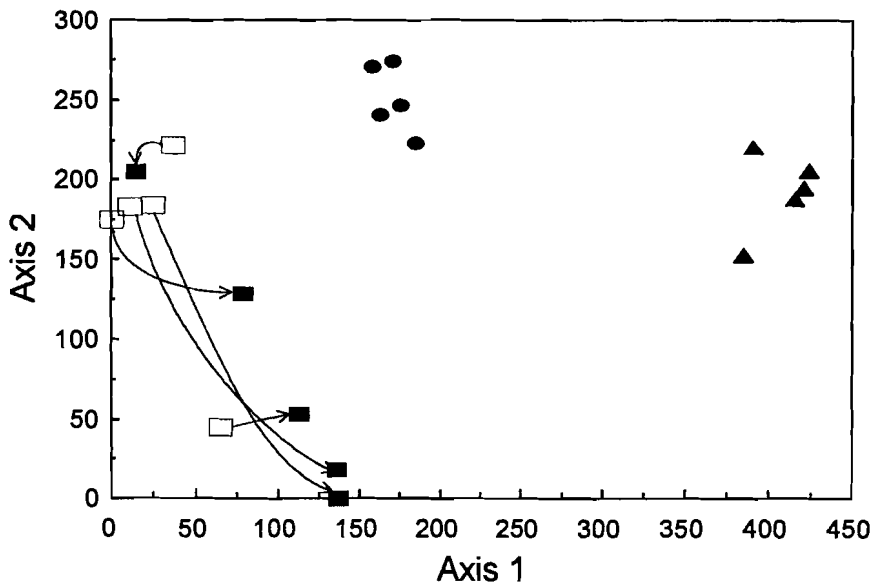
FIG. 1.—DCA analysis of plant community structure for sites in grazed (solid squares) and ungrazed grasslands (open squares), mesquite shrublands (solid ovals) and creosotebush shrublands (solid triangles). Arrows link matched ungrazed and grazed grassland sites (the curves are for graphic convenience and do not imply any trajectory in change in community structure)

ANTS

A total of 12 ant species were recorded removing seeds from the seed trays in all the habitats, with 9 species in the creosotebush shrublands, 9 in grazed grasslands, 7 in ungrazed grasslands and 4 in mesquite shrublands (Table 3). Both granivorous ant diversity (H', F = 5.37, df = 2,17, P = 0.016) and species richness (F = 4.96, df = 2,17, P = 0.02) differed among habitats. Only one species, *Solenopsis xyloni*, was common to all habitats. The mean number of ant species per tray, the number of ant species per site and the diversity of ants did not differ between grazed and ungrazed grassland sites (Student's-*t* < 0.85, df = 4, P > 0.05). However *Pheidole xerophila*, and an unidentified *Pogonomyrmex* sp. were not recorded in ungrazed grasslands (Table 3). In contrast to the plant communities, DCA of the ant communities showed no clear separation among the various habitats (Fig. 2). Ant communities from the grazed and ungrazed grassland sites did tend to cluster to the left along Axis 1, but were interspersed with the shrubland sites. Grazing of the grassland also produced no consistent shifts in ant community structure (Fig. 2).

RODENTS

The only species of rodent captured in the grassland grazing exclosure was Ord's kangaroo rat, *Dipodomys ordii* (Table 4). The highest abundance and species richness (six species) of rodents was in the creosotebush shrubland site (Table 4).

GRANIVORY

There were no differences in seed removal in grazed and exclosure grassland sites for either rodents or ants (Table 5, Student's-*t* = 0.94 and 0.87, respectively, df = 4, P > 0.05).

TABLE 3.—The frequency of granivorous ant species recorded in each habitat (summed for 100 trays), with the mean number of species per tray, and ant richness and diversity per habitat (n = 5). Size classes follow Chew and De Vita (1980)

Ant species	Size	Grasslands		Shrublands	
		Grazed	Exclosure	Mesquite	Creosote
Solenopsis xyloni	Small	53	66	29	8
Pheidole militicida	Small	17	14	0	6
Ph. rugulosa	Small	2	1	0	9
Ph. xerophila	Small	4	0	1	10
Ph. cerebrosior	Small	0	0	2	5
Tetramorium spinosum	Small	0	0	0	1
Aphenogaster cockerelli	Large	3	2	0	11
Pogonomyrmex rugosus	Large	2	3	0	0
P. desertorum	Large	24	13	0	7
P. imberbiculus	Medium	1	1	0	5
P. maricopa	Large	0	0	1	0
Pogonomyrmex sp.	Large	1	0	0	0
Total ant species		9	7	4	9
Ant species per tray		1	1.07	0.33	0.62
Ant species per site		4.6	3.4	1.4	5
Ant diversity (*H'*)		0.83	0.56	0.2	1.19

Seed removal by ants was significantly lower at the shrubland (mesquite and creosotebush) sites than the grassland (grazed or exclosure) sites (F = 10.54, df = 3,16, P = 0.0005). Seed removal by rodents was significantly higher at the creosotebush sites than the grasslands (grazed and exclosure) and the mesquite sites, but did not differ between the mesquite and grassland (grazed and exclosure) sites (F = 7.75, df = 3,16, P = 0.002, Tukey's range test).

Seed removal by ants was higher than that by rodents (Table 5) in both the grazed (F = 211.41, df = 1,198, P < 0.0001) and ungrazed grassland sites (F = 100.94, df = 1,198, P < 0.0001), but significantly lower in the creosotebush sites (F = 43.16, df = 1,198, P < 0.0001). Seed removal did not differ between ants and rodents in the mesquite sites (F = 0.43, df = 1,198, P = 0.518). Overall, ants removed significantly more of the smaller grass seeds (38.1 g/tray/72 h) than millet seeds (2.1 g/tray/72 h, F = 445.23, df = 1, 398, P < 0.0001).

The location of stations in relation to shrubs (in the open or beneath a shrub) did not significantly affect the removal of seeds by either ants or rodents in either the creosotebush or mesquite shrubland sites (F < 1.05, df = 1,98, P > 0.05).

DISCUSSION

VEGETATION CHANGES

Grazing by domestic livestock changed the structure of the perennial plant community in the desert grassland sites. This was characterized by a decrease of perennial grasses, particularly the dominant black grama (*Bouteloua eriopoda*) although there was no detectable increase in the perennial shrubs. The decrease in perennial grass cover was not a simple graminoid response, as there is some evidence for *Sporobolus flexuosus* increasing in abundance as *B. eriopoda* decreased. Decrease in cover of *B. eriopoda* with increase in dom-
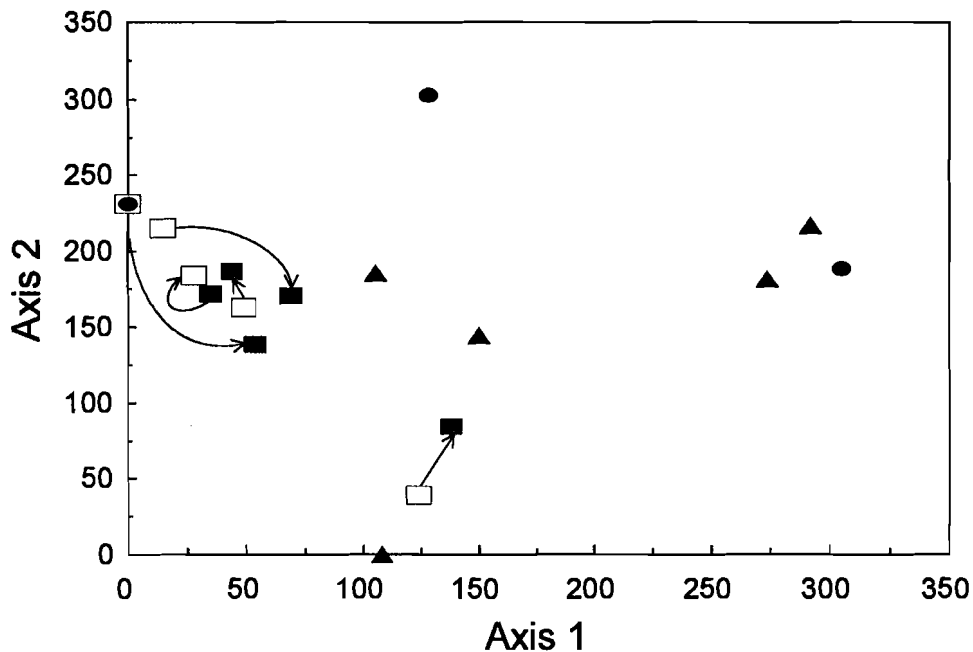
FIG. 2.—DCA analysis of ant community structure for sites in grazed (solid squares) and ungrazed grasslands (open squares), mesquite shrublands (solid ovals, including three overlapping sites on Axis 2) and creosotebush shrublands (solid triangles). Arrows link matched ungrazed and grazed grassland sites (the curves are for graphic convenience and do not imply any trajectory in change in community structure)

inance by *S. flexuosus* and *Aristida spp.* has been occurring in the black grama dominated grasslands since 1915 (Gibbens and Beck, 1988). Their work shows that plots dominated by *S. flexuosus* and *Aristida spp.* in 1915 were dominated by mesquite (*Prosopis glandulosa*) over the following 65 y. This shift from long-lived perennial grass (black grama) to the short lived grasses (*Sporobolus* and *Aristida*) has maintained the graminoid growth form in parts of this landscape long after the dominant species disappeared. Their data also confirm that in grazed pastures there was a trend from short-lived perennial grasses to shrub domination (Gibbens and Beck, 1988). Our vegetation analysis supports the historical data showing the

TABLE 4.—Relative abundances of rodents (number captured per 150 trap nights) in an ungrazed grassland, a creosotebush and a mesquite shrubland site

Species	Grassland	Mesquite	Creosotebush
Chaetodipus penicillatus	0	0	1
Dipodomys merriami	0	2	16
D. ordii	2	4	1
Peromyscus maniculatus	0	0	1
P. eremicus	0	0	1
Perognathus flavus	0	0	1

TABLE 5.—Seed removal (mean ± SE) from experimental seed trays by rodents and ants in grasslands (grazed and ungrazed) and mesquite and creosotebush shrubland sites. Differences between habitats for each taxon are indicated by differing letters, according to Tukey's range test. Habitats are represented by five samples, each comprising the mean seed removal rates from 20 stations. Ant/rodent comparisons are for 100 stations within each habitat

Habitat	n	Comparisons between habitats		Ant/rodent comparisons	n
		Ant seed removal (g/tray/12 h)	Rodent seed removal (g/tray/12 h)		
Ungrazed grasslands	5	14.2 ± 2.3 A	4.1 ± 1.4 A	P ≪ 0.05	100
Grazed grasslands	5	12.5 ± 1.5 A	2.1 ± 1.0 A	P ≪ 0.05	100
Mesquite shrublands	5	4.4 ± 0.4 B	4.0 ± 1.4 A	P > 0.05	100
Creosotebush shrublands	5	5.2 ± 1.4 B	9.9 ± 1.0 B	P ≪ 0.05	100

trend from black grama grassland (in the exclosures) to short-lived perennial tussock grasses in the grazed grasslands and finally the sites that have changed to an alternate stable state: the shrublands.

The shifts in the plant community composition of the grazed grasslands towards the shrublands along Axis 1 within the DCA (Fig. 1) supports the contention that grazing by domestic livestock converts desert grasslands to shrublands (Buffington and Herbel, 1965; Grover and Musick, 1990). These data confirmed that our choice of sites were appropriate for the investigation of the effects of cattle grazing and desertification on granivores and granivory.

The fact that a single grassland site showed the opposite tendency along Axis 1 of the DCA (Fig. 1) reinforces the need for appropriate experimental design if we are to understand the dynamics of these complex systems. Many studies have failed to demonstrate general responses to grazing of semiarid landscapes (e.g., Grant et al., 1982; Bock et al., 1984; Heske and Campbell, 1991; Kelt and Valone, 1995), but the interpretation of these findings is hampered by lack of replication. Lack of replication has hampered the recognition of predictable responses to grazing by livestock (cf., Brown and MacDonald, 1995), and many authors have had to invoke local factors to explain their observations, rather than contribute to the debate on the role of livestock in the degradation of rangelands.

FAUNAL RESPONSES

Rodents.—Our rodent data, although lacking replication, confirm widely published accounts of shifts in rodent communities associated with changes in vegetation structure. Thus grasslands typically support few rodents (Wood, 1969; Pulliam and Brand, 1975), whereas shrublands, with greater habitat heterogeneity, support more diverse rodent communities, typically dominated by granivores (Rosenzweig and Winakur, 1969; Whitford, 1976) and a much higher biomass of rodents (Wood, 1969). In a study comparing rodent communities in grassland and mesquite coppice dune habitats (locations used in this study), Alberico (1978) found that Dipodomys ordii was the most abundant species in both habitats. He reported densities of mesquite shrubland heteromyids that were 2× to 3× higher than in black grama grasslands. The increase in rodents in shrub habitats apparently reflect opportunities for coexistence through differential microhabitat use (Lemen and Rosenzweig, 1978; Price, 1978), resource dispersion (Harris, 1984; Price and Waser, 1985) or predator avoidance (Kottler, 1984).

The few studies that have documented the response of rodent communities to grazing by livestock (Alberico, 1978; Grant *et al.*, 1982; Bock *et al.*, 1984; Brown and Heske, 1990; Heske and Campbell, 1991) obtained conflicting responses (some increases, some decreases in response to removal of grazing). Interpretation of these contradictory findings is confounded by the lack of replication in these studies. Well-designed field experiments are needed to resolve this issue. Despite the documented shifts in rodent diversity, abundance and biomass between desert grassland and shrubland habitats, there have been few attempts to quantify the impacts of these shifts on ecosystem functioning.

Ants.—The absence of a pattern in the DCA (Fig. 2) of the composition of the seed harvesting ant communities is similar to the result obtained by pitfall trap sampling of the ant communities in many of these same habitats and grazing exclosures (Whitford *et al.*, 1999). The DCA pattern suggests that factors other than vegetation affect the structure of seed harvesting ant communities. Kirkham and Fisser (1972) were unable to detect differences in harvester ant abundance and species composition in pastures subjected to different grazing intensities 10 y after the initiation of a grazing study. They concluded that soil texture was the most important factor influencing harvester ant abundances. The absence of *Pheidole militicida* from the mesquite coppice dune area is probably the result of shallow soils in the interdune spaces since this species appears to require deep soils for its nests (Whitford *et al.*, 1999). The virtual absence of *Pogonomyrmex* seed harvesters from the seed trays in the mesquite coppice dunes reflects the lack of soil stability which reduces the potential nest sites (Whitford and Ettershank, 1975; Whitford, 1978). The ant species that dominated the seed trays in grassland habitats, *Solenopsis xyloni,* exhibited decreased frequency at seed trays in the mesquite and creosotebush habitats that was proportional to the decrease in seed removal by ants in those habitats. The *S. xyloni* nests that we found during searches for ant nests were located in grass tussocks. The paucity of suitable grass tussocks for nests in the mesquite and creosotebush habitats may be the primary factor affecting this species and its role as a seed harvester.

<div align="center">GRANIVORY</div>

The levels of seed removal by ants reported here are considerably higher than published levels for North American semiarid landscapes (Brown *et al.*, 1975; Mares and Rosenzweig, 1978, Parmenter *et al.*, 1984). The highest rates of seed removal by ants previously reported for North American deserts was approximately 11 g in 12 h (Mares and Rosenzweig, 1978). The average seed removal rate by ants in our desert grassland sites was 14.2 g in 12 h. This rate of seed removal by ants is the highest reported for any desert area in the world (Abramsky, 1983; Morton, 1985; Kerley, 1991; Lopez de Casenave *et al.*, 1998). The ants that dominated the seed trays were the small *Solenopsis xyloni* which recruit rapidly to dense food sources. *Solenopsis xyloni* selectively harvested grass seeds and did not forage on the millet seeds. *Pogonomyrmex desertorum* selectively harvested native millet seeds (pers. obs.). Most seed tray studies have used seeds larger than 1 mm in diameter (Brown *et al.*, 1975; Mares and Rosenzweig, 1978). Pulliam and Brand (1978) pointed out that large smooth seeds such as millet cannot be handled by some species of seed harvesting ants. More than 60% of the seeds collected by seven species of harvester ants (*Pogonomyrmex spp.* and *Pheidole spp.*) were smaller than 1 mm in diameter (Brown and Davidson, 1977). Seed tray studies that offered only seeds greater than 1 mm in diameter therefore probably underestimated the potential of seed harvesting ants to remove seeds.

We recorded five species of large seed harvesting ants, six species of small seed harvesters and one intermediate sized species (Table 3, size classes from Chew and De Vita, 1980). The most abundant, large, seed-harvesting ant in the Jornada basin is *Pogonomyrmex deser-*

torum which has a head width at the mandibles of 1.6 ± 0.06 mm (n = 7) and the most abundant small seed harvester is *Solenopsis xyloni* which has a head width at the mandibles of 0.7 ± 0.05 mm (n = 7). These values are good indices of the maximum size of seeds that can be carried by ants (Chew and De Vita, 1980). If we had offered only seeds larger than 1 mm in diameter, *S. xyloni* would have been physically limited in removing the seeds from the seed trays, supporting the above conclusion regarding the possible underestimation of seed harvesting by seed removal studies.

In the grassland sites the small seed harvesting ants dominated the seed trays (occupying 76% and 81% of the seed trays, respectively). In mesquite coppice dune sites small seed harvesting ants also dominated (97% of seed trays visited by ants) but overall, the number of trays found by seed harvesting ants was significantly lower in the dune sites than in the grassland sites. Small body size seed harvesters also dominated in the creosotebush sites (41% of seed trays vs. 23% of seed trays with large body size harvesters). Thus, underestimation of ant seed removal through using large seeds only in seed removal experiments would vary between habitats.

Although livestock grazed grasslands generally trended toward degraded shrublands in terms of seed removal, there was no measurable effect of grazing on seed removal by ants or on the ant species composition harvesting the seeds. There were significant differences in seed harvesting between the grassland sites and degraded shrubland sites with fewer species of seed harvesters at the trays and considerably less seed removal in the degraded shrubland sites. These patterns could not be predicted from responses of ant communities to changes in vegetational cover and composition resulting from the conversion of grassland to shrubland. When ant communities were sampled by pitfall trapping the differences in structure of the ant communities in grazing exclosures, grazed grassland and shrublands were small and inconsistent (Whitford *et al.*, 1999). The seed tray experimental approach may better represent the long-term effects of disturbance and degradation on the functioning of the ant community than species information provided by pitfall trap data.

Except for North America and Israel, ants are the dominant seed consumers in desert ecosystems (Brown *et al.*, 1975; Mares and Rosenzweig, 1978; Abramsky, 1983; Morton, 1985; Kerley, 1991, Lopez de Casenave *et al.* 1998), based on seed tray experiments. The data from this study shows that in Chihuahuan desert grasslands, ants remove significantly more seeds than do rodents, rodents and ants have similar impact on seed in mesquite coppice dune ecosystems, and in creosotebush ecosystems rodents remove significantly more seeds than ants. Several factors that contribute to these results differ from those of Brown *et al.*, (1975) and Mares and Rosenzweig (1978). The previous North American studies were conducted in desert shrubland. Desert shrublands typically have higher abundances of heteromyid rodents than do desert grasslands as shown in this study and others (Wood, 1969; Pulliam and Brand, 1975; Whitford, 1976; Alberico, 1978).

Desertification and granivory.—Desertification of the Chihuahuan Desert grasslands has obviously altered the process of granivory. One of the generally accepted features of the North American deserts is the dominance of rodent granivory over ant granivory, which is the reverse of the situation for deserts in other continents (Kerley and Whitford, 1994). Numerous explanations have been put forward to explain the anomalous levels of rodent granivory in North American deserts (Kerley and Whitford, 1994), ranging from Pleistocene extinctions to climatic variability. The findings of the present study suggest that elevated rodent granivory in North American deserts may be an anthropogenic effect brought about by grazing by domestic livestock and subsequent desertification increasing the availability of the preferred rodent habitat. This hypothesis should be tested in other desert ecosystems where grasslands are being converted to shrublands.

There is a need to further explore the implications of desertification on seed dynamics and other ecosystems processes. The elevated levels of rodent granivory observed here may influence the lack of recovery of degraded desert grasslands, with rodent granivory affecting plant regeneration. This suggests that removal of grazing by domestic herbivores will not lead to the spontaneous recovery of desertified landscapes and that other approaches need to be identified to rehabilitate these areas. These could include management of seed dynamics.

LITERATURE CITED

ABRAMSKY, Z. 1983. Experiments on seed predation by rodents and ants in the Israeli desert. *Oecologia,* 57:328–332.

ALBERICO, M. S. 1978. Species diversity of nocturnal rodents in disturbed desert-grassland habitats. Ph.D. Dissertation, New Mexico State University. Las Cruces, New Mexico. 80 p.

BAHRE, C. J. 1995. Human impacts on the grasslands of southeastern Arizona, p 230–264. *In:* M. P. McClaran and T. R. Van Devender (eds.). The desert grassland. The University of Arizona Press, Tucson.

BOCK, C. E., J. H. BOCK, W. R. KENNY AND V. M. HAWTHORNE. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. *J. Range Manage.,* 37:239–242.

BROWN, J. H. AND D. W. DAVIDSON. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science,* 196:880–882.

——— AND W. MACDONALD. 1995. Livestock grazing and conservation on Southwestern Rangelands. *Cons. Biol.,* 9:1644–1647.

———, J. J. GROVER, D. W. DAVIDSON AND G. A. LIEBERMANN. 1975. A preliminary study of seed predation in desert and montane habitats. *Ecology,* 56:987–992.

——— AND J. C. MUNGER. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology,* 66:1545–1563.

———, O. J. REICHMAN AND D. W. DAVIDSON. 1979. Granivory in desert ecosystems. *Annu. Rev. Ecol. System.,* 10:201–227.

——— AND E. J. HESKE. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science,* 250:1705–1707.

BUFFINGTON, L. C. AND C. H. HERBEL. 1965. Vegetational changes on a semidesert grassland range from 1958 to 1963. *Ecol. Monogr.,* 35:139–164.

CHEW, R. M. AND J. DE VITA. 1980. Foraging characteristics of a desert ant assemblage: functional morphology and species separation. *J. Arid Environ.,* 3:75–83.

GIBBENS, R. P. AND R. F. BECK. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *J. Range Manage.,* 41:186–192.

———, ———, R. P. MCNEELEY AND C. H. HERBEL. 1992. Recent rates of mesquite establishment in the Northern Chihuahuan Desert. *J. Range Manage.,* 45:585–588.

——— J. M. TROMBLE, J. T. HENNESSEY AND M. CARDENAS. 1983. Soil movement in mesquite dunelands and former grasslands of southern New Mexico from 1933–1980. *J. Range Manage.,* 36:145–148.

GRANT, W. E., E. C. BIRNEY, N. R. FRENCH AND M. SWIFT. 1982. Structure and productivity of grassland

small mammal communities related to grazing-induced changes in vegetative cover. *J. Mammal.*, **63**:248-260.

GROVER, H. D. AND H. B. MUSICK. 1990. Shrubland encroachment in southern New Mexico, U. S. A.: an analysis of desertification processes in the American Southwest. *Climatic Change*, **17**:305-330.

HARRIS, J. H. 1984. An experimental analysis of desert rodent foraging ecology. *Ecology*, **65**:1579-1584.

HENNESSY, J. T., R. P. GIBBENS, J. M. TROMBLE AND M. Cardenas. 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *J. Range Manag.*, **36**:723-726.

HESKE, E. J., J. H. BROWN AND G. Qinfng. 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia*, **95**:520-524.

——— AND M. CAMPBELL. 1991. Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, southeastern Arizona. *Southwest. Natl.*, **36**:89-93.

HOUGHTON, F. E. 1972. Climatic guide: New Mexico State University, Las Cruces 1851-1971. *New Mexico Agricultural Expl. Stat. Res. Rep.*, **230**:1-20.

KELT, D. A. AND T. J. VALONE. 1995. Effects of grazing on the abundance and diversity of annual plants in Chihuahuan desert scrub habitat. *Oecologia*, **103**:191-195.

KERLEY, G. I. H. 1991. Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *J. Arid Environ.*, **20**:63-69.

——— AND W. G. WHITFORD. 1994. Desert-dwelling small mammals as granivores: intercontinental variations. *Aust. J. Zool.*, **42**:543-555.

KIRKHAM, D. R. AND H. G. FISSER. 1972. Rangeland relations and harvester ants in northcentral Wyoming. *J. Range Manage.*, **25**:55-60.

KOTTLER, B. P. 1984. Predation risk and the structure of desert rodent communities. *Ecology*, **65**:689-701.

LEMEN, C. A. AND M. L. ROSENZWEIG. 1978. Microhabitat selection in two species of heteromyid rodents. *Oecologia*, **33**:3-9.

LOPEZ DE CASENAVE, J., V. R. CUETO AND L. MARONE. 1998. Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world? *Global Ecol. Biogeog. Lett.*, **7**:197-204.

MARES, J. A. AND M. L. ROSENZWEIG. 1978. Granivory in North and South American deserts: rodents, birds, and ants. *Ecology*, **59**:235-241.

MORTON, S. R. 1985. Granivory in arid regions: comparisons of Australia with North and South America. *Ecology*, **66**:1859-1866

MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York. 547 p.

ROUNDY, B. A. AND S. H. BIEDENBENDER. 1995. Revegetation in the desert grassland, p. 263-303. *In:* M. P. McClaren, and T. R. Van Devender (eds.). The desert grassland. The University of Arizona Press, Tucson.

PARMENTER, R. R., J. A. MACMAHON AND S. B. VANDERWAL. 1984. The measurement of granivory by desert rodents, birds and ants: a comparison of an energetics approach and a seed dish technique. *J. Arid Environ.*, **7**:75-92.

PRICE, M. V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology*, **59**:910-921.

——— AND N. WASER. 1985. Microhabitat use by heteromyid rodents; effects of artificial seed patches. *Ecology*, **66**:211-219.

PULLIAM, H. R. AND M. R. BRAND. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. *Ecology*, **56**:1158-1166.

ROSENZWEIG, M. L. AND J. WINAKUR. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology*, **50**:558-572.

WHITFORD, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. *J. Mammal.*, **57**:351-369.

———. 1978. Structure and seasonal activity of Chihuahuan Desert ant communities. *Insectes Sociaux*, **25**:79-88.

————. 1995. Desertification: implications and limitations of the ecosystem health metaphor, p 271–296. *In:* D. J. Rapport, C. L. Gaudet, and P. Calow (eds.). NATO ASI Series, Vol. 128. Evaluating and Monitoring the Health of Large-Scale Ecosystems. Springer-Verlag, Berlin.

———— AND G. ETTERSHANK. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environ. Entomol.,* **4**:689–696.

————, D. J. DEPREE AND P. JOHNSON. 1980. Foraging ecology of two Chihuahuan Desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus. Insectes Sociaux,* **27**:148–156.

————, ————, P. HAMILTON AND G. ETTERSHANK. 1981. Foraging ecology of seed-harvesting ants, *Pheidole* spp. in a Chihuahuan Desert ecosystem. *Am. Midl. Nat.,* **105**:159–167.

————, G. MARTINEZ-TURANZAS AND E. MARTINEZ-MEZA. 1995. Persistence of desertified ecosystems: explanations and implications. *Environ. Monit. Assess.,* **37**:319–332.

————, J. VANZEE, M. S. NASH, W. E. SMITH AND J. E, HERRICK. 1999. Ants as indicators of exposure to environmental stressors in North American desert grasslands. *Env. Monit. Assess.,* **54**:143–171.

WOOD, J. E. 1969. Rodent populations and their impact on desert rangelands. *New Mexico State Univ. Agric. Exp. Stat. Bull.,* **555**:1–37.

ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, New Jersey. 718 p.