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Effects of grazing and shrub removal on small mammal populations in southern New Mexico, USA

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Abstract

Between 1995 and 1997, grazing regimes and mesquite (*Prosopis glandulosa*) shrub removal were combined in a factorial arrangement to assess changes in small mammal communities on the Jornada Experimental Range in southern New Mexico. Small mammals were live-trapped biannually in winter and at the end of the growing season (fall). We examined changes in abundances, species richness, species and biomass diversity, and mean captures and biomass. Species richness did not change significantly with treatments but was seasonally higher in spring 1996 compared to the fall 1996. A decrease in species and biomass diversities were seen in fall 1996 and an increase in both diversities in fall 1997. No plots reached the same species richness, abundance, or diversity encountered during a pre-treatment study in 1993. Spring 1995 and fall 1996 revealed significant reactions to the combination of the applied treatments, yet no overall pattern can be elucidated. Environmental fluctuations such as variable rainfall and inherent stochasticity of the ecosystem may explain the lack of pattern, and only emphasizes the need for more long-term studies assessing the effects of vegetation alteration on dependent communities. © 2005 Elsevier Ltd. All rights reserved.

Keywords: American southwest; Chihuahuan desert; Grazing; Prosopis glandulosa; Shrub removal; Small mammals

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1. Introduction

The large scale changes in vegetation structure and economic productivity in desert grasslands during the past 150 years have been attributed to periodic drought, over-grazing by domestic livestock and suppression of fire (Bahre, 1995). While these play a role in degradation of arid rangelands, the impact of livestock grazing remains the most controversial. In recent years there has been growing interest in the effects of environmental changes in desert ecosystems on biodiversity (Whitford, 1997). In the Chihuahuan Desert grasslands, degradation has resulted in loss of grass cover and conversion of grasslands to shrublands dominated by mesquite (Prosopis glandulosa) or creosotebush (Larrea tridentata) (Buffington and Herbel, 1965; Grover and Musick, 1990; Gibbens et al., 2005). Coincident with vegetation changes are changes in the animal communities and their role in ecosystem dynamics (Whitford and Kay, 1999; Whitford, 2000). There are a number of studies focusing on the effects of grazing and/or rangeland degradation on small mammals (Grant et al., 1982; Johnson, 1982; Bock et al., 1984; Heske and Campbell, 1991; Kelt and Valone, 1995; Kerley and Whitford, 2000; Valone et al., 2002; Valone and Sauter, 2005). Small mammals in desert-grasslands have been intensively studied with respect the effects of vegetation change on their community structure and abundance and their contribution to the maintenance or degradation of grasslands (Alberico, 1978; Brown and Heske, 1990; Heske and Campbell, 1991; Heske et al., 1993). Those studies that have examined the effects of livestock grazing on small mammals have often reached different and/or conflicting conclusions ranging from no significant detectable differences to negative impacts. These conflicting results may be attributable to a variety of factors, including environmental variation and/or lack of replication.

In order to fully understand the effects of grazing and vegetation change on small mammal populations, experimental designs must be set up to look at the different permutations which may alter the environment in various ways. Lack of proper replication and repetition may result in conflicting or meaningless conclusions (Johnson, 1982). This study was one component of an larger experimental study established on the Jornada Experimental Range to investigate the effects of grazing and shrub removal on a variety of ecosystem components and properties, including vegetation, soil nutrient patterns, soil microtopography, ants, reptiles, and small mammals (Nash et al., 1998, 2004). The experimental design combined both the effects of livestock grazing and the removal of a dominant shrub species (*P. glandulosa*) to assess the interaction of these factors in addition to each separately. Here we report the results of these factors on the abundance and species composition of the small mammal community.

2. Methods

2.1. Study area

The Jornada Experimental Range is located approximately 40 km NNE of Las Cruces in southern New Mexico. The Multiple Stressor Experiment site (latitude $32^{\circ}35'$, longitude $106^{\circ}50'$) was in an ecotonal area between black grama grassland with sparse shrub cover and a mesquite shrubland with small coppice dunes. Black grama (*Bouteloua*)

•	—— I	Block One ·		▶◀	Block Two) ——•	• - E	Block Three	
10	SI	NI	NR 12	SI	NI 14	SR	WI 16	WR	5I 18
1	WI	2 WR	SR 3	4 WR	5 WI	NR 6	SR	NR 8	9 NI
W W SI	I W R W Si	/inter-graz/ /inter-graz/ immer-gra	ed, shrubs ed, shrubs zed, shrub	intact removed os intact			1		
SF NI	R Si I N	immer-gra on-grazed,	zed, shrub	s removed tact	1	Ν			
N	R N	on-grazed,	shrubs rea	moved					

Fig. 1. Design of the Multiple Stressor Experiment site on the Jornada experimental range. Each plot (n = 18) is 0.5 ha in size. Codes indicate treatment applied. Each treatment is replicated once per block (r = 3).

eripoda) accounted for more than 50% of the grass cover prior to the treatments, with *Sporabolus* sp., and *Aristida* sp. also relatively abundant. The study design consisted of eighteen fenced 0.5 ha plots. Study plots were set up in two rows of nine plots, with a combination of treatments randomly assigned to each plot (Fig. 1). Each treatment was a combination of: (1) removal or non-removal of honey mesquite shrubs (*P. glandulosa*) and (2) winter grazing, summer grazing, or ungrazed control. The factorial design was such that there were three replicate plots for every treatment combination. Grazed plots were stocked with 16–30 yearling steers. Before cattle were placed in paddocks the available forage was estimated using line-point transects. A stocking rate was adjusted to remove approximately 50% of available forage in approximately 36–48 h.

2.2. Data collection

Baseline data on relative abundance and species composition of the small mammal assemblage on the study site were obtained in 1993 before shrub removal and grazing treatments were initiated. Shrubs were removed between January and March 1994, and small mammal data was collected for the fall of 1994. Winter grazing began in January 1995, and summer grazing began in August 1995. Trapping sessions occurred in the spring and fall of each year from 1995 until 1997, lasting three consecutive nights each session. Due to the numerous plots and lack of sufficient manpower, all 18 plots were not trapped at the same time. Instead, grids were rotated (approximately three plots were trapped at a time), so one complete session lasted 2–3 weeks. A 6×6 trapping grid was set up on each of the 18 treatment plots, with 10 m intervals between trap stations. Traps were buffered 30 m from the fenced edges, leaving a maximum distance of 60 m between trapping grids on neighboring plots. One Sherman live trap was baited with a peanut butter and oat mixture and placed at each grid intersection. Traps were opened 1-3 h before sunset and checked within 2h of sunrise the following morning. All mammals caught were temporarily marked with individual codes with indelible colored ink on tails, ears, and head, and then released.

2.3. Data analysis

Because trapping occurred twice a year and only temporary marks were used, spring and fall seasons were analysed separately to avoid the assumption that animals caught in the fall were the same as those caught in the spring. We did not feel comfortable combining both seasons as we had no way of knowing if we were recapturing the same individuals, and this would compromise any conclusions drawn. Seasonal relative abundance was estimated as number of unique captures per 100 trap nights. Unique captures denotes firsttime captures and does not include recaptured animals. Shannon-Weiner species diversity indices (H') were calculated for each treatment combination in each sampling period (see Zar, 1999 for equations). Biomass diversity $(H_{\rm h}')$ was also calculated because this measure may be a more appropriate descriptor of community structure (Grant et al., 1982). Differences in these diversities between seasons were assessed with two sample Student's ttests, and differences among treatment types within each season were calculated with paired t-tests. Alphas were set at .05. Factorial ANOVAs were utilized to distinguish significant differences between the two treatments within each year and season for individual captures, total biomass, and individual species responses (proc GLM; SAS Institute Inc., 2002). Biomass calculations were either averaged from field data or, in the case of Onychomys leucogaster (whose mass was not recorded), derived from an average published mass (Burt and Grossenheider, 1980).

3. Results

3.1. Species richness and abundances

Because complete species richness cannot be absolutely known, for the purposes of this paper species richness simply indicates the number of different species captured and is in no way meant to represent the total variety of species in this environment. In the fall 1993 baseline study, 185 small mammals comprised of nine different species were trapped, more species than were trapped in any other year. In the 1994 pre-grazing session, only 50 individuals and seven species were trapped (27 in shrub intact plots, 23 in shrub removed). A total of 848 individuals were caught from 1995 to 1997 during 11,664 trap nights. Species caught and respective relative abundances for each year and season are presented in Table 1.

Dipodomys ordii was consistently found in every treatment combination in every season, except in spring 1995 when no animals were trapped on the winter grazed/shrub removed plots. Woodrats (*Neotoma*), kangaroo rats (*Dipodomys*) and grasshopper mice (*Onychomys*) were trapped every year in both seasons. Species richness was significantly higher on the treatment plots in spring 1996, compared to the fall session (t = 3.05, d.f. = 17, p = 0.0073). No other year had any detectable differences in species richness either among treatment types or between seasons.

The total number of captures in each season across all 3 years yielded significantly more small-bodied animals (animals < 100 g, i.e. *Onychomys, Perognathus, D. ordii*, etc.) than large-bodied (animals > 100 g, i.e. *Spermophilus, Neotoma, D. spectabilis*) (spring: t = 5.47, d.f. = 17, p < 0.001; fall: t = 6.41, d.f. = 17, p < 0.001) When *D. ordii* is removed from the analysis due to the its high rate of capture, the spring sessions resulted in more large-bodied rodents trapped than small-bodied (t = 2.83, d.f. = 17, p = 0.0116). There is no

Table 1

Total relative abundance of each species caught from 1993 to 1997. Abundance represented as number of unique individuals captured per 100 trap nights. 1993 was pre-treatment, 1994 pre-grazing, and 1995–1997 a combination of grazing and shrub removal

	1993	1994	1995		1996		1997	
			Spring	Fall	Spring	Fall	Spring	Fall
Dipodomys spectabilis	0	0.41	0.21	0.36	0.15	0.05	0.67	0.72
Dipodomys ordii	2.98	1.08	1.18	1.54	5.45	4.94	10.03	5.61
Neotoma albigula	0.46	0.15	0.05	0.21	0.05	0.10	0.21	0.67
Neotoma micropus	1.95	0	0	0	0	0.10	0	0.26
Neotoma sp. ^a	0	0	0	0	0	0	0.15	0.46
Onychomys arenicola	0.21	0.67	0.72	0.05	0.26	0.10	0.62	1.39
Onychomys leucogaster	0.93	0.10	0.05	0.00	0.21	0	0	0
Perognathus flavus	0.05	0	0	0.00	0.62	0.41	0.57	1.65
Peromyscus eremicus	0	0	0	0.15	0	0	0	0
Peromyscus maniculatus	0.41	0.10	0	0	0	0	0	0
Sigmodon hispidus	2.21	0	0	0	0	0	0	0
Spermophilus spilosoma	0.31	0.05	1.08	0.31	0.77	0	0.82	0.67
Total	9.52	2.57	3.29	2.62	7.51	5.71	13.07	11.42

^aNeotoma sp. represents juveniles that could not be confidently identified as N. micropus or N. albigula.

difference in the fall sessions between large- and small-bodied animals, with or without *D. ordii* included. Replacing total captures with biomass, large-bodied animals dominated the results when *D. ordii* was excluded from analysis (spring: t = 5.92, d.f. = 17, p < 0.001; fall: t = 4.11, d.f. = 17, p < 0.001).

3.2. Species and biomass diversity

As with number of species, species diversity (H') and biomass diversity (H_b') was variable with treatments and seasons (Table 2). Both diversity indices were significantly lower in the fall of 1996 (H': t = 2.67, d.f. = 17, p = 0.0160; H_b' : t = 2.50, d.f. = 17, p = 0.0229), whereas both indices reflected higher diversity in the 1997 fall session (H': t = 3.72, d.f. = 17, p = 0.0017; H_b' : t = 3.88, d.f. = 17, p = 0.0012). There were no differences between sessions in 1995 for either index. No indices were significantly different among treatment types.

3.3. Treatment effects

3.3.1. Mean captures

Significant effects of grazing and shrub removal on mean numbers of individual captures were investigated among and within each year with ANOVA. Alphas (α) were set at 0.05 for main effects (shrub or grazing treatments alone), and 0.10 for interaction effects (grazing and shrub treatments together). Least squares means was used to explain which grazing and/or shrub treatments contributed to the significant interactions. The only significant seasonal difference was in 1996 when more animals were captured in the spring session than in the fall, detected using Wilks' Lambda statistic ($F_{1,10} = 5.03$, p = 0.0487).

Table 2
Total number of species, individuals, species diversity (H) , and biomass diversity (H_b) for each season and treatment combination (each combination represented in
three plots) between 1955–1997. Summer, winter and none indicate grazing treatment; intact and removed indicate shrub treatment

		Spring				Fall			
		Number of species	Number of individuals	Species diversity (H')	Biomass diversity $(H_{\rm b}')$	Number of species	Number of individuals	Species diversity (H')	Biomass diversity (H _b ')
1995									
Summer	Intact	9	17	0.67	0.72	2	6	0.23	0.30
	Removed	1	5			5	8	0.65	0.48
Winter	Intact	4	19	0.47	0.52	3	6	0.30	0.44
	Removed	0	**0			4	7	0.55	0.49
None	Intact	3	10	0.45	0.35	3	8	0.32	0.43
	Removed	4	13	0.58	0.53	4	10	0.51	0.50
	Totals	9	64	0.59	0.59	9	51	0.56	0.61
9661									
Summer	Intact	5	18	0.47	0.39	3	24	0.15	0.22
	Removed	9	22	0.56	0.54	2	14	0.28	0.12
Winter	Intact	4	27	0.34	0.32	1	12		
	Removed	3	27	0.14	0.16	3	18	0.18	0.09
None	Intact	5	20	0.39	0.42	4	31^{**}	0.23	0.37
	Removed	5	32	0.45	0.42	3	12	0.25	0.25
	Totals	7	146	0.43^{*}	0.44^{*}	7	111	0.25	0.32
1997									
Summer	Intact	5	51	0.32	0.34	7	46	0.65	0.73
	Removed	5	42	0.42	0.44	6	33	0.61	0.71
Winter	Intact	9	50	0.50	0.56	7	45	0.75	0.80
	Removed	4	39	0.22	0.29	5	25	0.51	0.54
None	Intact	7	38	0.49	0.56	6	41	0.72	0.75
	Removed	3	34	0.15	0.19	9	32	0.64	0.75
	Totals	7	254	0.41	0.49	7	222	0.74^{*}	0.78*

*Indicates significant seasonal difference (p < 0.05). **Indicates significant difference in captures due to treatment (p < 0.05). In 1995, the spring session revealed a significant difference in captures due to the combination of treatments ($F_{2,10} = 6.04$, p = 0.0191). More animals were caught overall on shrub intact rather than removal plots ($F_{1,10} = 12.48$, p = 0.0054) and no animals were caught on winter grazing/shrub removal plots ($F_{1,10} = 9.58$, p = 0.0093; Table 2). For fall 1996, the grazing and shrub removal combinations did reveal a significant interaction ($F_{2,10} = 3.92$, p = 0.0552), contributed by the ungrazed control which had more animals (Table 2; $F_{1,10} = 6.49$, p = 0.0256). In fall 1997, fewer animals were caught on the shrub removal plots than the intact plots ($F_{1,10} = 6.94$, p = 0.0250). No species responded consistently to the treatments, and only one exhibited any significant response. In fall 1996, *P. flavus* was trapped more often in the summer-grazed, shrub removed plots than any other (summer-grazed: $F_{2,10} = 12.00$, p = 0.0047; shrub removed: $F_{2,10} = 4.50$, p = 0.0348). Block effects were tested for each year with no significant differences among the three blocks (see Fig. 1 for block arrangement).

3.3.2. Mean biomass

Mean biomass weights were analysed in the same manner as above. Only spring 1995 and fall 1996 yielded significant results. The overall grazing and shrub interaction in 1995 was significant ($\alpha = 0.10$, $F_{2,10} = 3.87$, p = 0.0568) because the winter grazed/removed plots had no animals, resulting in the significant difference ($F_{1,10} = 7.73$, p = 0.0166). Shrub-removed plots had far less biomass than those with shrubs intact ($F_{1,10} = 5.08$, p = 0.0479). In fall 1996, the combination of treatments yielded a significant interaction ($\alpha = 0.10$, $F_{2,10} = 3.07$, p = 0.0911). Shrub removal treatments resulted in significantly less biomass on those plots ($F_{1,10} = 6.10$, p = 0.0331). The non-grazed/shrub intact plots had higher biomass ($F_{1,10} = 6.29$, p = 0.0275). The block treatment had no significant effect on biomass.

4. Discussion

Rodent responses to habitat alterations are notoriously variable in field studies (i.e. Johnson, 1982; Heske and Campbell, 1991; Rosenstock, 1996; Valone et al., 2002). This study reveals a similar variable response. Diversity, richness, biomass and capture rates of the small mammal community exhibited no consistent response to the shrub removal and grazing treatments. Abundances were always higher during the spring sessions but not statistically significant (Fig. 2).

In terms of overall capture numbers, more small-bodied rodents (i.e. *D. ordii* and *Onychomys* spp.) were caught during the 3 year study period than large-bodied animals (*Neotoma* spp., *S. spilosoma* and *D. spectabilis*). Yet in terms of biomass the large-bodied animals "outweighed" the small-bodied animals, despite their high numbers. The large-bodied species were a more constant presence on the plots than the smaller sized rodents, and persisted in the plots despite changes in vegetation structure. The continued presence of large rodents may be due to the fact these species either build and/or live in elaborate dens in which they can readily store food and seek shelter. Small-bodied mammals are also specifically vulnerable to habitat perturbation, with increased predation risk (Eccard et al., 2000; Tabeni and Ojeda, 2003).

Shrub removal coupled with grazing often resulted in lower richness, diversity, and capture rates than in intact plots, although this difference was not always statistically noticeable. Given both the reduction in both forage availability and cover precipitated by



Fig. 2. Total precipitation and summer monsoonal precipitation (millimeters) plotted against relative abundance (captures/100 trap nights) of small mammals from 1993 to 1997 on the Multiple Stressor Site. 1993 was before any treatment, and 1994 was post-shrub removal but pre-grazing. Sampling occurred only the in fall for these two years. Grazing and shrub treatment combinations were in effect 1995–1997, and are totaled across spring and fall sessions.

shrub removal, this is an unsurprising yet still important result. The Jornada Experimental Range has experienced a marked replacement of grassland habitats with those dominated by mesquite and creosotebush (Buffington and Herbel, 1965; Gibbens et al., 2005). The effects of shrub removal on small mammals have rarely been studied (Kutiel et al., 2000). More studies are needed in the Chihuahuan Desert focusing on shrub-encroached areas and the effects of ongoing removal practices on the small mammal community.

While the fluctuation in total original captures between 1993 (pre-treatment) and 1997 cannot be readily explained by the various treatments, they may in part be explained by environmental factors. During this experiment, southern New Mexico was enduring a drought with long-term average rainfall well below normal (D.W. Thatcher, unpubl. data). Comparing the total and summer monsoon precipitation against abundances for each trapping session between, there seems to be a relationship between total abundances and available precipitation (Fig. 2). Rodent abundances reached a low of 2.57 in 1994 coincident with low summer rainfall of only 57.40 mm, and then peaked in spring 1997 at 13.07 with a difference of over 100 mm in total rainfall between those three years.

Three murid species either disappeared from the trappable population within a year of the experiment (*Peromyscus* and *Sigmodon*) or remained in very low numbers (*Onychomys*) until 1997 when summer rainfall increased over 80 mm from 1996. Similar reactions of murids to precipitation were also seen in an earlier study on the Jornada Experimental Range (Whitford, 1976). Heteromyids (*Dipodomys* and *Perognathus*) remained a constant presence on all plots and *D. ordii* in particular were caught consistently in high numbers despite low precipitation. Their ability to remain in such high numbers may be due to a foraging strategy of scatter hoarding (Jenkins and Breck, 1998). Desert rodents have a complex yet undeniable relationship with precipitation (Brown and Ernest, 2002). The responses of rodent abundances to precipitation in this study support this relationship.

Small mammals are well known for their variable responses to spatial and temporal dynamics (Whitford, 1976; Brown and Kurzius, 1989; Brown and Zeng, 1989). The variation in results from this as well as previous studies emphasizes not only the environmental stochasticity occurring but also the continued need for replication and experimental studies. This study was not exempt from the vagaries of environmental fluctuations, nor was it free from design flaws. Because the plot design was arranged not only to serve for small mammal monitoring but a myriad of other projects as well, the design could not be tailored specifically for a small mammal project. Plots were only 0.5 ha in size and were separated by cattle exclusion fencing, allowing rodents to move freely between plots and be recaptured in plots different from the site of original capture. However, these "crossing over" events were relatively few in view of overall capture rates and should not alter the conclusions. Less than 3% of the total captures were animals recaptured on a plot different from the site of first capture. Movements between treatments were documented on less than 50% of the 18 plots. A design with larger plots distanced from each other or the use of rodent-exclosure fencing could improve a similar study, yet the overall conclusions may not change.

Long-term studies are a necessary and productive way to obtain meaningful results and elucidate any patterns or responses. While no immediate pattern is evident here, the lack of a pattern is certainly not meant to imply no pattern exists. Instead a larger pattern could be at work that, given enough time, can shed light on how small mammal populations respond and cope with alterations to their surrounding environment. The current desertification of Chihuahuan Desert grasslands requires continued monitoring of vertebrate populations as these ecosystems are altered by external biotic and abiotic forces.

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References

- Alberico, M.S., 1978. Species diversity of nocturnal rodents in disturbed desert-grassland habitats. Ph.D. Dissertation, New Mexico State University, Las Cruces, NM.
- Bahre, C.J., 1995. Human impacts on the grasslands of southeastern Arizona. In: McClaran, M.P., van Devender, T.R. (Eds.), The Desert Grassland. The University of Arizona Press, Tucson, pp. 230–264.
- Bock, C.E., Bock, J.H., Kenney, W.R., Hawthorne, .M., 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. Journal of Range Management 37, 239–242.
- Brown, J.H., Kurzius, M.A., 1989. Spatial and temporal variation in guilds of North American granivorous desert rodents. In: Morris, D.W., Abramsky, Z., Fox, B.J., Willig, M.R. (Eds.), Patterns in the Structure of Mammalian Communities. Texas Tech University Press, Lubbock, pp. 71–90.
- Brown, J.H., Heske, E.J., 1990. Control of a desert-grassland transition by a keystone rodent guild. Science 250, 1705–1707.
- Brown, J.H., Zeng, Z., 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan Desert. Ecology 70, 1507–1525.
- Brown, J.H., Ernest, S.K.M., 2002. Rain and rodents: complex dynamics of desert consumers. Bioscience 52, 979–987.
- Buffington, L.C., Herbel, C.H., 1965. Vegetational changes on a semidesert grassland range from 1858–1963. Ecological Monographs 35, 139–164.
- Burt, W.H., Grossenheider, R.P., 1980. A field guide to the mammals: North America north of Mexico. Peterson Field Guides, third ed. Houghton Mifflin Company, Boston, MA.
- Eccard, J.A., Walther, R.B., Milton, S.J., 2000. How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. Journal of Arid Environment 46, 103–106.
- Grant, W.E., Birney, E.C., French, N.R., Swift, D.M., 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy 63, 248–260.
- Gibbens, R.P., McNeely, R.P., Havstad, K.M., Beck, R.F., Nolen, B., 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. Journal of Arid Environment 61, 651–668.
- Grover, H.D., Musick, H.B., 1990. Shrubland encroachment in southern New Mexico, USA: an analysis of desertification processes in the American southwest. Climate Change 17, 305–330.
- Heske, E.J., Campbell, M., 1991. Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, southeastern Arizona. Southwestern Naturalist 36, 89–93.
- Heske, E.J., Brown, J.H., Guo, Q., 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. Oecologia 95, 520–524.
- Jenkins, S.H., Breck, S.W., 1998. Differences in food hoarding among six species of heteromyid rodents. Journal of Mammalogy 79, 1221–1233.
- Johnson, M.K., 1982. Response of small mammals to livestock grazing in southcentral Idaho. Journal of Range Management 35, 51–53.
- Kelt, D.A., Valone, T.J., 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., Whitford, W.G., 2000. Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores, and granivory. American Midland Naturalist 144, 78–91.
- Kutiel, P., Peled, Y., Geffen, E., 2000. The effect of removing shrub cover on annual plants and small mammals in a coastal sand dune ecosystem. Biological Conservation 94, 235–242.
- Nash, M.S., Whitford, W.G., Van Zee, J., Havstad, K., 1998. Monitoring changes in stressed ecosystems using spatial patterns of ant communities. Environmental Monitoring and Assessment 51, 201–210.
- Nash, M.S., Jackson, E., Whitford, W.G., 2004. Effects of intense, short-duration grazing on microtopography in a Chihuahuan Desert grassland. Journal of Arid Environment 56, 383–393.
- Rosenstock, S.S., 1996. Shrub-grassland small mammal and vegetation responses to rest from grazing. Journal of Range Management 49, 199–203.
- SAS Institute Inc., 2002. SAS System for Windows, version 8.2, Cary, NC.
- Tabeni, S., Ojeda, R.A., 2003. Assessing mammal responses to perturbations in temperate aridlands of Argentina. Journal of Arid Environment 55, 715–726.
- Valone, T.J., Nordell, S.E., Ernest, S.K.M., 2002. Effects of fire and grazing on an arid grassland ecosystem. Southwestern Naturalist 47, 557–565.

- Valone, T.J., Sauter, P., 2005. Effects of long-term cattle exclosure on vegetation and rodents at a desertified arid grassland site. Journal of Arid Environment 61, 161–170.
- Whitford, W.G., 1976. Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy 57, 351–369.
- Whitford, W.G., 1997. Desertification and animal biodiversity in the desert grasslands of North America. Journal of Arid Environment 37, 709–720.
- Whitford, W.G., 2000. Keystone arthropods as webmasters in desert ecosystems. In: Coleman, D.C., Hendrix, P.F. (Eds.), Invertebrates as Webmasters in Ecosystems. CABI Publishing, Cambridge, MA, pp. 25–42.
- Whitford, W.G., Kay, F.R., 1999. Biopedturbation by mammals in deserts: a review. Journal of Arid Environment 41, 203–220.
- Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall, Upper Saddle River, NJ.