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CONSEQUENCES OF CATTLE INTRODUCTION IN A SHRUBSTEPPE ECOSYSTEM: INDIRECT EFFECTS ON DESERT HORNED LIZARDS (*PHRYNOSOMA PLATYRHINOS*)

T.A. Scott Newbold^{1,2} and James A. MacMahon¹

ABSTRACT—Livestock grazing is one of the most common forms of land use in the western United States, yet scientists struggle to accurately predict grazing impacts. This study examined the initial response of desert horned lizards (*Phrynosoma platyrhinos*) to cattle introduction at a site in northwestern Utah. We sampled 21 grazed and 7 ungrazed study plots before grazing (2001), after grazing (2002), and 1 year after the cessation of grazing (2003). We were specifically interested in whether grazing influenced lizards through biotic or abiotic pathways. Lizard response (based on scat counts) to the initial impact of grazing (<6 months after cattle introduction) suggests that lizards abandoned areas protected from grazing (i.e., ungrazed exclosures) presumably in favor of grazed areas. Avoidance of ungrazed plots by lizards coincided with a decline in shrub and grass cover on grazed plots and with no significant change in relative abundance or richness of prey (ants) on grazed plots. In 2003, one year after cattle had been removed from the site, prey species richness declined on ungrazed plots, and percent bare ground increased on previously grazed plots; however, we detected no response of lizards to these changes. Overall, these results add to a growing consensus that responses by small vertebrates to grazing are largely the result of changes to habitat structure (i.e., vegetation cover), rather than to changes in prey availability. Importantly, results from our relatively unique evaluation of *initial* grazing impacts corroborate results from more classic grazing studies conducted sometime after grazing has commenced and suggest that responses of small vertebrates to changes in habitat structure may be generalizable.

Key words: cattle grazing, desert horned lizard, *Phrynosoma platyrhinos*, initial impacts, habitat change, ants, vegetation structure, livestock exclosures, shrubsteppe ecosystem, indirect effects.

Globally, and specifically in the western United States, livestock grazing has become one of the most pervasive forms of land use, yet scientists struggle to fully understand and accurately predict grazing impacts. While factors such as grazing intensity (Menke 1992, Graff et al. 2007) and the evolutionary history of a particular system (Mack and Thompson 1982, Milchunas et al. 1988) are known to strongly influence impacts caused by livestock grazing, consensus on the consequences of grazing for particular taxa remains elusive (e.g., for ants, reviewed in Underwood and Fisher 2006).

Studies of responses by plant species to grazing have revealed a variety of potential mechanisms by which plants are affected by livestock grazing (e.g., direct loss of biomass, Lauenroth and Milchunas 1991; change in the soil microbe community, Sankaran and Augustine 2004; altered nutrient dynamics, Neff et al. 2005). In contrast, most studies on the effects of grazing on animals, especially those

on small vertebrates, investigate a single process: response by animals to structural changes in vegetation caused by grazing (e.g., for reptiles; Jones 1981, Bock et al. 1990, Fabricius et al. 2003). Livestock grazing tends to reduce vegetation cover (Fleischner 1994), which can negatively impact the animal community through loss of structure, and therefore, loss of available niches (Pianka 1966). Alternatively, some animal species, often considered “open space” specialists (e.g., some agamid lizards; Read 2002), may increase under a scenario of reduced vegetation cover. Undoubtedly, alteration of habitat structure is an important repercussion from grazing that has diverse consequences; however, other indirect effects of grazing are rarely evaluated to determine their potential influence on animal species. For example, though frequently recognized as important in the literature (e.g., Bock et al. 1984, Brooks 1999), how grazing affects a species’ biotic environment (i.e., predators, competitors, prey, etc.), and in turn, how effects of grazing on other

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members of the biotic community indirectly influence the focal species (e.g., Pringle et al. 2007) have been addressed by few studies.

Several of the 13 species of horned lizard (*Phrynosoma*) that inhabit North America have undergone significant population declines or range contractions. Both the San Diego coastal horned lizard (*Phrynosoma coronatum blainvillii*) and the Texas horned lizard (*P. cornutum*) are listed as threatened species in California and Texas, respectively, and are candidates for federal listing by the U.S. Fish and Wildlife Service (Donaldson et al. 1994, Brattstrom 1997, Suarez et al. 2000). Overall, the potential causes of horned lizard declines include fragmentation and loss of habitat (Turner and Medina 1982), and the effects of introduced species of ants on communities of native ants (Suarez et al. 2000), the main food source for horned lizards. Though livestock grazing has received some attention as a potential cause of horned lizard declines (Donaldson et al. 1994, Burrow 2000), our understanding of how grazing affects horned lizards is relatively limited.

Horned lizards are diurnal sit-and-wait predators that feed primarily on ants (Pianka and Parker 1975) and are generally associated with areas of sparse vegetation (Whiting et al. 1993, Sherbrooke 2003). Previous studies of the effects of grazing on horned lizards found increased abundance (Reynolds 1979, Fair and Henke 1997, Castellano and Valone 2006) and survivorship (Burrow 2000) in grazed areas; however, not all studies concur with this finding (e.g., Busack and Bury 1974, Jones 1981). Moreover, the pathways by which lizards are affected remain unclear. Though most studies speculate that effects on horned lizards are primarily a result of change in vegetation structure (Reynolds 1979, Fair and Henke 1997, Wilgers and Horne 2006), few studies rigorously test this hypothesis or pursue alternate pathways (e.g., changes in prey availability, but see Reynolds 1979, Fair and Henke 1997, Castellano and Valone 2006).

Here, we examined the indirect pathways by which cattle grazing affects desert horned lizards (*Phrynosoma platyrhinos*). We were interested in (1) how *P. platyrhinos* responds to the initial impact of grazing; and (2) whether grazing influences *P. platyrhinos* through changes in biotic components of the environment (e.g., ant availability), abiotic components (e.g., vegetation structure, soil attributes), or a

combination of the two. Our study has several important strengths. First, horned lizards may have strong affinities for certain vegetation and soil characteristics as a result of thermal constraints associated with ectothermy (e.g., shade-seeking and burrowing; Heath 1965), and non-thermal constraints associated with mobility (Mattingly and Jayne 2004, Newbold 2005a), the availability of prey, and the availability of refugia from predators. Changes to habitat characteristics as a result of grazing are therefore likely to have an impact on lizards via these pathways. Second, horned lizards show little sign of territoriality or interspecific competition (Tanner and Krogh 1973), and there were relatively few predators observed at our study site during the course of the study (S. Newbold personal observation, based on number of loggerhead shrikes [*Lanius ludovicianus*], leopard lizards [*Gambelia wislizenii*], and gopher snakes [*Pituophis catenifer*] encountered during 61 days of field sampling). Therefore, of the biotic forces operating at the site, prey availability is likely the strongest biotic force influencing desert horned lizards. Finally, our study examined the relatively unique initial effects of cattle introduction into a system previously ungrazed by cattle for over a century (see methods for a history of livestock grazing in the area). Such studies are uncommon (Fleischner 1994), mostly because of a lack of suitable rangeland areas that are unaffected, yet are the most likely to reveal the true magnitude and extent of grazing impacts (Fleischner 1994, but see Stohlgren et al. 1999 for a review of enclosure limitations).

METHODS

Study Site and Methodology

The study site was situated along a shrub-steppe bajada in the Great Basin at the southern end of the Grouse Creek Mountains, Box Elder Co., Utah (Zone 12, 281300E, 4594550N). The term "bajada" refers to the land formation that results from the deposition of alluvium forming an inclined plane extending from the mountains to the valley floor. Elevations along the bajada range from 1400 to 1575 m. Mean annual precipitation (15-year mean) on the basin floor is 196 mm, ranging from 121 to 276 mm. Annual precipitation varied little during the study (160 mm in 2001, 164 mm in 2002, and 145 mm in 2003; all measurements are

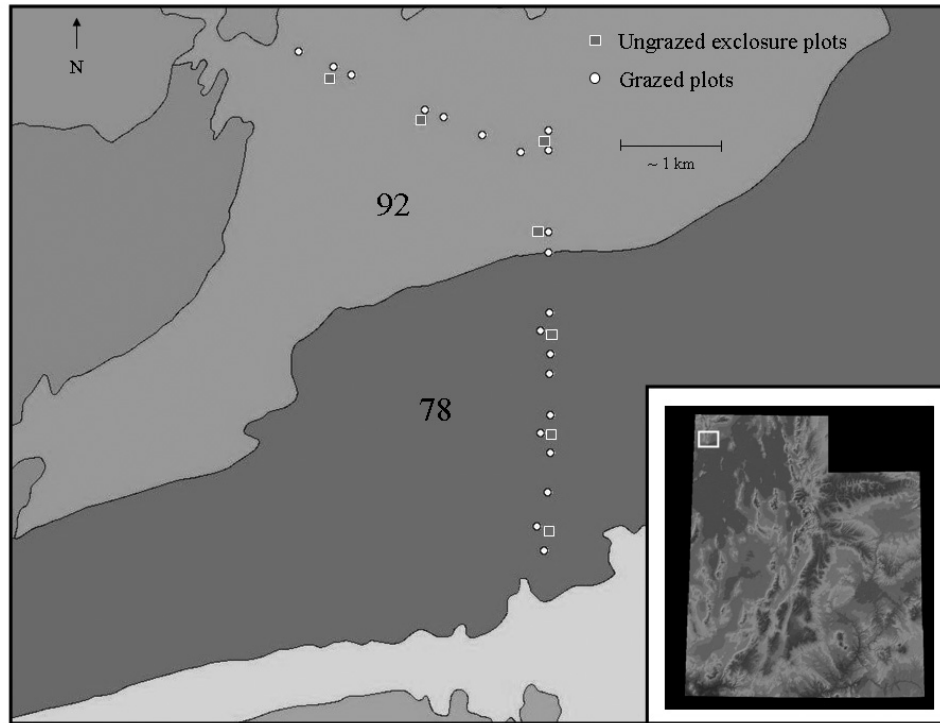


Fig. 1. Location of the study area and study plots in northwestern Utah. The map of Utah in the lower right corner of the figure shows the study area outlined with a white box. A GIS ArcView map illustrates the distribution of study plots and the location of cattle enclosures on the bajada. Ungrazed plots were located within the 30×30 -m enclosures, with at least a 5-m buffer between the edge of the sample plot and the enclosure fence. The plots are overlaid on a map of soil types, designated by their soil map unit number (92, 78; USDA Soil Survey, Loerch et al. 1985).

annual means). Slopes range from 10% to 20% at the highest part of the bajada, to nearly level (1% to 3%) in the lowest portions of the bajada. Soils are sandy-skeletal, mixed, mesic Xerollic Calciorthis in the upper bajada (soil type 92), and fine-silty, mixed, mesic Typic Natrargids in the lower bajada (soil type 78) (Loerch et al. 1985). Vegetation on the upper bajada includes singleleaf pinyon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*), and big sagebrush (*Artemisia tridentata* var. *wyomingensis*). The lower bajada is characterized by black sagebrush (*Artemisia nova*), shadscale (*Atriplex confertifolia*), spiny horsebrush (*Tetradymia spinosa*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and winterfat (*Krascheninnikovia lanata*).

In summer 2001, twenty-eight plots were established along the bajada. Plots were distributed >100 m apart across 2 soil types along a 7-km transect spanning upper-lower elevations. Soil map unit numbers (e.g., 92 and 78,

see Fig. 1) are used throughout the text to distinguish between soil types. Size of plots (20 m in diameter, ~ 315 m² each) was determined based on constraints imposed by intensive, systematic surveys of entire plots; this size is comparable to estimates of minimum home range size of horned lizards (e.g., 500 m² for *P. mcallii* [Turner and Medica 1982]). In fall 2001, before cattle were introduced to the study site, 7 of the 28 plots were fenced (30×30 -m enclosures) using traditional livestock fencing, resulting in 7 ungrazed, fenced plots and 21 grazed, unfenced plots (Fig. 1). There was at least a 5-m buffer between the edge of the sample plot and the enclosure fence, thus reducing edge effects.

The history of livestock grazing at this site suggests that prior to the commencement of our study in 2001 and for approximately the previous 100 years, grazing at this site was limited to relatively light sheep grazing in the winter (J. Pratt, Utah Division of Wildlife Resources,

TABLE 1. Probability values for repeated-measures ANOVA results from the impact phase (2001–2002) and the residual the 2001–2002 interval, but not during 2002–2003, and that 2001 values represent pre-grazing values. Plots were combined ($P < 0.05$) treatment \times year interactions (i.e., significant change in the response variable over time dependent on grazing *Crematogaster mormonum*; phenew, *Pheidole* sp.; forpru, *Forelius pruinosus*; monwhe, *Monomorium wheelerorum*; richness, bare soil cover (%); ppoint, penetrability between shrubs ($\text{kg} \cdot \text{cm}^{-2}$); pshrub, penetrability beneath shrubs ($\text{kg} \cdot \text{cm}^{-2}$); crust cover (%).

Study phase	Soil type	ANOVA model effect	Response variables								
			scat	pogsal	forobt ^a	cremor	phenew	forpru	monwhe	richness	totden
2001–2002	Soil 92	Treatment _{1,13}	—	0.062	0.586	0.475	0.695	0.077	—	0.685	0.528
		Year _{1,13}	—	0.100	0.260	0.021	0.357	0.350	—	0.014	0.061
		Treatment \times Year _{1,13}	—	0.724	0.944	0.257	0.759	0.377	—	0.662	0.457
Impact phase	Soil 78	Treatment _{1,11}	—	0.944	—	—	0.829	0.613	0.525	0.459	0.638
		Year _{1,11}	—	0.262	—	—	0.003	0.078	0.657	0.436	0.237
		Treatment \times Year _{1,11}	—	0.295	—	—	0.642	0.916	0.918	0.522	0.200
2002–2003	Soil 92	Treatment _{1,13}	—	0.052	0.439	0.664	0.537	0.046	—	0.610	0.657
		Year _{1,13}	—	0.005	0.621	0.151	0.416	0.402	—	0.510	0.432
		Treatment \times Year _{1,13}	—	0.123	0.619	0.706	0.760	0.363	—	0.902	0.926
Residual phase	Soil 78	Treatment _{1,11}	—	0.756	—	—	0.479	0.689	0.411	0.607	0.355
		Year _{1,11}	—	0.400	—	—	0.186	0.031	0.261	<0.001	0.192
		Treatment \times Year _{1,11}	—	0.352	—	—	0.810	0.963	0.477	0.051*	0.441
2001–2002	Soil 78 and 92	Treatment _{1,16}	0.084								
Impact phase		Year _{1,16}	0.001								
		Treatment \times Year _{1,16}	0.001*								
2002–2003	Soil 78 and 92	Treatment _{1,16}	0.290								
Residual phase		Year _{1,16}	0.068								
		Treatment \times Year _{1,16}	0.426								

personal communication). Only after a land-ownership change in 2001 were cattle introduced to the area. Because intensive grazing, especially by domestic ungulates, is not a part of the natural historic disturbance regime of the Great Basin shrubsteppe (Mack and Thompson 1982, Billings 1990, Young and Sparks 2002), and because grazing impacts by cattle and sheep differ (e.g., forage preferences [Rook et al. 2004, Celaya et al. 2007] and trampling impact [Spedding 1971]), we assumed that cattle grazing constituted a novel disturbance on the system. Cattle were introduced to this site in December 2001 and grazed during the winter (December 2001–March 2002) at a stocking rate of 4116 AUMs (animal unit months; an AUM is the amount of feed 1 adult cow with a calf eats in 30 days; Nash et al. 2004) within a 40,470-ha area, or 0.10 AUMs per hectare. Grazing intensity within the area was influenced by distance from water troughs and topography. During the following winter (November 2002–March 2003), there was no grazing.

Data were collected during summers 2001, 2002, and 2003. We compared data between summers 2001 (before grazing) and 2002 (immediately after grazing) to evaluate the initial

impacts of grazing (“impact phase”), and summers 2002 (immediately after grazing) and 2003 (1 year after grazing) to evaluate the response to a cessation of grazing (“residual phase”). While we refer to the comparison between 2002 and 2003 as the “residual phase,” we recognize that data collected during the summer of 2003, one year after grazing, may reflect a delayed response to grazing, recovery towards a predisturbance state, or a combination of these as well as other responses.

Lizards

All plots were systematically searched for fecal pellets (“scat”) from desert horned lizards during surveys conducted once per year between June and July in 2001, 2002, and 2003. During a pilot study in 2000, very few lizards were encountered during plot searches, even though lizards were apparently quite abundant in the area, based on encounters on nearby dirt roads. Scats, on the other hand, were conspicuous and relatively plentiful on plots. Data we analyzed from Turner and Medica (1982; Table 1) suggest that scat counts of horned lizards can be a good predictor of lizard counts. Here, we use scat counts as an index of lizard

phase (2002–2003) for 6 ant species and richness, 9 habitat variables, and lizard scat. Note that grazing occurred during from soil 78 and 92 for scat analyses because of small sample size and are shown separately. Asterisks indicate significant treatment). Response variable abbreviations are: pogsal, *Pogonomyrmex salinus*; forobt, *Formica obtusopilosa*; cremor, ant species richness; shrub, shrub cover (%); totden, shrub density (# shrubs/315 m²); grass, grass cover (%); baresoil, spoint, shear strength between shrubs (kg · cm⁻²); sshrub, shear strength beneath shrubs (kg · cm⁻²); crypsoil, cryptobiotic

Study phase	Soil type	ANOVA model effect	Response variables							
			shrub	grass	barsoil	crypsoil	ppoint	pshrub	spoint	sshrub
2001–2002	Soil 92	Treatment _{1,13}	0.593	0.749	0.623	0.8820 ^b	0.553	0.475	0.262	0.302
		Year _{1,13}	0.886	0.480	0.936	0.0966 ^b	<0.001	<0.001	<0.001	0.002
		Treatment × Year _{1,13}	0.496	0.149	0.265	0.9546 ^b	0.339	0.955	0.135	0.915
Impact phase	Soil 78	Treatment _{1,11}	0.324	0.695	0.932	0.887	0.651	0.973	0.955	0.700
		Year _{1,11}	0.274	0.256	0.050	0.006	<0.001	<0.001	<0.001	<0.001
		Treatment × Year _{1,11}	0.032*	0.423	0.668	0.298	0.710	0.766	0.803	0.425
2002–2003	Soil 92	Treatment _{1,13}	0.397	0.443	0.909	0.726	0.280	0.251	0.171	0.423
		Year _{1,13}	0.247	0.578	0.593	0.054	0.886	<0.001	0.216	<0.001
		Treatment × Year _{1,13}	0.535	0.621	0.045*	0.921	0.759	0.801	0.204	0.251
Residual phase	Soil 78	Treatment _{1,11}	0.152	0.761	0.679	0.961	0.525	0.624	0.713	0.449
		Year _{1,11}	0.042	0.032	0.445	0.132	0.448	<0.001	0.036	0.752
		Treatment × Year _{1,11}	0.988	0.245	1.000	0.302	0.777	0.391	0.777	0.752

^aDespite the occurrence of *Formica obtusopilosa* in both soil types (Table 2), this species was found in only 4 of 13 plots within Soil 78 and was excluded from analyses within that soil type.

^bOne plot was excluded from this analysis because of missing values (df = 1, 12).

use on plots following Newbold (2005a), assuming that plots with more scats represent more preferred habitat, regardless of the number of lizards responsible for depositing the scats. Scats from *P. platyrhinos* were distinguished from scats of other lizard species based on size and distinctive cylindrical shape (Newbold 2005b). Once counted, scats were collected from plots and brought back to the lab. Total number of scats per plot for each sampling period was used in analyses.

To account for the possibility that scats were more difficult to see in areas of dense grass or shrub cover, 5 plots were rechecked immediately for missed scats following the initial survey. No scats were found during these 2nd surveys.

Ants

Species composition of ants and their relative abundance were estimated on each plot using arrays of pitfall traps operated once per year between June and July in 2001, 2002, and 2003. Pitfall traps are commonly used for sampling ground-foraging ants in open habitats (Underwood and Fisher 2006). Each array consisted of 5 aluminum cans (78-mm diameter): 1 placed in each cardinal direction along the edge of the plot (~14 m between adjacent cans), with 1 can in the center (Suarez et al. 2000). Plots within exclosures had a minimum

distance of 5 m between cans on the edge of the plot and the exclosure fence. Traps were filled with a 1:1 mixture of animal-safe propylene glycol (SIERRA[®] Antifreeze, Safe Brands Corporation) and water. Peanut butter and Pecan Sandie[®] cookie crumbs served as bait and were distributed near the can's rim at the soil surface. Traps were set and then retrieved after 48 hours; contents were collected into Whirl-Pak[®] bags and refrigerated until the contents were cleaned and placed into vials with 70% ethanol. Ants were sorted, identified to species, and counted. Ant pitfall data were log-transformed at the trap level, and summed for each plot (Suarez et al. 2000). Ant identifications were verified by R. Snelling at the Los Angeles County Museum of Natural History and S. Cover at the Museum of Comparative Zoology (MCZ), Harvard University. Voucher specimens have been deposited at the MCZ.

Habitat Characteristics

We measured the following vegetation characteristics on each plot in August 2001, 2002, and 2003: density and percent cover of shrubs, percent cover of grasses, and percent cover of bare soil. Density and percent cover of shrubs were estimated using the point-quarter method. Ten randomly chosen points were sampled in each plot, yielding point-to-shrub distance and shrub-area measurements (2 orthogonal

Table 2. Comparison of ant species collected from pit-fall trapping arrays in study plots within Soil 92 and Soil 78 (USDA Soil Survey, Loerch et al. 1985). Species presence is indicated by an "X." Diet of *P. platyrhinos*, based on scat dissection, consisted of all ant species except *Messor lobognathus*, *M. smithi*, *Pheidole californica*, and *Temnothorax* sp.

Ant Species	Soil 92	Soil 78
Myrmicinae		
<i>Aphaenogaster uinta</i>	X	X
<i>Crematogaster mormonum</i> ^a	X	
<i>Messor lobognathus</i>	X	
<i>Messor smithi</i>	X	X
<i>Monomorium wheelerorum</i> ^a	X	
<i>Pheidole coloradensis</i>	X	X
<i>Pheidole</i> sp. (potential new species) ^a	X	X
<i>Pogonomyrmex salinus</i> ^a	X	X
<i>Solenopsis molesta</i>	X	X
<i>Temnothorax</i> sp.	X	X
Formicinae		
<i>Formica obtusopilosa</i> ^a	X	X
<i>Formica subpolita</i>	X	
<i>Myrmecocystus navajo</i>	X	X
<i>Myrmecocystus</i> sp.	X	X
<i>Myrmecocystus hammettensis</i>		X
<i>Myrmecocystus testaceus</i>	X	
Dolichoderinae		
<i>Dorymyrmex</i> morphospecies A	X	X
<i>Forelius pruinosus</i> ^a	X	X

^aAnt species that were used in analyses

diameter measurements) for 40 shrubs. At the same 10 sampling points, percent grass cover and bare soil were visually estimated using a 50 × 20-cm Daubenmire frame (Daubenmire 1959), and scored as a cover percentage category (1 = 0%–5%, 2 = 5%–25%, 3 = 25%–50%, 4 = 50%–75%, 5 = 75%–95%, 6 = 95%–100%).

Soil measurements included soil penetrability, shear strength of the soil surface, and percent cover of cryptobiotic crust. At each of the 10 randomly chosen points used for sampling vegetation within a plot, soil penetrability and shear strength were measured at paired points (shrub interspace and beneath shrub) using a pocket soil penetrometer (Durham Geo Slope Indicator, Stone Mountain, GA, #S-170) and Torvane[®] instrument (Durham Geo Slope Indicator, Stone Mountain, GA, #S-160), respectively. Soil measurements from shrub interspaces and from beneath shrubs allowed us to compare soil strength characteristics between these 2 microsites, which may be affected differently by grazing. Cover of cryptobiotic crust was estimated using the Daubenmire frame as a proportion of bare soil occupied by cryptobiotic crusts.

Grazing Intensity

As a surrogate for grazing intensity, we counted dung piles from cows on plots associated with grazing in winter 2001. Dung pile surveys were conducted during the systematic surveys for horned lizard scats in summer 2002, while dung piles were still intact and conspicuous. Counts of dung piles were used to estimate the relative intensity of use by cows on plots (Abensperg-Traun et al. 1996, Vulliamy et al. 2006) and to evaluate potential relationships between intensity of grazing and habitat characteristics.

Data Analysis

To assess changes over time in lizard use on plots, abundances and richness of ant species, and habitat characteristics (vegetation and soil), we conducted a separate repeated-measures 2-way analysis of variance (ANOVA) for each phase of the study: impact phase and residual phase. Within each phase, each plot was visited twice (e.g., 2001 and 2002 for the impact phase), requiring the use of a repeated-measures analysis. Each analysis investigated the impact of grazing treatment (grazed, ungrazed) and year (2001/2002 or 2002/2003) on the dependent variables (e.g., shrub cover). Data were evaluated independently for each soil type (Soil 92, $n = 11$ grazed, $n = 4$ ungrazed; Soil 78, $n = 10$ grazed, $n = 3$ ungrazed); this allowed us to avoid comparing dependent variables across soil types (see methods for soil type descriptions) when particular variables, such as ant species, occurred in only 1 soil type (e.g., *Crematogaster mormonum*, Table 2). Soil type was assumed to be influential when ANOVA results for particular variables differed between soil types. Scat data were combined across soil types because of the limited number of plots, especially ungrazed plots, with scat (ungrazed plots: Soil 92, $n = 1$ of 4 and Soil 78, $n = 2$ of 3; grazed plots: Soil 92, $n = 6$ of 11 and Soil 78, $n = 9$ of 10). Ant species with sufficient abundances across the 3 sampling periods were included in analyses; these included the 6 most common ants, 4 of which comprise a large percentage of *P. platyrhinos* diets at the site (Newbold 2005b). Statistical significance was evaluated using $\alpha = 0.05$. When necessary, data were transformed to meet assumptions of normality.

Though we report probability values for main effects, only the interaction between the

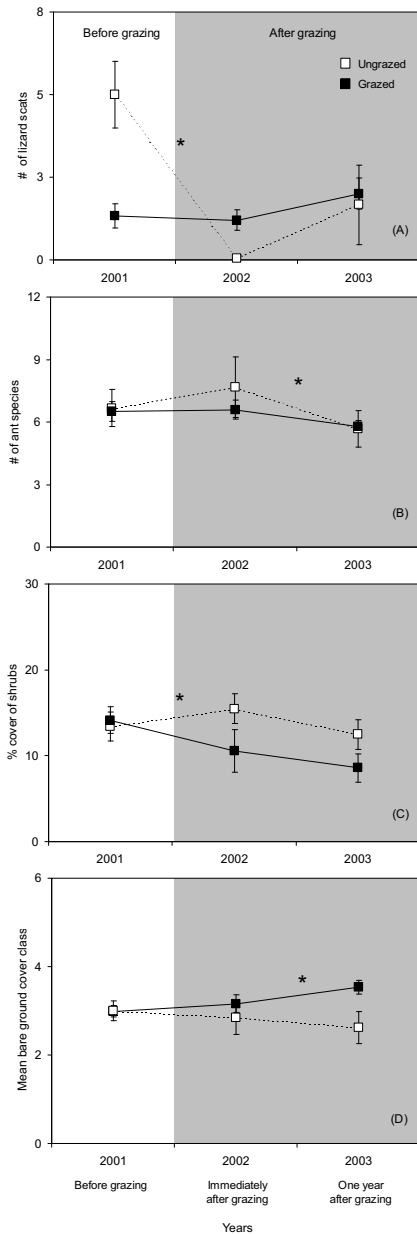


Fig. 2. Means of response variables on ungrazed and grazed plots before and after grazing. Shading distinguishes between pregrazing (2001) and postgrazing (2002 and 2003) conditions for each of the following response variables: (A) lizard scats per plot, (B) ant species per plot, (C) percent cover of shrubs, and (D) mean cover class of bare ground. Soil types are (A) Soil 92 and Soil 78 combined, (B) Soil 78, (C) Soil 78, and (D) Soil 92 (see methods for description of analyses). The naming convention used here (i.e., before grazing, immediately after grazing, 1 year after grazing) follows Read (2002). Asterisks indicate significant ($P < 0.05$) treatment \times year interactions (i.e., significant change in the response variable over time dependent on grazing treatment). Bars represent 1 standard error.

main effects of grazing treatment (grazed, ungrazed) and year (2001/2002 or 2002/2003) addresses our research question (Read 2002). In other words, what is most interesting is a significant change in the response variable over time that is dependent on the grazing treatment. In all cases, F -values in the text refer to the grazing treatment \times year interaction. Figures are provided for significant interactions only.

Finally, associations between grazing intensity estimated with dung pile counts and response data were examined using Pearson correlation coefficients. These potential associations inform the interpretation of our ANOVA results. All analyses were performed in SAS 9.0 (SAS Institute, Inc., Cary, NC).

RESULTS

Lizards

During scat surveys we collected 35 scats of *P. platyrhinos* in 2001, 18 in 2002, and 26 in 2003. During the impact phase (from 2001 to 2002), lizard use of plots as estimated by the number of scats per plot declined on ungrazed plots, while grazed plots showed no reduction in lizard use (Fig. 2a), with treatment \times year interaction significant ($F_{1,11} = 19.83$, $P = 0.001$; Table 1).

In contrast, there was no difference in scat abundance on grazed versus ungrazed plots during the residual phase (from 2002 to 2003; $F_{1,11} = 0.68$, $P = 0.426$; Table 1); both grazed and ungrazed plots showed a similar, slight increase (Fig. 2a).

Ants

Nineteen ant species occurred on the study area, and soil types supported different ant assemblages (Table 2). During the impact phase, there was no difference in the relative abundances of the 6 most common ant species or in ant species richness on grazed versus ungrazed plots (treatment \times year interaction terms, Table 1).

During the residual phase, there was a significant decrease in ant species richness on ungrazed plots relative to grazed plots (Soil 78; $n = 19$ species, $F_{1,11} = 4.81$, $P = 0.051$; Fig. 2b; Table 1). This decline in ant species richness was not attributed to uncommon species; when ants comprising $<1\%$ of the total ants trapped were excluded, the treatment \times year

interaction remained marginally significant ($n = 11$ species, $F_{1,11} = 4.23$, $P = 0.064$). The abundance of *Pogonomyrmex salinus*, a potentially critical component of *P. platyrhinos* diet (Newbold 2005b), showed a similar decline during the residual phase on ungrazed plots relative to grazed plots, but this decline was not significant (Soil 92; $F_{1,13} = 2.72$, $P = 0.123$; Table 1).

Habitat Characteristics

During the impact phase, percent shrub cover declined on grazed plots, while shrub cover on ungrazed plots within the exclosures increased (Fig. 2c), with treatment \times year interaction significant within Soil 78 ($F_{1,11} = 6.00$, $P = 0.032$; Table 1). Although the response was not statistically significant, percent grass cover responded similarly within Soil 92 ($F_{1,13} = 2.36$, $P = 0.149$; Table 1). These changes in vegetation coincided with a change in plot use by *P. platyrhinos* during the impact phase (Fig. 2a).

During the residual phase, there was a significant increase in percent bare ground on grazed plots relative to ungrazed plots within Soil 92 ($F_{1,13} = 4.92$, $P = 0.045$; Fig. 2d; Table 1). No other interaction effects for vegetation characteristics were significant during the residual period.

Soil characteristics were relatively unaffected during both the impact and residual phases. Although the effect was not statistically significant, soil shear strength in shrub interspaces increased on grazed plots relative to ungrazed plots during the impact phase (Soil 92; $F_{1,13} = 2.54$, $P = 0.135$; Table 1).

Grazing Intensity

Dung pile counts ranged from 1 to 19 dung piles per plot with 1 outlier for a plot where cows had congregated ($n = 69$ dung piles). Mean counts of dung piles did not differ between soil types (Soil 92, $\bar{x} = 8.5$, $n = 11$; Soil 78, $\bar{x} = 7.2$, $n = 9$, outlier removed; $F = 0.25$, $P = 0.623$). There was a significant negative association between dung pile counts and the difference in percent grass cover between 2001 and 2002 within Soil 78 ($r = -0.67$, $P = 0.045$, $n = 9$, outlier removed); plots with high grazing intensity experienced greater losses in grass cover than plots with low grazing intensity did. There were no significant associations between dung counts and any other response variable.

DISCUSSION

Somewhat surprisingly, in response to what could be considered a minor pulse of cattle grazing in a semiarid, slow-responding system, we detected a strong response by desert horned lizards to the initial impact of grazing; 1 year after cattle were introduced to the study site, lizards abandoned ungrazed areas (i.e., exclosures) presumably in favor of grazed areas. At the same time, shrub cover, and to a lesser extent grass cover, declined on grazed plots and increased on ungrazed plots, although the effect was not consistent between soil types. Variation in vegetation responses between soil types might be explained, in part, by differences in plant community composition among soil types (Newbold 2005b) and the palatability of those plant species to cattle. Given that there was no significant concomitant change in the availability of ants during the initial impact phase, our findings suggest that *P. platyrhinos* response reflects sensitivity to changes in vegetation structure (i.e., vegetation cover) rather than prey availability, which was unchanged as a result of grazing. In particular, *P. platyrhinos* appears to respond negatively to an increase in vegetation cover.

During the residual phase, lizard scats increased on ungrazed plots in 2003 after a steep decline to 0 in the previous year (Fig. 2a); however, this response to grazing treatment was not significant. At the same time, bare ground increased on grazed plots, and ant richness—perhaps less important to lizards than abundance of preferred ant species—declined on ungrazed plots, while vegetation cover was not significantly different from 2002 to 2003. Thus, despite presumably favorable conditions in grazed areas, effects of grazing on lizards appear to quickly dissipate once grazing is removed. Lack of response by lizards to these factors suggests that bare ground and ant species richness might not be as important to lizards as vegetation cover.

Vegetation structure has both direct (e.g., perch availability) and indirect (e.g., invertebrate prey availability, light quality, microclimate conditions) influences on animals, and responses to structural change vary based on the autecology of particular species. For example, because animals partition the environment based on habitat qualities (Schoener 1974), some species would be expected to do well

with structural change if that alteration positively affects an important niche axis (e.g., increase in perches with large stem diameters). Horned lizards tend to prefer sparsely vegetated habitats (Pianka and Parker 1975, Whiting et al. 1993, Beauchamp et al. 1998, Sherbrooke 2003), and, therefore, it is not surprising that, as in other studies with *Phrynosoma* spp. (Reynolds 1979, Fair and Henke 1997, Burrow et al. 2001, Castellano and Valone 2006, but see Busack and Bury 1974, Jones 1981), we found that *P. platyrhinos* responded positively to reduced vegetation cover as a result of grazing.

The influence of livestock grazing on ant community structure has received much attention (e.g., Read and Andersen 2000, Nash et al. 2001), yet despite the apparent usefulness of ants as ecological indicators of disturbance (Andersen and Majer 2004), there are no consistent trends in grazing impacts on ant assemblages or particular ant species (reviewed in Underwood and Fisher 2006). We found that ants were largely unaffected during the impact phase of grazing at our sagebrush-steppe study site. Lack of initial effects may demonstrate resistance to grazing by ants (Whitford et al. 1999, Read and Andersen 2000). Alternatively, initial effects of grazing may have been tempered by the short duration and timing (i.e., from December to March during the winter) of this disturbance. During the residual phase (i.e., 1 year after the cessation of grazing) ant species richness declined on ungrazed plots relative to grazed plots. This might suggest a lag response by ants to changes initiated during the impact phase (e.g., a delayed effect on the availability of food resources such as seeds) that was only manifested in the subsequent season.

The results of our study are largely consistent with the few previous studies that have examined responses by lizards to grazing-related changes in both habitat and prey characteristics. Read collected data on lizard (Read 2002) and invertebrate (Read 1999) responses to grazing and was able to evaluate changes in both vegetation and prey availability for the lizard *Ctenophorus fordi*, which primarily eats ants. Despite an increase in the abundance of ants under grazing, *C. fordi* declined in grazed areas, strongly suggesting a response by lizards to grazing-induced changes to habitat structure, rather than to ant availability (Read 2002). Three additional studies specifically related to

horned lizards drew similar conclusions (Reynolds 1979, Fair and Henke 1997, Castellano and Valone 2006). In contrast, a recent study by Pringle et al. (2007) found evidence that lizards responded to a combination of vegetation and prey changes associated with grazing. Perhaps with more frequent or intense grazing that temporally incorporates lag-time responses by ants, we would have found this biotic feature of the habitat to be more important to *P. platyrhinos*.

Why horned lizards respond positively to open areas remains unresolved. Potential explanations include increases in the probability of social interactions (Jones 1981), visibility of predators (Jones 1981), effectiveness of camouflage (Beauchamp et al. 1998), mobility (Whiting et al. 1993, Fair and Henke 1997), opportunities for thermoregulation (Jones 1981, Whiting et al. 1993, Burrow et al. 2001), or foraging efficiency (Whiting et al. 1993). Undoubtedly, many of these factors interact and influence habitat selection by lizards in complex ways, but some factors may be more influential than others. Recent studies suggest a potential association between vegetation structure and reduced locomotor performance for lizards (Jayne and Irschick 2000, Mattingly and Jayne 2004). This relationship was explored for *P. platyrhinos* in a concurrent study at our site, and it was suggested that *P. platyrhinos* tended to avoid areas of dense cheatgrass (*Bromus tectorum*), possibly because of its detrimental effects on mobility (Newbold 2005a). Thus, avoidance of ungrazed plots by lizards during the impact phase might be explained by lizard habitat preferences for open areas where movement is less hindered.

Though a link through vegetation seems well supported, alternative explanations for the response of *P. platyrhinos* to grazing, unrelated to vegetation or prey availability, remain untested. For example, cattle grazing, especially over long time periods, results in compaction of soils and redistribution of nitrogen through the deposition of urine and feces (Fleischer 1994, Hobbs 1996). In addition to providing nutrients that stimulate plant growth, which may, in turn, decrease open space availability, dung piles may serve an alternate purpose for lizards—elevated perch sites. In areas with few rock outcrops and very little topographical relief, lizards may use piles of dried dung as perching structures to bask on or to survey the

area from an elevated position. Two years after cattle grazed in our study area, side-blotched lizards (*Uta stansburiana*) were frequently observed perching on dung piles (Newbold 2007). Observations of horned lizards ($n = 1$) and their scats on ($n = 2$) or adjacent to ($n = 3$) dung piles suggest that *P. platyrhinos* individuals also use dung piles. Similar observations were made in a previous study of *P. coronatum* adults using dung piles (Tollestrup 1981). While these observations are intriguing, what role the availability of such microsites plays in the selection of habitat by lizards is unknown.

Replication of "control sites" (exclosures) in grazing studies is usually poor because the construction of exclosures is both cost- and time-prohibitive (Stohlgren et al. 1999). We caution that replication was similarly limited in our study, because it was necessary to evaluate the 2 soil types (92 and 78) independently, resulting in low numbers of ungrazed plots used in the analyses for each area (Soil 92, $n = 4$; Soil 78, $n = 3$).

Livestock grazing and its effects on natural systems are of great conservation concern. Because grazing alters the physical structure of vegetation communities, both directly (e.g., trampling and foraging [Spedding 1971]) and indirectly (e.g., promoting [Fleischner 1994] or reducing [Milchunas et al. 1992] the establishment and spread of exotic species), grazing has the capacity to influence a broad range of individual animal taxa as well as entire communities. Results from this study support an extensive literature that suggests that grazing-induced changes to vegetation structure, in this case plant cover, underlie the majority of responses observed in grazing-animal interactions. Further, because our study was initiated at a different state (i.e., unaltered, precondition) than most studies (i.e., previously grazed) yet shared similar findings with those previous studies, it suggests that these patterns hold up across a wider range of grazing conditions. The initial impact of grazing did not seem to have an adverse effect on desert horned lizards at our site, and may have enhanced lizard habitat by the creation of more open space. Moreover, lizard response was immediate (<6 months after grazing), but quickly disappeared 1 year after the cessation of grazing. By explicitly evaluating the response of ants to grazing, we were able to rule out, at least in the short

term, an indirect effect on desert horned lizards through this alternative biotic pathway (prey availability). Our study highlights the importance of considering multiple direct and indirect effects in future studies of grazing impacts on focal taxa, communities, and ecosystems.

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