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All Flesh Is Grass

Plant-Animal Interrelationships



HERBIVORE–PLANT INTERACTIONS AND DESERTIFICATION IN ARID LANDS

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1. Introduction

In a seminal paper on animals in ecosystems, Chew (1974) stated that, although only a small fraction of plant biomass is consumed by animals, the importance of animals as agents affecting the structure, properties, and processes of ecosystems must be evaluated. Chew based this evaluation of the function of animals in ecosystems on his research in the Chihuahuan Desert of eastern Arizona. The focus on animal activities that affect the structure and function of arid ecosystems provided the conceptual framework for animal studies for the past three decades. The most important animal activities are those which have direct or indirect effects on plants: establishment, growth and mortality, and/or spatial distribution. Arid lands around the world have experienced or are currently experiencing degradation that is known as desertification (Reynolds et al., 2007). Animal–plant interactions that have an effect on desertification are among the most important functions of animals in arid ecosystems (Whitford, 1993).

Desertification has been defined as land degradation in arid and semiarid areas that is the result of various factors, including climate variation and human activities (Williams and Balling, 1996). The interactions between animals and plants affect desertification in arid environments in a number of ways. These interactions may exacerbate desertification processes or contribute to the stability of desertified ecosystems. Some animal–plant interactions are direct, e.g., herbivory, while others are indirect, e.g., seed dispersal and soil modification. Animal–plant interactions that contribute to changes in the structure of plant communities or the spread of alien plant species may enhance some degradation processes such as soil erosion or contribute to soil stability and resistance to degradation.

Most studies that provide data useful for examining the effects of animal–plant interactions on desertification or the contribution of animal–plant interactions to the resilience of desertified ecosystems were conducted in arid and semi-arid regions, where desertification began approximately 1.5–2 centuries ago, coincident with the introduction of the livestock industry. In these landscapes, the structure of some of the component ecosystems is in a state of flux while other component

ecosystems appear structurally stable. In these environments, animal–plant interactions may be direct, e. g., herbivory, or indirect, e.g., seed dispersal and soil modification. In degrading or relatively stable degraded ecosystems, herbivory can contribute to changing plant species composition or modifying the morphology of dominant plant species. Animals are frequently agents of seed dispersal, which may be critical for the expansion of native shrubs into areas where they were absent earlier. Animals that modify soil may affect the distribution of critical resources (water and nutrients), which has been identified as one of the most important consequences of desertification (Whitford, 2002). Here, we review studies that have addressed animal–plant interactions and desertification.

2. Herbivory – Plant Architecture

The behavior of some insects can have a marked effect on the architecture of woody perennials. For example, insects that kill part of live stems in the process of creating a safe environment for oviposition, can have an effect on the physiological response of the plant to the loss of apical dominance. One such insect is *Oncideres rhodosticta* (Coleoptera, Cerambycidae). *Oncideres rhodosticta* is a twig-girdling beetle that utilizes mesquite (*Prosopis glandulosa*) stems for oviposition and larval development sites. Female beetles chew girdles around mesquite stems, severing the phloem and xylem, disrupting water and nutrient transport and killing the stem above the girdle (Polk and Ueckert, 1973). The beetle then oviposits distally from the girdle, allowing the egg to avoid being coated in sap flowing down the stem in response to the girdle (Whitford et al., 1978; Dussourd and Eisner 1987). Mesquite responds to *O. rhodosticta* girdling behavior by producing new stems from nodes below the girdle, compensating for photosynthetic area loss on the dead girdled stem, and potentially increasing the stem density of individual plants (Whitford et al., 1978). Increase in stem density when multiple stems are produced below the girdle changes the morphology of the shrub and, more importantly, how the shrub functions in the landscape. In a study designed to compare the effects of *O. rhodosticta* girdling on mesquite in grasslands with mesquite plants in coppice dunes, there were no differences in the number of old or new girdles on mesquite plants among the dune and grassland plots (Fig. 1). Mesquite in grassland produced more new stems per girdle after 1 year than the coppiced shrubs of the dunes. The new stems below the girdles were longer in the grassland than in the dunes. The volume of plant-captured soil was correlated with shrub stem density (Duval and Whitford, 2008). Positive correlations of mesquite volume with both old and new girdles suggest a feedback loop where girdling increases stem density, stem dense shrubs provide greater resources to emerging female *O. rhodosticta* the following year, and the plant responds by growing more new stems. Beetles contribute to the increase of resources (oviposition sites and food) in the form of compensatory growth stems for the next generation of beetles that will emerge from the girdled stems. This interaction of the beetle and *P. glandulosa* shrubs supports the resource regulation hypothesis of Craig et al. (1986).



Figure 1. Mesquite dune landscape.



Figure 2. Small mesquite seedling with long stems browsed off by rabbits.

There is a correlation between soil capture and stem density, which provides evidence that increases in plant-stem density increases soil capture by individual *P. glandulosa* shrubs (Van de ven et al., 1989). As girdling by *O. rhodosticta* increases stem density, mesquite plants capture more aeolian sand, which is deposited around the base of the shrub. This is the mechanism of dune formation around mesquite plants that eventually results in coppice dune landscapes. Since coppice dune landscapes represent the end point in degradation of desert grasslands, the girdling of mesquite by this beetle increases the probability that the landscape will eventually convert to the most desertified state. Continued girdling of emergent stems from developing dunes provides a positive feedback that maintains the dunes in the landscape.

Browsing by jackrabbits (*Lepus californicus*) has been found to modify the morphology of small honey mesquites (*Prosopis glandulosa*) (Fig. 2). Jackrabbit browsing on small mesquites results in a net loss of biomass. However, the most

important effect of browsing was the change in architecture of the *P. glandulosa* shrubs. Unbrowsed mesquite had long branches and extended crown cover. Browsed mesquite had many stems packed into a compact matrix armed with spines. The compact, spiny, stem matrices produced one or more shoots that were sufficiently tall to escape browsing by the jackrabbits (Martinez and Lopez-Portillo, 2003). The high stem density of the browsed, small mesquite produces a trap for aeolian sand. Compact mesquite will serve as focal plants for the formation of coppice dunes in areas with low grass cover. The effects of stem girdling cerambycid beetles and browsing by native lagamorphs that change stem density and architecture of mesquite, were documented in studies on the expansion of *P. glandulosa* into black grama grassland (Hennessy et al., 1983). The study included areas that had been grazed by livestock and areas from which livestock had been excluded. Vegetation changes in the 45 years since the initial measurements documented complete dominance of mesquite, loss of black grama grass, and the formation of many new mesquite coppice dunes in both grazed and ungrazed areas.

Herbivory by rabbits was found to have an effect on the morphology and distribution of the Mediterranean woody shrub, *Retama sphaerocarpa*. Herbivores produced an open shrubland with fewer, thicker-branched, large, *R. sphaerocarpa* compared to areas subjected to mechanical cutting of the shrubs. Mechanical cutting is a management procedure used to maintain the *Retama* savanna shrublands. Intense herbivory during exceptionally dry periods was reported to produce some effects similar to mechanical cutting, i.e., denser aerial biomass (Sal et al., 1999). The distribution patterns and morphology of *R. sphaerocarpa* and the maintenance of the structure of the Mediterranean savanna-like shrublands are largely attributed to herbivory on the dominant shrub.

3. Herbivory – Plant Vigor and Mortality

Desertification in the southwestern United States and northern Mexico is generally described in terms of expansion of invasive native shrubs (mesquite, *P. glandulosa* and creosotebush, *Larrea tridentata*) into desert grasslands. Creosotebush expansion has been down slope from bands of *L. tridentata* on rocky, well-drained soils at the top of hill slopes or piedmont slopes to the finer textured sandy to sandy-loam soils on the low-slope angle basin slopes (Whitford, 2002). Jackrabbits (*Lepus californicus*) sever most of the stems of some of the multistem *L. tridentata* shrubs during the usually dry winter months in the Chihuahuan Desert. Jackrabbits selectively browse those shrubs with the highest stem water content (Steinberger and Whitford, 1983). Most of the stem with leaves attached is dropped adjacent to the browsed shrub. The stem and leaf wastage decomposes at a different rate than the naturally senesced material. However, the differences in decomposition appear to have little, if any, effect on the physiological status of the shrubs or on soil processes.

Following stem browsing by jackrabbits, *L. tridentata* shrubs exhibit compensatory growth, producing multiple, new shoots from nodes below the cut (Steinberger and Whitford, 1983). In many cases, heavy browsing changes the plant morphology, creating a shrub volume smaller than expected, with much denser foliage in comparison to unbrowsed shrubs. It has been suggested that heavy browsing enhances plant vigor and survivorship due to compensatory growth. In creosotebush-dominated shrubland, the shrubs with the highest stem density cause deposition of wind-transported soil fines and plant litter that form small mounds below the shrub canopy (Whitford et al., 1996). The development of finer textured soil mixed with decomposing litter under the shrub canopies produces a soil patch that supports higher density of soil biota than surrounding soils (Santos et al., 1978). Subcanopy soil with fine texture and organic matter contributes to the nitrogen-rich soils under shrubs (Schlesinger et al. 1996). The change in morphology of heavily browsed *L. tridentata* also affects water redistribution by the shrubs. There is significant stem flow of rainfall intercepted by the canopy of creosotebush that is funneled to deep soil storage by transmission along roots (Martinez-Meza and Whitford, 1996).

Herbivory that involves severing of stems of shrubs can have significant effects on the plant species composition of areas that are still subject to degradation processes. Tarbush, *Flourensia cernua*, is a native woody shrub species that was distributed along ephemeral water courses prior to the initiation of desertification processes. This species moved from the margins of ephemeral streams into areas receiving overland flow from the streams. Thus, on the lower slopes of the piedmonts, tarbush and creosotebush established in areas where grass cover was reduced. On the upper piedmont, creosotebush is dominant with some tarbush on the interfluvial ridges. On the ridges, approximately 35% of the tarbush shrubs were heavily browsed compared to only 4% of the creosotebush. Along the drainage channels on the upper piedmont, jackrabbits heavily pruned 21% of the tarbush but less than 1% of the creosotebush. Jackrabbits preferentially pruned tarbush shrubs in both locations but the differences in proportion of *F. cernua* shrubs pruned compared to *L. tridentata* shrubs was greatest in the drainage channels (Roth et al., 2007).

Creosotebush was slightly more abundant on lower piedmont slopes, with tarbush accounting for 41% of the shrubs per unit area. Nearly half of the tarbush shrubs were dead compared to less than 5% of the creosotebush. Most of the dead tarbush exhibited evidence of moderate to heavy browsing before the shrubs died. The dead tarbush shrubs were only 50% of the predicted size based on basal stem diameters. There was no evidence of compensatory stem growth in *F. cernua* shrubs that were moderately or heavily browsed by jackrabbits in any of the locations. Even in monotypic stands of *F. cernua*, the plants with severed stems exhibited no evidence of compensatory growth by new stems from lateral nodes below the severed end of the stem. Both *F. cernua* and *L. tridentata* are browsed by jackrabbits during the dry winter months. Pruning of stems of one-shrub species (*L. tridentata*) by jackrabbits resulted in increased vigor as a result of compensatory growth and, in the other species (*F. cernua*), pruning of stems by jackrabbits resulted in reduced vigor and mortality (Roth et al., 2007).

The long-term implication of these differences in response to browsing by rabbits is change in community dominants in degraded grasslands that underwent transition to tarbush in the past and are now shifting to creosotebush dominance. The process of vegetation change in desertification may change drivers, e.g., from domestic livestock overgrazing to selective browsing by a native herbivore. This change in drivers can change plant-species composition and spatial distribution of essential resources before temporally stable plant communities are established.

The resilience by compensatory growth of arid region shrubs to herbivory varies not only with the amount of biomass lost to herbivory but with season (wet or dry season) and rainfall (Oba et al., 2000). Long-term studies of herbivory effects on the dwarf shrub *Indigofera spinosa* showed that overcompensation occurred under some conditions but not others. *I. spinosa* exhibited overcompensatory growth for three consecutive years, with 30% biomass removal by clipping during the wet season. In 2 of the 5 years of the study, there was overcompensation when shrubs were defoliated in the dry season but not in the other three years of the study. Moderate to severe (50–90%) defoliation resulted in undercompensation, i.e., failure to return to the preclipping biomass. Full year defoliation resulted in undercompensation even at the light (30%) clipping regime (Oba et al., 2000). The results of this study suggest caution in making generalizations based on single-year or single-season studies of herbivory and compensatory growth in arid-region shrubs.

Growth and survivorship of mesquite in vegetation arcs were found to be a function of stem browsing by jackrabbits and packrats (*Neotoma* sp.) (Fig. 3). Herbivory by these animals had a greater effect on growth and survival of young *P. glandulosa* than water availability (Lopez-Portillo et al., 1996). In landscapes characterized by vegetation arcs separated by gentle erosion slopes, herbivory affected the survivorship of young plants, thereby affecting the plant-species composition of the vegetation arcs.



Figure 3. *Yucca elata* with foliage browsed by woodrats (*Neotoma* spp.).

The spread of mesquite (*Prosopis* spp.) into historical grasslands has been enhanced by the management decision to extirpate black-tail prairie dogs (*Cynomys ludovicianus*) from arid rangeland grasslands. Eradication programs in the western United States reduced the area occupied by prairie dogs to less than 1% of their former distribution and have resulted in an effort by conservation groups to have the species listed as an endangered species (Ceballos et al., 1993). An experimental study found that prairie dogs and the herbivores and granivores associated with their colonies probably maintained grassland and savanna by preventing the establishment of mesquite and other woody species. Mesquite seeds and pods disappeared three to 99 times greater on prairie-dog colonies than off-colony areas (Weltzin et al., 1997). Survival of *Prosopis* spp. seedlings that were protected from vertebrate herbivory was the same on and off colonies. On prairie dog colonies, prairie dogs and associated herbivores girdled and destroyed mesquite seedlings within 2 days after seedlings were planted on colonies. One-year-old mesquite seedlings were reduced by 50% on prairie-dog colonies. Repeat aerial photography showed that *Prosopis* spp. canopy cover on a colony eradicated in 1950 (27%) increased to a level of off-colony mesquite stands (approximately 65% canopy cover) within 23 years (Weltzin et al., 1997). This is an example of how the failure to appreciate the importance of a herbivore in the maintenance of a grassland-savanna has probably contributed to desertification in the southwestern United States. Prior to European settlement, the fossorial mesomarsupial, the burrowing bettong (*Bettongia lesueur*) had the widest distribution of any native mammal in Australia. Following European settlement of interior Australia, the burrowing bettong was extirpated by hunting and poisoning for the same reasons that prairie dogs were largely extirpated in North America (Noble et al. 2007b). The burrowing bettong is now considered rare and endangered. "There is now mounting evidence that *B. lesueur*, together with other mesomarsupials such as the ubiquitous *B. penicillata* (brush-tailed bettong) and *Onychogalea fraenata* (bridled nailtail wallaby), collectively contributed to several other fundamental ecosystem processes including promoting the dispersal of mycorrhizal spores and seeds" (Claridge and May, 1994; Noble, 2001) and by selective browsing, together with episodic fire, regulating populations of native shrub species now regarded as "woody weeds" (Noble, 1996; Noble and Grice, 2002). In pre-European Australia, frequent fire and burrowing bettongs kept shrub and small tree populations low. The results of a modeling study are particularly revealing. With low-shrub density and high-fire frequency, the final densities of plants remained low both in the presence of *B. lesueur* (100 shrubs/ha) and in their absence (200 ha⁻¹). At low-fire frequencies, burrowing bettongs were predicted to keep shrub densities low (250 ha⁻¹). However, in the absence of bettongs and low-fire frequency, shrubs were predicted to increase to high levels (>1,000 ha⁻¹) (Noble et al., 2007a). With more than a half-century of fire suppression and elimination of bettongs, reintroduction of fire for shrub control was insufficient to change the dense shrub ecosystem to a more open savanna-like ecosystem.

Frequent fire resulted in post-fire coppicing of many shrub species that provided green biomass at or near ground level during drought. Some native mammals probably depended on such vegetation for forage. Intense browsing on

resprouting shrubs would impose sufficient physiological stress on the plants to kill a large percentage of the population. These studies provide evidence that herbivory by mesomarsupials, especially burrowing bettongs, were essential for maintaining the open savanna-like ecosystems before the arrival of Europeans. This has led to attempts to reintroduce burrowing bettongs into areas that are dense shrubland in order to use frequent fire and bettong browsing to return the system to a savanna parkland (Noble et al., 2007a).

Noble et al. (2007a) reviewed anecdotal evidence that other mesomarsupials contributed to the regulation of shrub populations by browsing shrubs seedlings and coppices that regenerated after fire. Another rare and endangered mesomarsupial, the nail-tail wallaby, *O. fraenata*, consumed large quantities of shrub foliage. The rufous bettong (*Aepyprymnus rufescens*) browsing of seedlings of the white cypress pine (*Callitris glaucophylla*) in combination with fire maintained the region in northern New South Wales as an open savanna woodland.

Exclosure studies in Western Australia clearly demonstrated that fire and browsing by the mesomarsupial, the quokka (*Settonix brachyurus*), prevented tree-seedling recruitment. Experiments in mallee regions of New South Wales provided evidence that macromarsupials, especially the western gray kangaroo, could eliminate seedlings of mallee pine (*Callitris verrucosa*) by selective browsing (Noble, 2001).

Rodent and insect herbivory is the main factor eliminating the establishment of trees in the northern Mongolian steppe. In experiments where larch, *Larix sibirica*, was planted in plots from which livestock were excluded by fences, grasshoppers and rodents damaged the seedlings during the entire growing season (Dulamsuren et al., 2008). This study documented the importance of grasshopper and rodent herbivory in maintaining the steppe grassland free of trees.

In the Monte Desert of Argentina, the fossorial herbivorous rodent, the tuco-tuco (*Ctenomys mendocinus*), is reported to damage 39% of the total shrubs. *C. mendocinus* was recorded as browse damaging 65% of the *Larrea divaricata*, 41% of the *Lycium chilensis*, 38% of the *Junellia seriphoides*, and 33% of the *Mendoza decemfida* shrubs (Tort et al., 2004). There were no data provided on the long-term growth responses of these shrubs to herbivory by the tuco-tuco in this study. However, since *Larrea tridentata* is closely related to *L. divaricata*, it is likely that this species would exhibit compensatory growth of stems from below the severed ends of the stems. However, other shrub species browsed by the tuco-tuco may parallel tarbush (*F. cernua*), with cumulative damage causing death of the shrub. We suggest that herbivory by the tuco-tuco is an important factor affecting the species composition of the shrub communities in the Monte Desert.

Herbivory is also an important animal plant interaction that affects the physiological status, survivorship, and abundance of perennial herbaceous plants, which are important components of desert ecosystems. In the Chihuahuan Desert, several species of prickly-pear cacti are relatively abundant and important plants contributing to faunal diversity. These plants are also subjected to intense herbivory by

lagomorphs (*L. californicus* and the desert cottontail, *Sylvilagus auduboni*) during the dry winter months. Plant size and not spinescence appears to be the key determinant of presence or absence of browsing. Lagomorph herbivory is not directed at seedlings or small individuals with less than ten cladodes (pads). *Opuntia* with more than 30 cladodes were little affected by herbivory. Because of the large volume and architecture of large *Opuntia* sp., browsing is predominately on the peripheral, older cladodes. The large size insures that there is sufficient photosynthetic area and primordia for new cladodes, flowers, and production of fruit provided by interior cladodes. Thus, heavy browsing on the mid-size cacti reduces the number of cladodes, reduces flower and fruit production, and may even kill the plant if browsing is intense (Hoffman et al., 1993). Since browsing by rabbits does not have adverse effects on seedlings and small individuals or on large prickly-pear, herbivory on these plants is relatively benign.

A South American rodent (*Microcavia australis*) gnaws the bark of the Monte Desert shrub *Geoffroea decorticans* and plants that are heavily gnawed do not survive the loss of bark. *G. decorticans* plants with large diameter trunks have greater survival after bark loss than shrubs with small diameter trunks. Also, shrubs that are a long distance from *M. australis* burrows are subject to less damage by the rodents. The size-distance relationships of the *G. decorticans* shrubs from *M. australis* burrows has long-term effects on the abundance and spatial distribution of the shrub (Tognelli et al., 1999).

In the arid regions of Israel, the dorcas gazelle (*Gazella dorcas*) feeds on different parts of the lily *Pancratium sickenbergeri*. In the summer months, gazelles dig in the sand to remove all or part of the bulb. Partly eaten bulbs have a lower probability of leaf production the following winter (the rainy season) and probably have lower lifetime flower production (Saltz and Ward, 2000). In lily populations subjected to gazelle herbivory, the plants respond by greater depth of bulb growth than recorded in populations with no herbivory. In winter, gazelles browse only on the tips of leaves because of the calcium oxalate concentrations in the leaves, resulting in little effect on the physiological status of the lily. However, in experiments where the lily was subjected to various levels of simulated browsing of leaves (0%, 25%, and 50% of leaves clipped), plants in the intermediate clipping treatments overcompensated in leaf area produced after clipping. Even the highest level of clipping had no significant effect on the number of fruits per plant (Ruiz et al., 2008). Compensatory growth that exceeds photosynthetic area lost is important for the maintenance of *P. sickenbergeri* and is an important adaptation for plant species subjected to herbivory in arid ecosystems.

In the autumn, gazelles eat most of the flowers. Some of the plants produce a second flower that may or may not be eaten by gazelles (Saltz and Ward, 2000). Gazelle-lily interactions appear to be either benign (summer feeding on leaf tips) or negative during the other seasons. Dorcas gazelles are probably more important than edaphic features of the landscape in determining the abundance and distribution of the lily.

Herbivory may have negative effects on certain plants by affecting reproduction by destroying inflorescences and indirectly eliminating specialist pollinators. *Yucca elata* (Agavaceae) is a common evergreen perennial in the arid regions of the southwestern United States and northern Mexico. Young *Y. elata* plants grow as a rosette of narrow, sharp-tipped leaves. In mature plants, the leaf rosette is supported by a fibrous caudex. The inflorescence stalk grows rapidly and bears several hundred flowers. The young inflorescence stalks and flowers are highly desired by cattle, and ranchers manage their herds for maximum utilization of the *Yucca* inflorescences. This management strategy has the effect of reducing populations or eliminating *Y. elata* from the ecosystem. Cattle also browse *Yucca* leaves, especially during the dry winter and spring months (Herbel and Nelson, 1966).

Cattle browse young vegetative growth in the center of the rosette, causing a loss of apical dominance of the browsed rosettes. Browsing rosettes leads to an increase in the number of caudices per plant. The most important effect of browsing on central leaves in the rosette is the reduction in floral inflorescences in the browsed *Y. elata*. This has long-term implications for maintenance of viable populations of this important plant (Kerley et al., 1993).

Yucca elata is pollinated exclusively by the mutualistic yucca moth *Tegeticula yuccasella*, for which *Y. elata* seeds are the obligate habitat and food source for the larvae. If cattle eat all or almost all of the flowers, the year's cohort of *T. yuccasella* will fail to reproduce. If intense browsing of the flower crop continues for several years, the yucca moth may become locally extinct. Yucca moths are weak fliers, suggesting poor dispersal to unaffected *Y. elata* populations. Thus, local *Y. elata* populations may become infertile and incapable of sexual reproduction (Kerley et al., 1993). In Mexico, human harvest of *Yucca fillifera* flowers for food has extirpated the specialist yucca moth, *Tegeticula mexicana*. As a consequence, there are large regions in northern Mexico where *Y. fillifera* flowers are not pollinated and there is no fruit production (Ridaura-Sanz, 1979). Since the dried inflorescence stalks are nest and/or perch sites for several species of birds, loss of inflorescence stalks and/or reduction in abundance of *Yucca* sp. may have serious consequences for biodiversity in areas where this plant is a subdominant.

Differential mortality of shrubs results not only from vertebrate herbivory but also has been reported to result from activities of invertebrates. Seed harvester ants, *Pogonomyrmex rugosus*, were reported to alter the vegetation in the *Larrea tridentata*-*Ambrosia dumosa* shrubland of southern Nevada. Thirteen of seventeen species were absent from nest discs and immediate vicinity of the nests. Woody vegetation was sparse and less variable in composition at the nest discs and edges of nests (Lei, 1999). *P. rugosus* frequently defoliates or severs the stems of woody plant germinants on the nest discs and in close proximity to the nest (Whitford, W. G., 1972–1975, unpublished observations). This behavior of harvester ants contributes to the spatial structure of shrub-dominated ecosystems and to the maintenance of zones of low shrub densities in the vicinity of the nests.

4. Herbivory and Graminivory

While herbivory on some shrubs has effects on ecosystem structure and function as well as on the trajectory and end points of desertification, herbivory on other shrubs, grasses, or herbaceous plants may be benign or contribute to desertification or resilience of desertified ecosystems as a function of the abundance of the target plants in the landscape. Overgrazing of desert grasslands frequently results in increased abundance of an evergreen, subshrub, *Gutierrezia sarothrae* (snakeweed), which is poisonous to livestock (Ralphs, 2002). Snakeweed is multistemmed, with a crown of dense inflorescence stems bearing seeds. *G. sarothrae* stems are severed close to the soil surface during dry winter months by jackrabbits (*L. californicus*). The incidence of herbivory on the stems of snakeweed is virtually the same in mesquite coppice dunes, overgrazed grassland, and ungrazed grassland (Roth et al., 2008). There is no evidence that herbivory by jackrabbits on *G. sarothrae* has an effect on size or mortality of this species. However, rodents sever the inflorescences containing seeds. Because of the low mass relative to the large volume of the severed inflorescences, the cut material is easily moved by wind. It is very likely that wind-blown seed heads disperse the seeds of this undesirable plant species. Thus, herbivory on snakeweed by rodents may contribute to higher abundance of *G. sarothrae* in overgrazed grassland.

While jackrabbit browsing had no effect on mortality and population size of *G. sarothrae*, these parameters were affected by the specialist, snakeweed grasshopper, *Hesperotettix viridis* (Insecta, Orthoptera). In an experiment using caged grasshoppers on individual *G. sarothrae*, mortality was positively related to the number of grasshoppers per plant. One grasshopper per plant killed 53% of the plants, three grasshoppers per plant killed about 69% of the plants, and five grasshoppers per plant killed 91% of the plants (Thompson et al., 1996). A natural population explosion of *H. viridis* resulted in the death of most of the snakeweed in the area and an increase in grass biomass. However, there were no increases in grass biomass during years with low to medium density grasshopper populations (Thompson et al., 1996). While a specialist grasshopper may cause a short-term reversal of a desertification trajectory (increasing abundance snakeweed and reducing grass production), it only occurs during population outbreaks. During most years, *H. viridis* herbivory on *G. sarothrae* is benign.

Most research on desert rodents has focused on granivory and the effects of granivory on soil seed banks. However, most desert rodents feed on plants or plant parts during some or all of the year and may, thereby, have an effect on desertification (Kerley and Whitford, 1994). In the Chihuahuan Desert, several species of kangaroo rats, *Dipodomys* spp., are known to cut large numbers of tillers from a variety of grasses (Kerley et al., 1997; Sipos et al., 2002). Fourteen species of perennial grasses, three species of annual grasses, and one invasive alien species (*Eragrostis lehmanniana*) were reported to be subject to removal of flowering and vegetative

tillers by rodents. Rodents also severed stems of three of the most abundant perennial herbs and three of the most abundant annual herbs (Kerley and Whitford, 2009). This indicates that rodent herbivory is not limited to a few grass species or just monocotyledons. The herbivorous behavior of rodents has largely been unrecognized but recent experimental evidence documents the extent and contribution of this behavior to the maintenance of ecosystems in a degraded state.

In an experiment comparing the effects of tiller cutting of the bunch grass *Sporobolus flexuosus* by rodents, caged grass tussocks that were protected from rodents were compared to plants subject to browsing. Plants subjected to rodent-pruning exhibited very little regrowth of tillers even when pruned tussocks were protected from further herbivory. The lack of recovery (growth) of severed tillers is probably due to the loss of the apical meristem (Briske, 1991). Loss of vegetative tillers markedly reduced the vigor of the grass tussocks. Most of the tillers were severed before seed set. Although medium-size kangaroo rats consume relatively few grass seeds (Reichman, 1975), the effect of rodent graminivory was to reduce the average seed production by a factor of 65. This supports the hypothesis (Kerley et al., 1997) that kangaroo rat graminivory may have a large effect on seed dynamics of desert grasses.

In another experiment where graminivory was examined in relation to tussock size and distance to neighboring tussocks, graminivory was highest on the smallest plants and considerably higher on small plants that were surrounded by bare soil. Graminivory did not occur on tussocks that were in contact with other tussocks. These relationships suggested that graminivory would be highest in overgrazed areas where small and germinant grasses are surrounded by bare soil (Kerley and Whitford, 2009).

The contribution of graminivory by rodents to the prevention of recovery of overgrazed grassland was recently documented in a study of paddocks that were intensively grazed for 1 or 2 days a year between 1995 and 1997 (Roth et al., 2009). Grazed plots had very little grass cover when compared with the ungrazed controls although grazing had been excluded from all plots for more than 5 years. Rodent graminivory reduced the canopy cover of the grasses in the overgrazed plots between 73% and 95% (Table 1) in comparison with little reduction in canopy

Table 1. Proportion of tillers cut by rodents on ungrazed plots and plots intensively grazed by cattle relative to the total percentage of cover of each grass species measured at the end of the growing season. Proportions of total cover clipped by rodents that are different ($p < 0.05$) are indicated by different letters. (Modified from Roth et al., 2008.)

Grass species	Ungrazed plots	Grazed plots
	Proportion of total clipped	Proportion of total clipped
<i>Bouteloua eripoda</i>	5.1% a	73.3% b
<i>Aristida purpurea</i>	3.3% a	73.3% b
<i>Aristida ternipes</i>	24.7% a	77.5% b
<i>Sporobolus</i> spp.	16.2% a	97.0% b

area of the grasses in the ungrazed control plots. The level of rodent graminivory in the overgrazed plots has undoubtedly contributed to the lack of recovery of grass cover in the absence of grazing.

These data also demonstrate that in grasslands that are only moderately degraded by expansion of undesirable shrubs such as mesquite, graminivory by rodents is benign, with little effect on the structure of the grassland.

Graminivory on seedlings contributes to the virtual absence of grass in shrublands. In a study of survival of transplanted black-grama grass (*Bouteloua eriopoda*) seedlings in grassland, shrub-grass matrix ecotone, and shrubland, there was higher loss of seedlings to herbivory by small mammals in the shrubland than in the grassland or ecotone areas.

5. Indirect Effects of Animals on Plants

While graminivory and herbivory are important processes that contribute to desertification or to the maintenance of desertified ecosystems as alternate stable states, there are less direct but similar effects of animals on plants in arid regions. For example, animals may serve as the primary dispersal agents of seeds of woody plants that are undesirable in rangelands. Phytophagous insects may contribute to the growth and vigor of shrubs in desertified shrublands by affecting soil processes. Several types of soil disturbance are known to affect the patch dynamics of arid ecosystems and may contribute to the resilience of desertified ecosystems.

Prior to the introduction of the livestock industry, honey mesquite (*Prosopis glandulosa*) distribution was limited to the margins of ephemeral streams and ephemeral lakes (Johnston, 1963). The dispersal of mesquite from riparian habitats into upland grasslands has been attributed to domestic livestock. Livestock consume the seed-pods and seeds of mesquite, which are reported to have enhanced germinability after passing through a herbivore-digestive tract. Livestock deposit the seeds in nutrient-rich dung in areas that are frequently distant from the parent plants (Brown and Archer, 1989). While livestock are agents for long-distance dispersal of mesquite, heteromyid rodents (*Dipodomys* spp., *Chaetodipus* spp., *Perognathus* spp.) are thought to be agents of short distance dispersal and to enhance germination by seed scarification and by burying seeds in shallow, scatter hoard, caches (Duval et al., 2005). The germination and establishment of mesquite depends on weather conditions prior to the dispersal of the seeds and the abundance of rodents. In an experiment examining the germination and establishment of mesquite in three microsites in a desert grassland, all of the seeds and seedlings were removed from cattle dung pats in all locations. During the growing season of this experiment, no grasses or herbaceous annuals flowered and the only plants that set fruit were mesquite. The dry conditions and lack of other foods probably account for the destruction of dung pats and excavation of all of the caches.

Experiments in the following 2 years examined germination and establishment of mesquite in simulated rodent caches with rodent exclusion cages over one-half

of the caches. Despite relatively high rates of germination in both caged and open caches, over-winter survival was zero in all microsites except for the rodent exclusion caches in burned grassland. In the repeat experiment the following year, high rates of germination were followed by relatively high over-winter survival of seedlings in the burned-site caged caches (28.6%) and unburned grassland open sites (50%). The most frequently documented cause of mortality was rodent or rabbit browsing. Thus, rodent dispersal of mesquite seeds and successful establishment is dependent on weather patterns, rodent population size, and cache microsite.

In Australia, one of the invasive, undesirable shrubs in salt-bush (*Atriplex vesicaria*) rangeland is nitrebush *Nitraria billardieri* (Zygophyllaceae). Nitrebush is a conspicuous component of many overgrazed salt-bush areas. Emus (*Dromaius novehollandiae*) congregate in areas with abundant nitrebush during the late summer fruiting season. The fruits are small drupes that are consumed in large quantities by Emus. During the peak fruiting period, nitrebush seeds comprise more than 90% of the crop and proventriculus (Noble, 1975). Germination studies showed much higher germination of nitrebush seeds after passing through Emus (67% after 24 days) compared to 17% germination of hand-collected seeds. Germination of Emu-digested seed was much faster (50% within 4 days vs. 3% in 4 days for hand-collected seeds (Noble, 1975)). The relationship between Emus and nitrebush is similar to that of cattle and mesquite seeds with respect to dispersal and enhanced germination. Although woody weeds that produce large fruits and seeds are primarily dependent on animals for dispersal, most plants in relatively intact and desertified arid ecosystems are wind-dispersed. In desertified systems with large patches of barren soil, most seeds are either deposited with litter under shrubs that create eddy currents in winds or in animal produced soil pits (Whitford, 2002). One example of digging and diversity and productivity of plants in the soil disturbed patch, was documented in studies of vegetation on residual burrowing bettong warrens. Species diversity and biomass of forbs and grasses were higher on warren sites compared with off-warren sites (Noble et al., 2007b). Similar results have been reported for banner-tail kangaroo rat (*Dipodomys spectabilis*) mounds in the Chihuahuan Desert of North America (Mun and Whitford, 1990), for crested porcupine (*Hystrix indica*) excavations in the Negev Desert, Israel (Boeken et al., 1995), and for the Cape porcupine (*Hystrix africaeaustralis*) in the semi-arid regions of South Africa (Bragg et al., 2005). Warrens of bettongs, mounds of kangaroo rats, and excavations of porcupines and other large, relatively persistent soil disturbances, frequently represent fertile patches within a relatively infertile matrix and patches with higher infiltration and water storage. These features may therefore serve as refugia for plant species that cannot establish and/or survive in the low-resource areas between patches. Nests of some ants (harvester ants: *Messor* and *Pogonomyrmex*) are well documented as representing nutrient-rich patches and as supporting higher biomass and species richness of annual plants on the periphery of the nest discs (Whitford et al., 2008).

Even small, short-lived excavations can serve as seed traps and contribute to the stability of ecosystems. In banded mulga (*Acacia aneura*), the excavations produced by the large varanid lizard (*Varanus gouldii*) in the process of digging

out ground-nesting spiders, serve as traps for seeds of grasses, forbs, and mulga (Whitford, 1998). The varanid pits are concentrated at the interception zones of the vegetation bands. The seed trapping pits produced by *V. gouldii* contribute to the dynamics of the banded vegetation by concentrating seedlings and young plants at the upslope edges of the bands where run-off water accumulates. In North American deserts, heteromyid rodents collect and store seeds in burrows and scatter hoard seeds in spatially dispersed, shallow excavations (Price et al., 2000). The scatter-hoard caches are important germination and establishment sites for plant species that produce seeds selected by the rodents. Establishment of plants from seed initially scatter-hoard-cached by kangaroo rats (*Dipodomys merriami*) was an order of magnitude higher than those from seed that escaped harvest by rodents or ants (Longland et al., 2001). Even scatter-hoard caches that are retrieved by the rodents serve as traps for litter and other seeds. These are examples of indirect effects of animals that affect the structure and function of both desertified and relatively undisturbed ecosystems.

Herbivory by insects can have an effect on the vigor of invasive shrubs. Growth of an invasive shrub, creosotebush (*L. tridentata*), is both water- and nitrogen-limited (Fisher et al., 1988). In a study designed to examine the contribution of herbivorous insects to short-term nitrogen cycling in creosotebush (*Larrea tridentata*) shrublands, these insects contributed approximately 20% of the canopy to soil nitrogen flux. Sap-sucking phytophagous insects were the most abundant arthropods but leaf-chewing phytophagous insects accounted for the highest biomass of the foliage arthropods (Lightfoot and Whitford, 1990). Leaf-chewing insects produced more frass (fecal material) of partially or wholly digested leaf material. Sap-sucking insects excrete a variable volume of liquid that is dependent in-part on the amino acid content of the plant fluid. The frass of sap-sucking insects is also a dilute solution of simple carbohydrates. The frass not only supplies nitrogen to the soil, and eventually the plant, but the simple carbohydrates provide a readily useable energy source for the microbes in the subcanopy litter and soil. Microbial biomass in arid ecosystems is dependent on the supply of labile carbon, and rates of nutrient cycling are dependent on the microbial biomass (Parker et al., 1984). Phytophagous insects on desert shrubs can indirectly contribute to the growth and reproduction of the shrubs via their contribution to nutrient cycling and, thus, to the resilience of shrub-dominated desertified ecosystems.

6. References

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Biodata of **Dr. J. Patrick Kociolek**, author of “*Microscopic in Size: Macroscopic in Impact. Diatom–Human Interactions*”

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