Structure and Function of Chihuahuan Desert Ecosystem
The Jornada Basin Long-Term Ecological Research Site
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Chihuahuan Desert Fauna: Effects on Ecosystem Properties and Processes

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This chapter focuses on the direct and indirect effects of animals on ecosystem processes and/or their effects on ecosystem properties. This set of effects has been the primary focus of animal studies on the Jornada Experimental Range (JER) and the Chihuahuan Desert Rangeland Research Center (CDRRC) during the twentieth century. Early studies dealt with animal species that were thought to reduce the amount of primary production that was available to support livestock. With the establishment of the International Biological Programme (IBP) in the late 1960s and its premise that ecosystems could be modeled based on energy flow, animal studies were designed to measure energy flow through consumer populations. Those studies yielded estimates of consumption of live plant biomass between 1% and 10% of the annual net primary production (NPP) (Turner and Chew 1981). From these studies Chew (1974) concluded that in most ecosystems consumers process only a small fraction of the NPP as live plant material but play important roles in ecosystems as regulators of ecosystem processes rather than energy flow. Chew's hypothesis was then the focus of animal studies in the Jornada Basin for nearly 30 years. Studies of animals as regulators of ecosystem processes led to the

expansion of Chew's hypothesis to include the effects of animals on ecosystem

properties, such as patchiness.

Many of the studies examined in this chapter support the hypothesis that animals

affect spatiotemporal heterogeneity and in turn are affected by it. Because this research

focused on the role of animals in ecosystems, studies of animal populations were

conducted simultaneously with functional studies. Population and behavioral studies were

considered an integral part of the central theme because they supported an understanding

of the spatial and temporal variation of desert ecosystem properties.

The Distribution and Abundance of Animals and Their Effects

We review animal studies that focused on spatial patterns in the distribution and

ecosystem effects of several taxa and guilds. Large-scale ecosystem degradation and

vegetation changes in the Jornada Basin occurred prior to studies of animal populations

(Buffington and Herbel 1965). Therefore, it is important to bear in mind that the

published data on animal populations reflect vegetation and ecosystem conditions that are

very different from the conditions in which many Chihuahuan Desert species existed only

a century before (see chapter 10).

Factors affecting the distribution of vegetation types have probably had strong

effects on small mammal diversity. Overall, the most abundant and widespread rodents

on the Jornada belong to the family heteromyidae (kangaroo rats [*Dipodomys* spp.], silky

pocket mice [*Perognathus* spp.], and coarse-haired pocket mice [*Chaetodipus* spp.]).

Merriam's kangaroo rat (*Dipodomys merriami*) is most abundant in the shrub-dominated

habitats, and Ord's kangaroo rat (*Dipodomys ordii*) is most abundant in the grassland

habitats. The banner-tailed kangaroo rat (*Dipodomys spectabilis*), a grassland specialist

that plays a keystone role in these ecosystems (Mun and Whitford 1990), is absent in the

desertified mesquite (*Prosopis glandulosa*) coppice dunes and creosotebush (*Larrea*

tridentata) and tarbush (*Flourensia cernua*) shrublands. Nonetheless, both the abundance

and species richness of rodents were higher in shrub-dominated areas than in desert

grassland (Wood 1969; Whitford 1976; Whitford et al. 1978b). The subdominant species

in desert grasslands included grasshopper mice (*Onychomys* spp.), spotted ground

squirrels (*Spermophilus spilosoma*), and silky pocket mice (*P. flavus*). Dry lake basin

grasslands and tobosa (*Pleuraphis mutica*) grass swales are thought to support cotton rats

(*Sigmodon hispidus*) (Wood 1969), whereas pocket gophers (*Thomomys bottae*) are

limited to the piedmont grassland at the base of Mount Summerford of the Dona Ana

Mountains (see figure 2-1 in chapter 2). Studies in other regions of the Chihuahuan

Desert suggest that vegetation growth form, vegetation cover, landscape position, and soil

texture determine the spatial distribution patterns of rodents. Black-tailed prairie dogs

(*Cynomys ludovicianus*) occurred in scattered colonies in the basin prior to 1917. During

World War I these populations were exterminated by government programs to increase

forage area for livestock to promote red meat production during the war period. These

populations have not returned (Oakes 2000).

Black-tailed jackrabbits (*Lepus californicus*) and desert cottontails (*Sylvilagus*

auduboni) are important midsize herbivores. Their abundance fluctuates greatly over time

in response to rainfall patterns, desertification status, and productivity of the landscape

units on the Jornada. Mean annual abundance of black-tailed jackrabbits was 36/km^2 in

mesquite shrublands, 30/km^2 in mesquite coppice dunes, and approximately 8/km^2 in

creosotebush and tarbush shrublands. Mean annual abundance in grassland was 5.7/km^2.

Desert cottontail abundance varied from 1.0 to 7.2/km^2 in shrublands but only 0.25/km^2

in grasslands.

Rodents and other small mammals may create spatial heterogeneity through their

digging activities. Foraging pits serve to trap windblown seeds and plant litter

(Steinberger and Whitford 1983a). When the pits are filled in by eolian sand or water-

transported sediments, the seeds in the pit escape collection by harvester ants and

probably escape other seed feeders. More than half of tagged foraging pits in black grama

(*Bouteloua eriopoda*) grassland produced threeawn (*Aristida* spp.) seedlings and/or

seedlings of globe mallow (*Sphaeralcea subhastata*) (Jackson and Whitford unpublished

data). Furthermore, rodent digging activities may accelerate erosion rates when loosened

sediment is washed away (Neave and Abrahams 2001).

Birds and rodents exhibit similar patterns of abundance and species richness.

Breeding bird densities in black grama grasslands (9.8 breeding pairs/km^2) were

considerably lower than in the creosotebush shrublands (28.8 pairs/km^2) (Raitt and Pimm

1978). Intact grasslands supported fewer species and lower abundances of breeding birds

than the most degraded areas (mesquite coppice dunes) (Whitford 1997). The breeding

birds in desert grassland were insectivores. Breeding/nesting birds were completely

absent from the desert grassland site in a year with below-average growing season

rainfall. The grassland breeding birds nested in soapweed (*Yucca elata*) and in mesquite >

3 m tall, providing evidence for the importance of vegetation height diversity for breeding bird abundance and species richness. It also documented dependence of desert grassland breeding bird abundance and species richness on rainfall.

Breeding bird densities on a creosotebush-dominated bajada averaged 28.8 breeding pairs/km^2 during the two years of study (Raitt and Maze 1968). Nests of the most abundant species, black-throated sparrows (*Amphispiza bilineata*), were primarily in creosotebushes at the margins of small drainage channels (86% of the nests). Nests of verdins (*Auriparus flaviceps*), the second most abundant species, were predominantly in whitethorn (*Acacia constricta*) growing along the margins of large and small drainage channels (79% of the nests). The nests of other species recorded in this study were located in large, riparian shrubs growing in the channels or margins of large arroyos (cactus wren [*Campylorhynchus brunneicapillus*], crissal thrasher [*Toxostoma dorsale*], black-tailed gnatcatcher [*Pilioptila melanura*], and loggerhead shrike [*Lanius ludiovicianus*]). Other species that were recorded on the study area included scaled quail (*Callipepla squamata*), mourning dove (*Zenaida macroura*), and roadrunner (*Geococcyx californianus*).

Dissemination of seeds and production of safe germination sites are among the important processes contributed by birds. Nest construction by cactus wrens concentrates many viable seeds of grasses and forbs in the materials collected. Common plants used in cactus wren nests were bush muhly (*Muhlenbergia porteri*) and the exotic Lehmann's lovegrass (*Eragrostis lehmanniana*) (Milton et al. 1998). Nest material that was subjected to germination trials produced 375 seedlings, mostly monocots, from 20-g samples from

12 nests. Seed in the nest material is dispersed when the nest is abandoned and disintegrates. The inclusion of an exotic lovegrass in the nest construction material may contribute to the dispersal of this species, which is a competitor with native grasses.

The most abundant lizard species on the Summerford watershed was the western whiptail (*Cnemidophorus tigris*). Densities of this species ranged from 30–50/ha on the playa fringe and creosotebush bajada. There were 12 species of lizards recorded in the various habitats on the watershed. Several species were transients or immigrants from nearby source habitats, including the Chihuahuan spotted whiptail (*Cnemidophorus exsanguis*), Great Plains skink (*Eumeces obsoletus*), and lesser earless lizard (*Holbrookia maculata*). Only four species were permanent residents of the creosotebush bajada: western whiptail, checkered whiptail (*C. tesselatus*), round-tailed horned lizard (*Phrynosoma modestum*), and long-nosed leopard lizard (*Gambelia wislizeni*). The greater earless lizard (*Cophosaurus* [*Holbrookia*] *texana*) was limited to the large arroyo habitats on the bajada. The side-blotched lizard (*Uta stansburiana*) was associated with the dense vegetation of the feeder arroyos and the large arroyos. Seven lizard species were residents in the mesquite–Mormon tea area fringing the playa lake basin*:* western whiptail, checkered whiptail, Texas horned lizard (*Phrynosoma cornutum*), round-tailed horned lizard, side-blotched lizard, desert spiny lizard (*Sceloporus magister*), and long-nosed leopard lizard (Whitford and Creusere 1977). The abundance and diversity of lizards was higher in mesquite coppice dunes than in adjacent grasslands. The higher species richness in desertified habitats is the result of the addition of shrubland species to the grassland lizard assemblage.

Five species of anurans inhabit several areas of the Jornada Basin around ephemeral lakes. Estimated densities of adult anurans (based on mark and recapture) at a playa lake were: western spadefoot (*Scaphiopus hammondi*), 238/ha; Plains spadefoot (*Scaphiopus bombifrons*), 206.3/ha; Couch's spadefoot (*Scaphiopus couchi*), 79.4/ha; green toad (*Bufo debilis*), 39.7/ha; and Great Plains toad (*Bufo cognatus*), 11.9/ha (Creusere and Whitford 1977). As soon as the playa lake flooded, species of breeding frogs began to occupy different parts of the playa. Western spadefoots were concentrated in open water with depth greater than 12 cm, Plains spadefoots and green toads were concentrated in areas of sparse vegetation with green toads in the shallower water, and Couch's spadefoots were concentrated in shallow water areas with dense vegetation.

Anurans may play a role in moving nutrients from areas of nutrient concentration, that is, ephemeral lakes, which serve as collection points for runoff and transported sediments. Juvenile toads move to areas of sandy soil around the margins of the playa, where they burrow into the soil to estivate until the next growing season. Overwintering juvenile toads suffered high mortality (70–80%) during the first winter and 50–58% during the second winter (Creusere and Whitford 1977). Survival of juvenile toads is dependent on the quantity of fat the toads can accumulate prior to burrowing into the soil for winter and on the moisture of the burrow sites (Whitford and Meltzer 1976). Juvenile toads that die in their overwinter burrows return nutrients concentrated in their natal ponds to the surrounding area. Based on the conservative estimate of juvenile toads of 18,333/ha, this can be an important mechanism of spatial redistribution of nutrients from a nutrient sink to the surrounding landscape.

Studies of arthropods have focused on those taxonomic groups that have a role in seed dispersal and the fate of seeds, decomposition and nutrient cycling processes, and/or the formation of patch heterogeneity of Chihuahuan Desert landscapes. Because of their effects on decomposition, nutrient cycling, water infiltration, and spatial distribution patterns of organic matter, subterranean termites are considered keystone species in the Chihuahuan Desert (Whitford 2000). The abundance and spatial distribution of subterranean termites (primarily Isoptera: Termitidae, *Gnathamitermes tubiformans*) was studied by use of bait rolls (Johnson and Whitford 1975; Nash et al. 1999). These studies found that subterranean termites were equally abundant in all desertified and undegraded habitats, except for those areas inundated for periods of a month or more (ephemeral lake basins). These keystone insects have not been affected by vegetation change resulting from desertification. The average live biomass of termites, estimated from numbers of termites removed from bait rolls, on the Desert Biome watershed was 3.6 kg/ha. The ratio of termite biomass to livestock biomass based on average stocking rates was 4.4, indicating the potential importance of termites in energy flow in Jornada ecosystems (Johnson and Whitford 1975).

Abiotic processes (heat and ultraviolet light) decompose detritus located on the soil surface (MacKay et al. 1987a; Moorhead and Reynolds 1989a) or is consumed by invertebrate detritivores and decomposed in their guts by the symbiotic microflora and microfauna (Crawford 1988). There were large differences in ground-dwelling arthropod communities at the base and on the piedmont slopes of the IBP Desert Biome (Summerford) watershed. The most abundant ground-dwelling arthropods were

tenebrionid beetles and orb spiders (mostly black widow spiders). Most of the taxa

reported for the creosotebush bajada habitat were also reported for desert grasslands in

the Jornada Basin. However, in the grasslands, small tenebrionid beetles (*Araeoschizus*

decipiens) were several times more abundant than any of the other ground-dwelling

arthropods. Another difference between the bajada shrubland and the basin grassland is

the abundance of sand roaches, Polyphagidae (mostly *Arenivaga* spp.) (Whitford et al.

1995). The abundance of dung beetles in the traps in the grassland sites represents

dispersing individuals that were trapped en route to adjacent areas that were grazed by

livestock. Overall, the most abundant taxa in both shrubland and desert grasslands are

detritivorous (scarabids, tenebrionids, polyphagids, and gryllacridids). The gut symbionts

of these detritivores include bacteria, fungi, protozoans, and nematodes (Crawford 1988).

Gut symbionts allow relatively high assimilation efficiencies (30–70%) even when the

animals consume dead plant materials that are primarily cellulose and lignin. Several

species of stink beetles (*Eleodes* [Coleoptera: Tenebrionidae]) have been observed

feeding on the chaff accumulations around the nest disks of seed-harvesting ants

(Whitford 1974). Desert cockroaches (*Arenivaga* spp.) feed on decaying leaves and roots

of desert shrubs (Hawke and Farley 1973). Because most of the annual, aboveground

NPP enters the dead plant material or detritus pool, detritivores are the most abundant

Chihuahuan Desert animals and account for the highest biomass of primary consumers

(Ludwig and Whitford 1981).

The spatial distribution of the most abundant seed-harvester ant species appears to

be primarily related to soil texture characteristics (Whitford et al. 1976, 1999). Although

there is overlap in the distribution of the two widespread species (rough harvester ant

[*Pogonomyrmex rugosus*] and desert harvester ant [*Pogonomyrmex desertorum*]), *P.*

rugosus is absent from mobile and stabilized sand dune areas, and *P. desertorum* is

absent from the clay and silt soils of the tobosa grass swales. In a broom dalea (*Dalea*

scoparia) sand dune area, Maricopa harvester ant (*Pogonomyrmex maricopa*) replaces

rough harvester ant as the large harvester ant in the system. The large nests of these

harvester ants in turn contribute to patchiness in soil properties due to the to the

concentration of nutrients to nests, bioturbation, and chemical alterations of soil via the

vertical redistribution of calcium carbonate (Whitford and DiMarco 1995; Wagner et al.

1997; Whitford 2002).

Soil texture appears to be the most important factor limiting the distribution of

most of the other ant species in Chihuahuan Desert ant communities (Whitford et al.

1999; Bestelmeyer and Wiens 2001a). Creosotebush shrublands on the gravelly soils of

the Summerford bajada had the highest site species richness (36 species) recorded in the

Jornada Basin. The Summerford bajada is a valuable environment from a biodiversity

perspective because it is a source of newly discovered (and potentially rare) ant species

(MacKay and MacKay 2002) and possesses a higher richness than similar environments

elsewhere (e.g., the Sevilleta LTER; Bestelmeyer and Wiens 2001b). Within sandy soils,

however, mesquite cover may be a key factor governing species abundance (Bestelmeyer

2005). For example, an attine ant species (*Trachymyrmex smithii neomexicanus*) that is

absent in grasslands occurs in high abundance in adjacent mesquite coppice dunes and

has also been recorded in creosotebush communities on deep sandy soils (Wisdom and

Whitford 1981). The attine ant species collect senesced leaves and senesced floral parts (petals and sepals) (Schumacher and Whitford 1975). The leaves and floral parts are broken down by fungi cultured by the ants in fungal gardens (Gamboa 1975).

The earliest studies of microarthropods found that their densities were directly correlated with the amount of surface litter (Santos et al. 1978). They reported that nanorchestid mites were found in all habitats sampled on a creosotebush-dominated bajada. Prostigmatid mites were the most numerous acari in all but one area: litter under dense shrubs on margins of an arroyo. In the arroyo margin area, cryptostigmatid (oribatid) mites were the most abundant order of acari. There were 18 orders of soil microarthropods recorded from 12 sites on the Summerford watershed (Wallwork et al. 1985). Mites and collembolans dominated all sites and, except for a honey mesquite site at the edge of the ephemeral lake, mites were more abundant than collembolans. The collembolan density at the honey mesquite site was estimated at $24,460/m^2$. Genera of several families of prostigmatid mites dominated most of the sites in the Jornada Basin (Nanorchestidae: *Speleorchestes* sp., *Nanorchestes* sp.; Tarsonemidae: *Tarsonemus* sp.; Tydeidae: *Tydeus* sp., *Tydaeolus* sp.). These genera were the most abundant mites in black grama grassland, tobosa grass swales, mesquite coppice dunes, and tarbush shrublands (Steinberger and Whitford 1984, 1985; Silva et al. 1989a; Kay et al. 1999).

Cryptostigmatid mites were dominant only where the organic matter content of the soil was > 30%. In leaf litter, the highest density of mites was recorded from juniper (*Juniperus* spp.) litter ($29,486/m^2$), and the lowest density was recorded in creosotebush litter ($8,274/m^2$). Among the most abundant cryptostigmatid mites reported from the

LTER watershed was a previously undescribed species, *Jornadia larreae* (Wallwork and

Weems 1984).

Microarthropods were isolated from honey mesquite rhizosphere soils from

depths up to 13 m (Silva et al. 1989b). Many of the microarthropods that characterized

the rhizosphere fauna at depths > 1 m were species that were abundant in surface soils,

that is, prostigmatids (*Speleorchestes* sp., *Tarsonemus* sp., *Nanorchestes* sp., and

Tydaeolus sp.), cryptostigmatids (*Bankisonoma ovata* and *Passalozetes neomexicanus*),

and the collembolan (*Brachystomella arida*).

The initial stage of decomposition of belowground litter is primarily via soil

bacteria. The bacteria are grazed by protozoans, primarily naked amoebae, and by

bacteriophagous nematodes. The numbers of protozoans and nematodes are regulated by

several species of omnivorous microarthropods (Acarina) that prey on the nematodes

(Santos et al. 1981). When microarthropods were eliminated from buried litter by a

broad-spectrum insecticide, bacteriophagus nematode numbers increased dramatically.

The large numbers of nematodes overgrazed the bacteria, thus reducing the rate of

decomposition. In mesic ecosystems, microarthropods affect decomposition and

mineralization processes by masticating the litter and passing it through their guts. This

increases the surface area and inoculates the litter with microflora from the gut of the

arthropods. The dominant soil acari in mesic systems are cryptostigmatid (oribatid mites).

Oribatids constitute a small fraction of the soil acari community in arid and semiarid

ecosystems (Wallwork 1982; Wallwork et al. 1985). Thus, in arid and semiarid regions,

the role of microarthropods as regulators of the rate of decomposition is indirect via

predation on nematodes and/or fungi, rather than directly by consumption of dead plant material.

The later stages of decomposition and mineralization in dry soils are regulated by some of the same species of omnivorous mites feeding on fungi. Fungi replace bacteria as the primary microfloral decomposers in dry soils. Experiments in which microarthropods were removed showed that rates of nitrogen mineralization were significantly reduced compared with the rates measured when microarthropods were present (Parker et al. 1984b). Elimination of fungivorous and omnivorous mites resulted in a large increase in fungal biomass. Mineral nitrogen from soil surrounding dead roots or buried litter is incorporated into fungal biomass. The fungi use the carbon in litter or roots as energy sources but scavenge nitrogen from the surrounding soil to produce fungal biomass. The nitrogen incorporated into fungal biomass is considered immobilized, that is, not available to be absorbed by plant roots. Soil microarthropods that graze on fungal hyphae release immobilized nitrogen as mineral nitrogen in the form of excretory products. These experiments demonstrate that mineralization of nitrogen in desert ecosystems requires the activities of soil microarthropods.

Arthropods can indirectly affect spatial patterns of plant growth by stimulating the activity of the soil microflora or by supplying soluble nitrogen directly to the soil beneath the plant canopies. The most abundant insects on shrubs in deserts are sucking insects (*Homoptera* and *Hemiptera*) (Lightfoot and Whitford 1987; Schowalter 1996; Schowalter et al. 1999). The frass and honeydew production from these insects fertilizes the litter under the shrub canopies with soluble carbohydrates and nitrogen. This readily available

form of carbon and nitrogen stimulates the growth of microflora on the litter (Lightfoot

and Whitford 1987). Rapid growth of soil microflora as a result of inputs of high-carbon,

low-nitrogen substrates results in the immobilization of soil nitrogen in the rapidly

growing microbial biomass (Parker et al. 1984b). Nitrogen immobilization imposes

severe nitrogen limitations on the biomass production of shrubs and of ephemeral and

perennial herbaceous species.

Synthesis Topics

In this section we review additional animal studies with respect to seven key topics in

ecology that have guided Jornada research over the last three decades.

Pulse-Reserve and Source-Sink Models

In deserts, where many animal species live close to their limit of physiological tolerance

for one or more abiotic factors, the responses of species populations to fluctuations in the

abiotic environment must be understood before questions concerning the role of animals

in ecosystems can be addressed. The pulse-reserve paradigm has been the primary

conceptual model for responses of desert organisms to the abiotic environment (Noy-

Meir 1974). Following this conceptual model, a rainfall pulse stimulates reproduction and

growth of animal populations. Population reserves may be in the form of desiccation-

resistant eggs, specialized "replete" workers that store food in honey pot ants

(*Myrmecocystus*), or stored energy as fat reserves.

Whereas the pulse-reserve model addresses temporal heterogeneity, the source-sink conceptual model addresses the consequences of spatial variation in the transfer of individuals (and resources) between elements of landscape mosaics. This model considers landscapes to be composed of three types of habitats: (1) source habitat, in which reproduction exceeds mortality and the expected per capita growth rate is greater than one; (2) sink habitat, in which limited reproduction is possible but will not (on average) compensate for mortality, and the per capita growth is between zero and one; and (3) unusable habitat through which animals disperse, which comprises the matrix of all habitats that are never exploited by the species in question and in which patches of source and sink habitats are embedded (Danielson 1992). Results from several vertebrate studies (e.g., the cotton rat and amphibian cases reviewed earlier) can be interpreted according to an integration of the pulse-reserve and source-sink conceptual models.

Bottom-Up or Top-Down Population Regulation

Temporal and spatial variation in terrestrial herbivore populations has generated controversial hypotheses concerning the regulation of herbivore numbers (Strong 1988; Matson and Hunter 1992). The top-down hypothesis focuses on the impacts of predators and/or parasitoids on animal numbers, and the bottom-up hypothesis focuses on the consequences of resource quality. Top-down impacts on creosotebush canopy phytophages were studied by experimentally excluding avian and arthropod predators from creosotebushes. In the two years of the study, exclusion of predators resulted in increases in densities of phytophagous insects (Floyd 1996). The effects of bird and

arthropod predation on phytophage populations was additive one year but were compensatory the following year. In the second year of the study, predatory arthropod numbers were lower on creosotebushes from which birds had been excluded than on the shrubs from which birds had not been excluded. The relative effects of predators on herbivore populations varied among seasons and among sites in both years. The impacts of predators on the herbivorous insects were not correlated with known gradients of climatic or of resources quality heterogeneity. The results of this study "confirm the important direct and cumulative effects of multiple predator guilds, even against a complex background of temporal and spatial heterogeneity" (Floyd 1996).

Two studies of creosotebush arthropods provided evidence of bottom-up regulation of herbivorous insect abundance. Herbivorous arthropods were more abundant on creosotebushes on nitrogen-fertilized plots than on creosotebushes on irrigated or control plots (Lightfoot and Whitford 1987). The morphology of creosotebush affects the nutrient status of soils under the shrubs. Insect abundance was higher on high-nutrient shrubs than on low-nutrient shrubs, confirming in part the bottom-up regulation (Lightfoot and Whitford 1989, 1991). A study of the effects of plant stress using "rain-out" shelters to impose drought stress revealed that only 2 of the 44 insect species studied increased in abundance on the stressed creosotebushes. Eight species of phytophagous insects exhibited increased abundance on creosotebushes in irrigated plots. The abundances of the remaining species did not change significantly among treatments (Schowalter et al. 1999). These studies show that phytophagous insects on creosotebush are regulated by both top-down and bottom-up processes.

The Roles of Social Insects

By virtue of their collective activities and ecological success, eusocial insects exert a strong effect on the functioning of desert ecosystems (MacKay 1991). Ants, for example, are among the most abundant arthropods in most of the world's deserts. The high forager abundance and flexible foraging habits of ants are two reasons for their success. Seed-harvester ants of the genus *Pogonomyrmex* are among the most abundant and widely distributed ants in the Chihuahuan Desert. The numbers of foragers in colonies varied among species: 1,000–6,000 in rough harvester ants (*P. rugosus*), approximately 1,000 in California harvester ants (*P. californicus*), and 200–600 in desert harvester ants (*P. desertorum*) (Whitford and Ettershank 1975). Peak foraging activity of rough harvester ants measured as percent of colonies foraging and rate of foragers returning to colonies, occurred following periods of drought. Rough harvester ants foraged at night during midsummer and colonies ceased foraging when granaries were filled. Desert harvester ants and California harvester ants exhibited only diurnal foraging behavior and did not exhibit larder-hoarding satiation. Soil surface temperature and saturation deficit accounted for 10–40% of the variation in foraging activity in harvester ants. Foraging in harvester ants was primarily affected by forage availability and secondarily by microclimate (Whitford and Ettershank 1975).

Scavenging and honey dew collection are other important activities performed by ants (Van Zee et al. 1997). Nearly all small arthropod cadavers that reach the ground are scavenged by ants, particularly the piss ant (*Forelius* or *Iridomyrmex* spp.) and the bicolored crazy ant (*Dorymyrmex* or *Conomyrma bicolor*). Larger ants and ants adapted

to high soil surface temperatures tend to remove these materials over larger distances to their nests. The abundance of these two kinds of species at the Jornada leads to scales of redistribution that are nearly seven times that found in the shortgrass steppe biome (Bestelmeyer and Wiens 2003).

Chihuahuan Desert ant species vary widely in their daily activity patterns, including species that have specialized to nearly lethal diurnal temperatures (the piss ant and honey-pot ants *Myrmecocystus* [Endiodioctes subgenus]) to nocturnality (*Myrmecocystus* [Myrmecocystus subgenus]). The numbers of active colonies of seed-harvesting ants (*Pheidole* spp.), long-legged ants (*Aphaenogaster* [*Novomessor*] *cockerelli*), crazy ants (*Dorymyrmex* [*Conomyrma*] spp.), piss ants, fire ants (*Solenopsis xyloni*), perpilosa formica ants (*Formica perpilosa*), honey-pot ants, and New Mexico leaf-cutter ants (*Trachymyrmex smithii*) also vary seasonally, generally with peak numbers of active colonies in midsummer but with some important exceptions among years (Whitford 1978). As with harvester ants, the foraging activity patterns of these species appear to primarily reflect variation in forage availability and secondarily microclimate. Experimental studies of foraging ecology of long-legged ants demonstrated the importance of forage quality as a factor affecting foraging activity. When long-legged ant colonies were provided both grass seeds and tuna fish, those colonies provided with tuna fish extended their foraging time and remained active until soil surface temperatures reached lethal levels (Whitford et al. 1980a). Colonies provided with seeds ceased foraging at midmorning, the same time that colonies provided with no supplemental forage ceased foraging. It was concluded that foraging activity of ant species is only

partly a function of microclimate, in other words, soil surface temperatures and air relative humidity. Most of the ant species responded to availability of preferred forage and to quantities of food stored in the nests. Ant species exhibited satiation when luxury amounts of preferred forage was available, and colonies ceased foraging when satiated. Because many ant species store food in their nests (i.e., harvester ants, honey-pot ants, fire ants, long-legged ants, and desert leaf-cutter ants) and behave as larder hoarders, stored food is an important regulator of colony foraging activity. Overall, the suite of foraging behaviors used by ants ensures that their populations and foraging activities are sustained even through the most stressful periods.

Although less diverse and apparent than ants, the collective activities of termites may drive nutrient cycling to a greater degree. Where studies have been conducted on quantities of materials consumed by termites, it was estimated that they processed between 3% and 50% of the annual input of detritus and herbivore dung (Whitford et al. 1982) (table 12-1).

The large variation in the fraction of dung consumed by termites (15.1–95.6%) was attributed to the rate at which foragers located individual dung pats. The variation in the fraction of creosotebush leaf and stem litter consumed by termites was found to be related to the availability of other preferred plant species, that is, some grasses and annuals. On the Jornada, there was no annual plant production and very low abundance of fluff grass on the creosotebush bajada in the only year in which creosotebush leaf and stem litter was consumed by termites (Fowler and Whitford 1980; Whitford et al. 1982; MacKay et al. 1987b). In the Chihuahuan Desert, subterranean termites also consumed

Table 12-1. Estimated annual percent of total input of dead plant material and dung consumed by subterranean termites in the Chihuahuan Desert

Shrubs		Reference
Larrea tridentata (dead stems)	3.0%	MacKay et al. (1989)
Larrea tridentata (leaves and twigs)	40.0%	Whitford et al. (1982)
Larrea tridentata (leaves and twigs)	0.0%	Fowler & Whitford (1980); MacKay et al. (1987b)
Yucca elata (flowering stalks)	12.0%	Whitford et al. (1982)
Grasses		
Erioneuron (Tridens) pulchellus (roots)	50.0%	Whitford et al. (1988a)
Erioneuron pulchellus (standing dead)	30.0%	Silva et al. (1985)
Erioneuron pulchellus (standing dead)	43.0%	Whitford et al. (1982)
Aristida purpurea (standing dead)	40.0%	Schaefer & Whitford (1981)
Annual Plants - aboveground		
Crypthantha (spp)	45.0%	Schaefer & Whitford (1981)
Lepidium lasiocarpum	50.0%	Whitford et al. (1982)
Lepidium lasiocarpum	30.0%	Schaefer & Whitford (1981)
Eriastrum diffusum	2.6%	Whitford et al. (1982)
Eriastrum diffusum	4.0%	Schaefer & Whitford (1981)
Eriogonum trichopes	4.2%	Whitford et al. (1982)
Eriogonum rotundifolium	5.0%	Schaefer & Whitford (1981)
Astragalus spp.	0.0%	Schaefer & Whitford (1981)
Baileya multiradiata	45.0%	Whitford et al. (1982)
Baileya multiradiata **(roots)**	50.0%	Whitford et al. (1988a)
Cattle dung	46.5%	Whitford et al. (1982)

large quantities of dead roots of grasses and annuals (Whitford et al. 1988a). There is

indirect evidence that termites consume a large fraction of dead roots of shrub species, if

termites locate the roots (Mun and Whitford 1998). Although there are no quantitative data on the fraction of litter and dung consumed by termites in desert grassland, mesquite coppice dunes, mesquite-grass mosaic, and tarbush habitats in the Jornada Basin, recent studies on termite galleries and sheeting in these habitats suggest that termites may be consuming a larger fraction of the detritus than has been reported for the creosotebush-dominated bajada.

The processing of dead plant material by the gut symbionts of termites has important implications for the organic matter content of soils and the cycling of nutrients. The gut symbionts of some species of termites have the capacity to decompose lignins and other recalcitrant organic molecules (Butler and Buckerfield 1979). Thus, termites produce only small quantities of feces. Termite feces contain very little recalcitrant carbon to contribute to the soil organic matter pool. The soil organic matter content of soil patches on a Chihuahuan Desert watershed was found to be strongly negatively correlated with the abundance/activity of subterranean termites (Nash and Whitford 1995). Since the rates of processes such as nitrogen mineralization are directly related to the soil organic matter content (Whitford et al. 1986), termites can indirectly affect the availability of essential nutrients for plant growth.

There are other characteristics of termites that contribute directly to nutrient cycling processes. Many species of termites have been shown to fix atmospheric nitrogen via hindgut symbionts (Beneman 1973; Schaefer and Whitford 1981; Bentley 1984), which allows termites to use foods with high carbon:nitrogen ratios. This nitrogen enters the nitrogen cycle in desert ecosystems primarily through the many predators that feed on

termites (Schaefer and Whitford 1981). Termites also contribute significantly to cycling of other soil nutrients, such as phosphorus and sulfur, via this same pathway (Schaefer and Whitford 1981). The materials used to construct sheeting over potential food materials are also enriched with such nutrients as calcium and potassium (Bagine 1984).

All ecosystem processes and properties that are modified by the activities of termites taken together make a strong case for considering subterranean termites keystone organisms in Chihuahuan Desert ecosystems. Termite consumption of a large fraction of the input of dead plant material and dung affects spatial patterns of soil organic matter and spatial variability in macroporosity resulting from foraging galleries. Soil turnover and nutrient turnover resulting from construction of surface galleries and sheeting further contribute to variation in water infiltration, water storage, and soil nutrient concentrations. This spatial variation in soil water content and nutrients affects the species composition and productivity of the plant community.

The Roles of Soil Microfauna in Decomposition

Although termites and other macroinvertebrates are the primary processors of dead plant materials that remain on the soil surface, the decomposition of roots and litter that is buried occurs through the interactions of a complex of soil micro- and mesofauna and the microflora. Plant materials trapped in animal-produced pits may be buried by windblown soil or by runoff water sediment (Steinberger and Whitford 1983a). The decomposition and nutrient mineralization of buried materials and dead roots differs greatly from the processing of plant materials retained on the soil surface. Soil microarthropods, especially prostigmatid mites (Tydeidae and Tarsonemidae), contribute significantly to

the decomposition of buried litter (Santos and Whitford 1981). When microarthropods were eliminated from decomposing litter by an insecticide, decomposition rates were significantly reduced.

Because of their importance in decomposition and mineralization processes, a number of studies examined temporal variation in community composition and abundance of soil microarthropods. Experimental studies of timing and characteristics of rainfall, the characteristics of leaf litter accumulations on composition, and abundance of soil microarthropods and other soil invertebrates were conducted by irrigation studies and by use of rain-out shelters. Microarthropod abundance on decomposing roots was relatively independent of rainfall (including supplemental irrigation) (Whitford et al. 1988b). The prostigmatid mite genera that were most abundant in the vicinity of shrub roots and herbaceous plant roots were the same genera associated with the live roots of mesquite. The abundance of microarthropods associated with decomposing roots peaked in the warm-wet season (July–September) and decreased dramatically as soils cooled to minimum annual temperatures. Breeding activity in Chihuahuan Desert mites coincides with the summer rainfall season (Wallwork et al. 1986). The seasonal breeding pattern was not affected by irrigation during other seasons of the year. The strict seasonality of reproduction in mites was interpreted as an outcome of strong selection pressure to recruit only when food quality and quantity is maximal and when soil microclimate is most favorable. One species, Joshua's orabitid (*Joshuella striata*), which is widely distributed species found in summer and winter rainfall deserts of North America,

produced eggs in response to winter rainfall and during the summer wet season

(Wallwork et al. 1986).

Because soils dry rapidly after small rain events, protozoans and nematodes that

are active only in water films on soil particles encyst or enter anhydrobiosis. In desert

soils, protozoans and nematodes are in an inactive state most of the time because soils are

at soil water potentials of approximately –6.0 MPa much of the year (Whitford 1989).

Approximately 50% of the protozoan population is encysted at a soil water potential of –

0.1 MPa, and virtually the entire protozoan population is inactive at –0.4 MPa (Whitford

1989). Ninety-nine percent of the nematode population is anhydrobiotic at water

potentials between –3.0 MPa and –5.0 MPa (Freckman et al. 1987). Therefore, in Jornada

desert soils, taxa of soil microarthropods are the only active microfaunal component of

soil food webs during much of the year.

The Roles of Granivores and Native Herbivores

The removal of seeds by vertebrate and invertebrate granivores was recognized as a

potentially important ecosystem process early in the Desert IBP program. Studies of seed

consumption, effects of granivory on the seed bank, and the impacts of various groups of

granivores on vegetation composition have produced clear answers regarding the

significance of granivory on desert ecosystems.

Seed consumption by ants (*Pheidole* spp. and *Pogonomyrmex* spp.) was estimated

by collecting the booty of returning foragers and counting the rate of return of foragers to

the nests (Whitford 1979; Whitford et al. 1981a). The numbers of seeds transported to ant

nests were compared to the estimated seed production by the plants in the area. The three species of *Pogonomyrmex* harvester ants harvested varying percentages of the monthly seed production of the dominant forbs and annual grasses. For example, the harvester ants harvested approximately 100% of the seed production by the annual grass six weeks grama (*Bouteloua barbata*) in August but only 32% of the seeds of this annual grass in September (Whitford 1979). The seeds of six weeks grama and four species of forbs (desert marigold [*Baileya multiradiata*], mealy goosefoot [*Chenopodium incanum*], Abert's buckwheat [*Eriogonum abertianum*], and little desert trumpet [*Eriogonum trichopes*]) accounted for most of the seeds harvested by harvester ants. Large *Pogonomyrmex* harvester ants concentrated their seed harvesting activity in the summer months (June–September), and small *Pheidole* harvesters concentrated their seed-harvesting activity in the late summer and early autumn (August–November). *Pheidole* harvested nearly 10 times more seeds than were harvested by *Pogonomyrmex*. It was estimated that *Pheidole* harvested 3.44×10^8 seeds/ha in creosotebush communities on a bajada, 3.11×10^8 seeds/ha in a mesquite Mormon tea community at the base of a watershed, and 9.7×10^8 seeds/ha in a black grama grassland community. *Pheidole* collected large quantities of seeds from fluff grass (*Tridens* [*Erioneuron*] *pulchellus*). However, there were large differences in the percentages of grass seed collected by the two most abundant species. More than 50% of the seeds collected by small militant harvesters (*Pheidole militicida*) were seeds of annual forbs, whereas ~ 75% of the seeds collected by small arid harvesters (*Pheidole xerophila*) were grass seeds (Whitford et al. 1981a). Based on these studies, it was concluded that small seed-harvesting ants had a

larger effect on the seed reserves than did the larger harvester ants and that ants consumed a significant fraction of the seed production of some species of grasses and annual forbs.

The impacts of herbivory by native animals differ from those of livestock, especially with regard to shrubs. Observations on the large numbers of terminal stems that were killed by girdlers or node borers led to a study that examined the effects of stem girdlers and node borers on the growth of mesquite (Whitford et al. 1978a). Stems killed by Bostrichids represented approximately 1% of the total stem biomass and between 1.4% and 53.4% of the leaf biomass of the shrubs sampled. Twig girdlers (*Oncideres rhodisticta*) killed stems on 45% of the mesquite shrubs on the site. The girdled mesquite stems provide oviposition sites and larval development sites for a number of other insects: buprestid, cerambycid, clerid, and scolytid beetles, as well as some butterflies and moths (*Lepidoptera* spp.). Scolytid beetle larvae were the most abundant insect larvae found in one- and two-year-old girdled stems of mesquite (Whitford et al. 1978a). Simulated girdling of 40–80% of the appropriate size branches of mesquite demonstrated that there was no reduction in shoot and leaf growth in either natural or simulated girdled plants in comparison to ungirdled controls. Girdling has the effect of pruning mesquite plants and stimulating growth of new stems from lateral nodes below the girdle. The removal of terminal stems of creosotebush by rabbits results in compensatory growth with several stems originating from below the severed stem (Whitford 1993). Creosotebushes that are pruned by rabbits on a regular basis develop a dense canopy and a hemispherical morphology.

Predator Ecology

Autecological studies of predators can provide information about the regulation of herbivore, granivore, and detritivore guilds and the structure of food webs (Polis 1994). In this regard, studies of coyotes (*Canis latrans*) would have been extremely useful, but such studies were not advisable at the Jornada because coyotes were subjected to control practices until the late 1980s. Recent studies of coyote behaviours have been limited and of short duration, though still insightful (Windberg et al. 1977).

Among other predators, the most abundant avian insectivore in the Jornada shrublands is the black-throated sparrow (*Amphispiza bilineata*). Black-throated sparrows nest from early April through the summer. The adult birds forage intensively to feed the chicks. Zimmer (1993) reported that when creosotebush and tarbush were flowering, there was an increase in abundance of foliage arthropods. Black-throated sparrows are opportunistic predators. Following summer rains that stimulated the emergence of termite alates (winged reproductives) the sparrows shifted to termites and brought loads of 3–10 alates per trip to the nest. When there was an unusual emergence of mydas flies (Mydidae), for about one week the mydas flies became the second most frequent prey item. In black-throated sparrows, the clutch size was regulated by prey availability. Clutch sizes were larger in years when grasshoppers were abundant. Approximately one-third of the clutches were lost to predators (Zimmer 1993).

The only large raptor that breeds in the Jornada Basin is the Swainson's hawk (*Buteo swainsoni*). Average density of nesting pairs during the summers of 1974 and

1975 was one pair per 9.4 km^2 (Pilz 1983). Forty-eight percent of the hatchling hawks fledged in 1974, and 72% fledged in 1975. The average number of chicks produced per nest was 2.4–2.5. Prey items brought to the chicks were 55% reptiles (22% of the biomass). Small mammals accounted for 42% of the prey items but accounted for 79% of the prey biomass. The most frequent prey were horned lizards, which were 14% of total prey items but only 7% of the biomass, and western whiptails, which were 33% of the total but only 8% of the biomass. Rabbits (jackrabbits and desert cottontails) accounted for 36%; spotted ground squirrels, 19%; banner-tailed kangaroo rats, 15%; and lizards, 14% of the prey biomass brought to the nestlings. Other mammals taken by Swainson's hawks included Ord's kangaroo rats, packrats and woodrats (*Neotoma* spp.), and hispid cotton rats. Other reptiles included the lizards (round-tailed horned lizard, long-nosed leopard lizard, and desert spiny lizard), and the snakes (glossy snake [*Arizona elegans*] and coachwhip [*Masticophis flagellum*]). The variety of prey taken by these hawks suggests that predation by Swainson's hawks has little effect on the abundance of the prey species.

The abundance of ants in the Chihuahuan Desert supports specialized predators: horned lizards of the genus *Phrynosoma*. Texas horned lizards were reported to feed mostly on two species of harvester ants, *Pogonomyrmex rugosus* and *P. desertorum* (Whitford and Bryant 1979). Although the average number of ants taken per feeding stop (15) was higher when lizards were positioned near nest disks or near columns of foragers (feeding stops, 14), horned lizards made more feeding stops (46) in areas not associated with nests or columns of foragers (average per feeding stop = 4.7). Individual Texas

horned lizards consumed between 30 and 100 ants per day. Simulated predation on rough

harvester ant and desert harvester ant colonies revealed that colonies losing

approximately 25% of the estimated forager population ceased foraging for up to five

days. It was concluded that horned lizard densities are regulated by the abundance and

productivity of *Pogonomyrmex* ants. Round-tailed horned lizards are considerably

smaller than Texas horned lizards and select much smaller ants as their primary prey.

The most dependable prey for round-tailed horned lizards were honey-pot ants (Shaffer

and Whitford 1981). Hairless honey-pot ants and mimicking honey-pot ants

(*Myrmecocystus depilis/mimicus*) collected honey dew and leaf exudates from mesquite.

Round-tailed horned lizards consumed foragers returning from the shrub canopy. The ant

species composition of *P. modestum* changed its diet following summer rainfall and

increase in activity of ants other than honey-pots. Species of large harvester ants, crazy

ants, small seed harvesters, and long-legged ants contributed a significant proportion of

the round-tailed horned lizard's diet during the warm-wet season. Other Chihuahuan

Desert lizards that exhibit extreme prey specialization are the western whiptails and other

whiptail (*Cnemidophorus*) species. On the Jornada, western whiptails and checkered

whiptails are very effective in finding termites by rooting through leaf litter under shrubs

(personal observation). At the Mapimi Biosphere Reserve in the southern Chihuahuan

Desert, termites accounted for 79% of all of the prey items in the stomachs of whiptails

(Barbault et al. 1978).

Possibly the most important predator–prey interactions are those in the detrital

food webs in the Chihuahuan Desert. One of the most unexpected findings in studies of

the soil microfauna was that soil mites of the family Tydeidae fed on nematodes and

depressed nematode numbers (Santos and Whitford 1981). Nematophagy by soil

microarthropods has since been reported as common in short-grass steppe and in the

Rocky Mountains (Walter 1988). Many microarthropod species that were thought to be

mycophagous were found to be omnivorous. Omnivorous and predaceous mites that prey

on bacteriophagous, fungivorous, and omnivorous nematodes are key elements in detrital

food webs (Elliot et al. 1988).

The Relationship of Native Animals to Desertification

In the Jornada Basin, the transformation of desert grasslands to honey mesquite coppice

dunes, mesquite-grass mosaics, tarbush shrubland, and creosotebush shrubland (chapter

10) has had a number of effects on animal populations and on the processes and

properties that they affect. Studies of rodent and rabbit populations in the Jornada Basin

have consistently documented low abundance and species diversity in desert grasslands

and higher abundance and diversity in the desertified shrublands (Wood 1969; Whitford

1997). This consistency is remarkable considering that the studies cover a span of 40

years with considerably different rainfall and productivity patterns in the years preceding

the trapping studies. Studies of rodent populations were initiated in the 1960s because

"their populations can represent a large portion of the vertebrate weight, or biomass, of an

area and often impose a greater impact on the community than the more conspicuous

game or livestock species" (Wood 1969). Wood's study suggested that feedbacks

between vegetation change and rodent community structure could contribute to

maintaining desertified ecosystems in a stable, altered state. Wood (1969) reported the rodent biomass in mesquite coppice dune areas (0.72 kg/ha) was double that of the black grama grassland (0.35 kg/ha). Although species populations fluctuated throughout the study (1960–63), the mean rodent biomass in the grassland and other communities sampled remained stable. The rodent biomass in the mesquite coppice dune site, however, fluctuated from a high of 0.94 kg/ha to a low of 0.60 kg/ha.

The spatial and temporal variation in rodent populations may exacerbate the desertification processes and contribute to the irreversibility of the desertified state (Whitford 1993). In places and times of high rodent abundance, rates of herbivory and graminivory may increasingly constrain grass seed production even as grass cover declines (Dabo 1980; Kerley et al. 1997). Rodent cache pits and soil disturbances, on the other hand, may increase the germination rates of some grass species. Thus it is possible that the activities of animals may produce either positive or negative feedbacks on the ecosystem structure, but it is not yet clear which of these effects is most important.

Conclusions

Taken together, the body of research on animals at the Jornada reveals three intriguing patterns; (1) patterns of shrub cover and water redistribution are dominant elements structuring the environments of Chihuahuan Desert animals, (2) feedbacks from animals influence nutrient availability and plant demography via several direct and indirect pathways, and (3) the contributions of native animals to desertification remains unclear.

The idea that variation in habitat complexity and differentiation is important for animal diversity is well established in ecology, but this idea has seldom been connected to desertification. Although certain species are associated with grasslands, data for several taxa indicate that shrubs play a positive role for animal diversity (table 12-2) despite the suggestion that shrubs do the opposite (Muldavin et al. 2001).

The role of water redistribution patterns in creating habitat differentiation is less well understood but has important contributions to the development of arroyo vegetation and ephemeral water bodies used by distinct animal groups. Because run-off is increased as grass cover declines, it is possible that grassland degradation has accentuated habitat differentiation in some cases. The relationship of conventional notions of degradation to biodiversity involves several mechanisms and is not always clear cut (Bestelmeyer et al. 2003b).

The importance of animals for nutrient flux and other feedbacks to ecosystem properties lends support to Chew's hypothesis. This is especially true of termites and the detrital pathway, as has been found in other desert systems (Stafford Smith and Morton 1990). Perhaps more remarkable is the diversity of indirect pathways that has been uncovered (table 12-2). Only through detailed studies of natural history could such diversity be revealed. These observations also suggest a further modification to Chew's hypothesis: A given taxon may have more than one important effect on ecosystem properties (e.g., limiting N availability but increasing infiltration). The consequences of these effects for plants and soils may reinforce or counteract one another to varying

Table 12-2. A summary of the key relationships described in this chapter, including the effects of variation in ecosystem structure on different taxa or functional groups as well as the feedbacks exhibited by taxa on ecosystem properties.

Taxon/functional group	Effect of ecosystem structure	Feedbacks to ecosystem
Rodents and lagomorphs	Increased density in shrublands	Graminivory, herbivory reduces grass reproduction
		Foraging pits favor seed germination for some grasses
Birds	Increased density/richness in shrublands	Redistribute grass seeds (natives and exotics)
	Arroyo vegetation used by some species	
Lizards	Increased density/richness in shrublands	Consumption of ants and termites
Anurans	Positively affected by water redistribution	Redistribute nutrients to surrounding watershed in their bodies
Ants	Additional species in shrublands	Granivory effects on plant reproduction
		Nutrient concentration in nests and soil patchiness
		Bioturbation and vertical redistribution in soils
		Food for specialist predators (*Phrynosoma*)
Termites	Ubiquitous except in inundated areas	Rapid breakdown of roots, litter, and dung
		Reduce soil carbon and N mineralization rates
		N fixation via hindgut symbionts
		Increase macroporosity and water infiltration
Phytophagous insects	Specialized to shrubs	Frass locally alters nutrient availability
Macro-detritivores	Species sort among grasslands/shrublands	Decomposition of litter
Microarthropods	Track litter amounts, but ubiquitous	Regulate fungi and N availability to plants
		Control nematode predation on bacteria, decomposition rates

degrees. Such considerations are critical in establishing the true functional roles and redundancies of species in ecosystems (Rosenfeld 2002).

The multiple effects of different animal taxa for different ecosystem properties preclude simple statements about the role of animals in desertification or other landscape change. We do not have enough information to gauge the relative importance of various animal effects for plant recruitment and mortality, especially against a background of livestock grazing, historical legacies, and soil and climate variability. Nonetheless, the research summarized here allows us to frame the next generation of questions much more effectively.