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Diversity, Spatial Variability, and Functional Roles of Invertebrates in Desert Grassland Ecosystems

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Any analysis of the community structure and functional roles of desert grassland invertebrates is constrained by the fact that there are few, if any, patches of grasslands undisturbed by humans and their domestic livestock. The desert grasslands currently exist as scattered patches surrounded by large expanses of desert scrub or as a grassland matrix with shrubs. Much of the area that was desert grassland in the 1850s is now classified as desert scrub (Buffington and Herbel 1965; York and Dick-Peddie 1969). Further, the remaining desert grassland remnants are diverse in terms of soil characteristics and grass species composition. In some areas, exotic introduced grasses have become dominant; in others, remnant grasslands are dominated by species of grasses that are relatively unpalatable to domestic livestock.

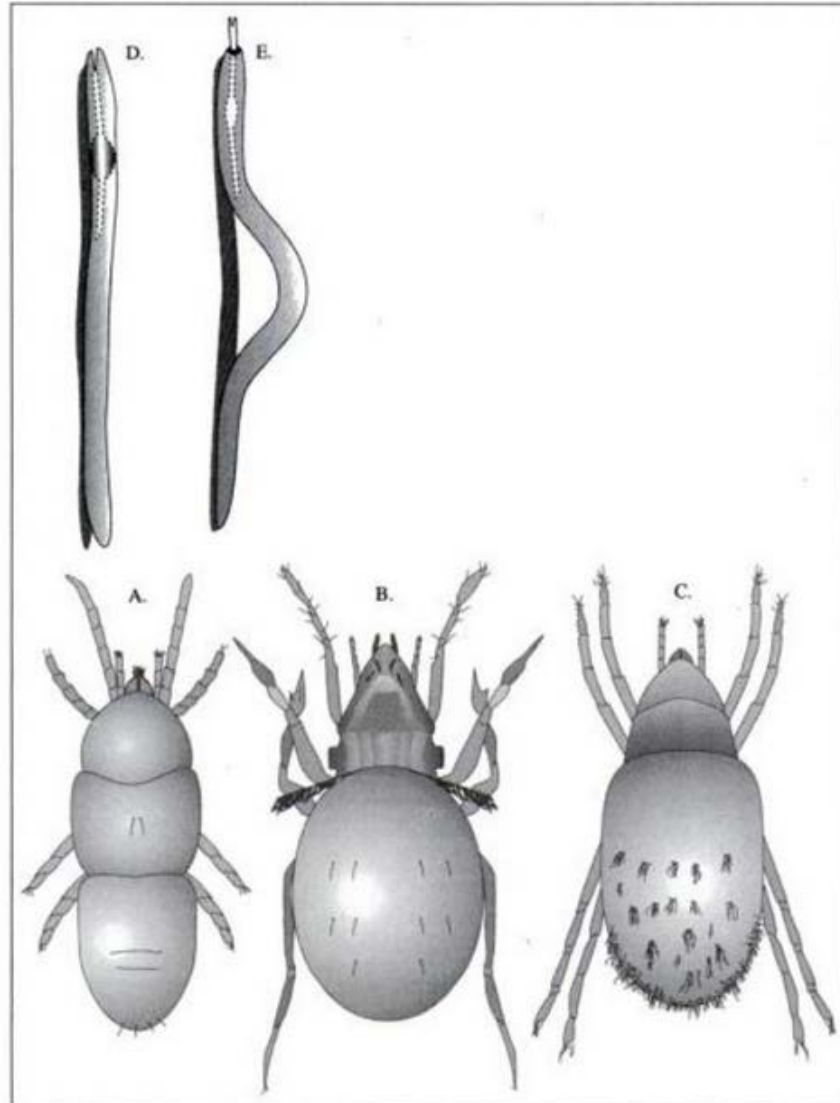
The invertebrate fauna of desert grasslands is incredibly diverse and includes several phyla. While mammal, bird, reptile, and vascular plant species occur in the tens to hundreds, invertebrate species in desert grasslands number in the thousands or tens of thousands, and many of the less conspicuous species have never been described by taxonomists. Much of this fauna is never seen by the casual observer. If you were asked, "What invertebrates did you see on your morning walk in the desert grassland?" your

response would probably be "ants." Ants are the most conspicuous and, along with unseen subterranean termites, the most numerous macroinvertebrates in arid environments. However, the fauna of desert grasslands includes many microscopic organisms and many large but cryptic species as well as the obvious and familiar ones (Crawford 1981; Wallwork 1982). Most of what we know about desert grassland invertebrates and their general life history characteristics is based on data from economically important species (Crawford 1981).

The Invertebrate Fauna of Desert Grasslands

Protozoans (single-celled animals that feed on bacteria and single-celled plants) populate the soil of all desert grasslands, but practically nothing is known of their distribution and biology. Naked amoebae predominate, along with smaller numbers of other orders of protozoans. The abundance of protozoans in desert soils is astounding: there are 25,000 naked amoebae, 4,900 flagellates, and 700 ciliates in every gram of dry soil (Parker et al. 1984). These numbers are deceiving, however, because most of the protozoans in dry soil are encysted (in an inactive physiological state; Whitford 1989). After a rain they quickly resume activity and remain active until the soil dries and they once again encyst.

Nematodes represent another group of extremely abundant microscopic soil animals. There are approximately 100,000 bacteria feeders, 1,000 fungus feeders, 10,000 omnivore-predators, and 10–1,000 plant root feeders (root parasites) per square meter of soil (Freckman et al. 1987). Nematodes are aquatic animals confined to single-molecule-thick water films surrounding soil particles, although they are well adapted to deal with dehydration. As the water films disappear in a drying soil, the nematodes enter an inactive state called anhydrobiosis, which is immediately reversible when the soil is wetted. Anhydrobiotic nematodes can survive desiccation for days to years at any stage of their life cycle. Despite the ubiquity of free-living nematodes, however, there have been few studies of their ecology, and many species are undescribed. Nematodes are often classified into feeding groups based on their morphology. The bacteria-feeding forms have a muscular buccal pump (a structure in the throat region) and a sucking mouth. The fungus feeders have oral stylets (hypodermic needle-like mouthparts) with which they pierce the fungal hyphae and suck out the cellular contents (fig. 6.1). The stylets and modified mouths of the omnivore-predators allow them to feed on fungi and other nematodes.



The soil mites (Acarina) are the smallest of all the arachnids—the group that contains spiders and their relatives. Most mites are large enough to be visible to the unaided eye (about the size of grains of ground pepper) but not large enough to allow determination of their morphological characteristics. The mite fauna in desert grassland soils includes more than 30 families and 100 species (Cepeda-Pizarro and Whitford 1989). The most abundant are the generalist microbe feeders such as the nanorchestid and tydeid mites (fig. 6.1). Some mite species feed on nematodes as well as fungi, yeasts, and bacteria. Included in this fauna are a variety of predators

that capture and eat other mites and nematodes. The most abundant mites in desert soils are prostigmatids; the soils in more mesic environments (forest ecosystems) are dominated by cryptostigmatid mites (sclerotized mites about as large as the head of a pin). The ratio of prostigmatid to cryptostigmatid mites in desert grassland soils is between 10:1 and 20:1; in forest soils this ratio is reversed. Unlike the nematodes and protozoans, soil mites do not depend on water films, and they remain active even in very dry soils (MacKay et al. 1988).

Many of the larger arachnids live in burrows or in plant litter and are active on the surface at night, and hence are infrequently seen. Among these are some of the most interesting and feared of all desert animals: sun spiders (Solifugae); vinegaroons, or whip scorpions (Uropygi: Thelyphonidae); pseudoscorpions (Pseudoscorpiones); and the true scorpions (Scorpiones). Although they occur throughout desert grasslands, their population densities are low in most settings ($<1/m^2$). In addition, a number of relatively common short-lived spiders inhabit desert grasslands. Several kinds may become locally abundant during some periods and are associated with certain plant species. For example, crab, jumping, and orb-weaving spiders are abundant on soaptree yucca (*Yucca elata*) when it flowers but are rare at other times. Tarantulas, wolf spiders, and funnel-web spiders are relatively common, occurring at densities in the tens per hectare.

The detritus-feeding millipedes (Diplopoda), represented by the large (>20 cm long, >1 g) desert millipede (*Orthoporus ornatus*: Spirostepidae) and centipedes (Chilopoda) such as the giant desert centipede (*Scolopendra heros*; up to 20 cm long), are among the largest invertebrates in desert grasslands. These animals occur at low densities except in particularly favorable habitats. Their activity periods on the soil surface are largely confined to early morning, evening, and nights during the rainy season (Crawford 1981).

Cockroaches (Blattodea), crickets and grasshoppers (Orthoptera), ant lions (Neuroptera: Myrmeleonidae), beetles (Coleoptera), butterflies and moths (Lepidoptera), flies (Diptera), bees and wasps (Hymenoptera), and true bugs (Hemiptera) make up the desert grassland insect fauna. Their numbers fluctuate over orders of magnitude depending on immediate past climatic conditions. Little is known of the life histories of most of these organisms. The few quantitative data available regarding grassland insects show biomass in the range of less than 1 mg to 16 mg dry mass per square meter; peak biomass and species diversity occur at the end of the summer

rainy season (Whitford 1974). The biomass determined by Whitford (1974) was divided among 139 kinds of insects recognized as distinct species based on morphology and included large numbers of species of beetles, flies, and plant-sucking bugs.

Life Spans and Reproduction

Desert grassland invertebrates run the spectrum of life spans, ranging from a few days to months or years. Those with the shortest life spans include protozoans, nematodes, aphids, thrips, and mirid bugs. Several groups of flies produce several generations per year whenever environmental conditions are suitable (Crawford 1981). Populations of some species of aphids increase rapidly by asexual reproduction (parthenogenesis) when high-quality food is abundant. When the quantity and quality of resources decline, they switch back to sexual reproduction. Most desert invertebrates are annual species (one generation per year), including most grasshoppers and crickets, many beetles, butterflies, moths, flies, wasps, bugs, sun spiders, and many spiders. Some species reproduce at fixed times determined by photoperiod, degree-days, or other predictable environmental cues; other species are more flexible and reproduce when environmental conditions (temperature, moisture, and food availability) approach some optimum.

Some desert grassland invertebrates—including millipedes, collembolans, cicadas, some beetles, whip scorpions, tarantulas, some wolf spiders, and scorpions—live for more than one year. They survive stress with long periods of dormancy, and their reproduction is generally coordinated with favorable environmental conditions.

Adaptations and Microhabitats

It is reasonable to classify most desert invertebrates as “avoiders,” because their behavior allows them to avoid desiccation and thermal stress (Crawford 1981). Most surface-dwelling desert invertebrates avoid physiological stress by limiting their activity to periods of the day and times of the year when the physical environment is relatively benign. Generally they are nocturnal, sometimes extending their activity to the early morning hours when temperatures are still moderate. During the driest and hottest periods these animals escape the lethal conditions of the soil surface by entering burrows in the soil where relative humidities remain above 90 percent

and temperatures rarely exceed 35°C. Invertebrates that live in the vegetation canopy are not exposed to the high temperatures found on the soil surface. The temperature in the canopy half a meter above the soil surface will remain at 40°C when the midday soil surface temperature is above 60°C. Grass canopies do not provide the microclimatic moderation that shrub canopies provide. This may be one reason why arthropods are generally more abundant and diverse in desert scrub than in grassland.

Desert macroinvertebrates exhibit few unique physiological specializations, although some arthropods have an epicuticle that reduces the loss of water through the cuticle, and some can absorb water from moist surfaces (Crawford 1981). The other physiological and morphological features that allow invertebrates to survive in deserts, such as their water-conserving excretory physiology, are not limited to invertebrates that inhabit deserts, and hence do not represent special adaptations.

Jornada del Muerto Basin Study Area

Much of the data presented in this chapter was collected on sites in the Jornada del Muerto Basin (32°30' N, 106°45' W) 40 km north-northeast of Las Cruces, Doña Ana County, New Mexico. The basin lies between 1,300 and 1,350 m elevation at the northern edge of the Chihuahuan Desert. The desert grasslands of the Jornada are structurally similar to those in southeastern Arizona and have had a similar history of land use and vegetation change (Bahre, this volume; McClaran, this volume). Data from this area should therefore also apply to desert grasslands in northern Mexico and southeastern Arizona in terms of species composition and functional attributes of faunal assemblages.

The data were collected in a number of different types of desert grasslands. The black grama (*Bouteloua eriopoda*) grasslands remain as remnant patches in the basin floor on sandy to sandy loam soils (fig. 6.2) and on montane piedmonts, or bajadas. The most extensive grasslands are areas dominated by a variety of relatively short-lived perennial grasses such as dropseeds (*Sporobolus* spp.) and threeawns (*Aristida* spp.) on sandy soils. The dominant shrubs in these areas are honey mesquite (*Prosopis glandulosa*) and creosotebush (*Larrea divaricata*). Many of the data on invertebrates in this grassland habitat were collected on the lower slopes of a watershed. A number of desert grassland habitats are located on clayey soils, including playa lake basins dominated by vine mesquite (*Panicum obtusum*) and swales



Figure 6.2. An ungrazed black grama (*Bouteloua eriopoda*) and mesa dropseed (*Sporobolus flexuosus*) grassland viewed from inside a grazing enclosure in the Jornada del Muerto Basin, Doña Ana County, New Mexico.

dominated by tobosa (*Hilaria mutica*), alkali sacaton (*Sporobolus airoides*), and burrograss (*Scleropogon brevifolius*) (fig. 6.3). The dominant shrub on clayey soils is tarbush (*Flourensia cernua*).

Diversity and Biology of Selected Groups

The soil biota. The biota of desert grassland soils is very similar to that of other water-limited subtropical ecosystems; any differences are likely related to the basic energy source for the food web. In desert grasslands, most of the energy-releasing decomposition occurs when the grasses are in the standing-dead state, not as leaf litter on the soil surface, and the basic energy source for soil food webs is thus the dense root systems of desert grasses. Invertebrates that live in litter layer patches under shrubs in desert scrub are not present in the desert grassland.

The biota of the soil food web includes bacteria and fungi, the primary

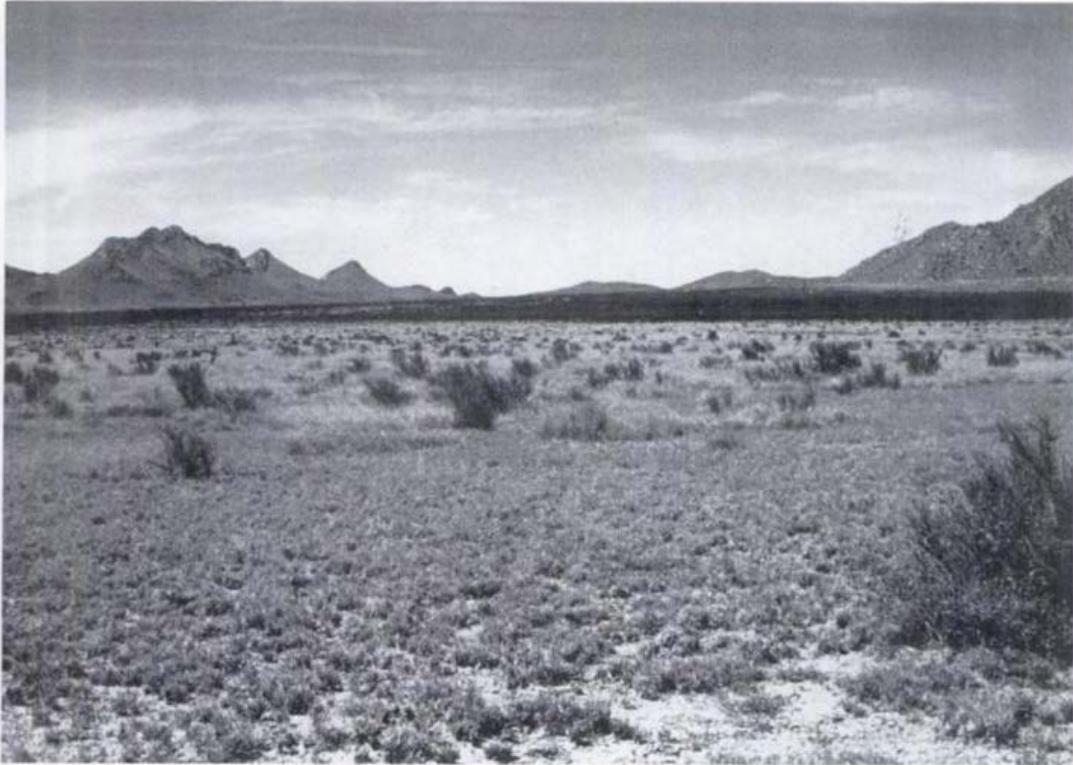


Figure 6.3. A burrograss (*Scleropogon brevifolius*) and tobosa (*Hilaria mutica*) swale on the Jornada Experimental Range, Doña Ana County, New Mexico. The burrograss is the short grass in the foreground; the tall grass in the background is tobosa.

consumers of dead and dying roots (fig. 6.4). This microflora provides the energy base for the soil microfauna: protozoans, nematodes, mites, collembolans, and insect larvae. The rhizosphere (the cylinder of soil immediately adjacent to a root) microflora is dominated by fungi that serve as food for the microfauna. Stanton (1988) reported that between 16 and 26 species of fungi served as the substrate for the microfauna in a semiarid grassland in Colorado. The rhizosphere microfauna was dominated by protozoans, which were estimated to occur in the hundreds of millions per square meter of soil (Stanton 1988). Microarthropods (microscopic mites and insects) occur at much lower densities than protozoans and nematodes (tables 6.1 and 6.2).

Most of the dominant species of microarthropods in the rhizosphere of desert grasses feed on both fungi and nematodes. Except during the brief periods following rains, most of the soil microfauna exists in an inactive state. As soils dry, the protozoans encyst, nematodes and collembolans

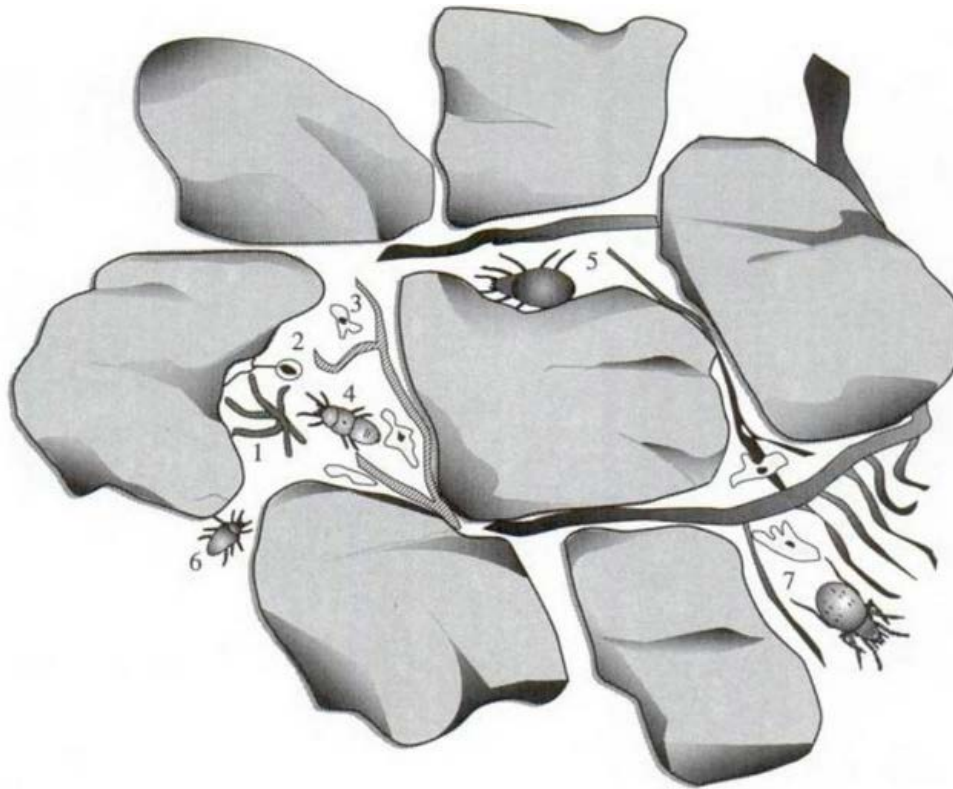


Figure 6.4. Microscopic view of the soil biota in a desert grassland soil: (1) bacteria-eating nematodes, (2) flagellate protozoan, (3) naked amoeba, (4) fungus-eating mite, (5) predatory mite, (6) collembolan, and (7) oribatid mite.

Table 6.1. Soil microarthropods extracted from rhizospheres of native black grama (*Bouteloua eriopoda*), introduced Lehmann lovegrass (*Eragrostis lehmanniana*), and unvegetated soil between grass clumps.

Taxon	<i>Bouteloua eriopoda</i>	<i>Eragrostis lehmanniana</i>	Unvegetated
Microbe-eating mites	14,109	11,343	7,124
Predatory mites	577	796	398
Collembola	816	1,890	298
<i>Speleorchestes</i> spp.	2,189	1,512	1,612
Tydeidae	4,597	4,995	2,334
Prostigmata/Cryptostigmata	17	23	42

NOTE: Data are numbers per square meter in the upper 10 cm of soil.

Table 6.2. Population densities (no./m²) of soil microarthropods in areas grazed by domestic livestock in summer or all year versus densities in ungrazed exclosures.

Taxon	Summer Grazing Only		Yearlong Grazing	
	Grazed	Exclosure	Grazed	Exclosure
Collembola	5,975	3,781	716	915
Microbe-eating acari	8,915	9,910	13,452	9,194
Predatory acari	358	398	796	159
<i>Speleorchestes</i> spp.	876	1,552	2,145	2,706
Tydeidae	1,353	3,144	2,985	3,065
Prostigmata/Cryptostigmata	21	33	19	4

become anhydrobiotic, and some species of soil acari enter a cryptobiotic (literally, "hidden life"; inactive but not dead) state (Whitford 1989). Thus, during most of the year the active component of the desert grassland soil biota consists of a few species of mites feeding on fungi (MacKay et al. 1987; Whitford 1989).

The abundance of soil microarthropods depends on the availability of food. Microarthropods are twice as numerous in soil cores collected from the rhizospheres of perennial grasses than in cores from unvegetated patches between grass clumps (table 6.1). There are no obvious differences in the abundance and diversity of microarthropods extracted from the rhizosphere of the native black grama grass and those from introduced Lehmann lovegrass (*Eragrostis lehmanniana*) (table 6.1). Apparently there is little difference between the quality or quantity of organic matter available to the soil microarthropod fauna in the rhizospheres of native grasses and introduced grasses. A similar relationship was apparent in soil core data from grazed and ungrazed grasslands (table 6.2). The absence of differences among sites suggests that vegetation composition has little effect on soil microarthropods.

Ants. Ants are the most conspicuous invertebrates in many ecosystems, and this generally holds true for desert grasslands as well. Most desert grassland ant species are diurnal and frenetically active when food supplies are available. They tend to be either seed harvesters or omnivores, although even the species usually classified as seed harvesters are omnivorous to some ex-

tent (Whitford 1978a,b). The nests of desert grassland ants tend to be conspicuous and abundant. The construction and maintenance of the subterranean nests affect the structure and function of desert grassland ecosystems by altering soil nutrient distribution and water infiltration.

A variety of techniques can be used to estimate the density, species composition, and activity patterns of ants. Colony densities can be estimated by recording their presence in randomly placed quadrants, in belt transects, or by plotless techniques (Whitford 1978b). Qualitative information can be obtained by using bait boards, seed trays, and pitfall traps. The data reported in this section were obtained using all of these methods, depending on the question being addressed and the suitability of the technique for use in the particular habitat.

The species composition, species richness, and density of ant colonies in desert grasslands depend on the landscape and soil characteristics. Grasslands at the lowest elevations are generally characterized by clay to clay-loam soils. These heavy soils with their characteristic low infiltration rates frequently have standing water on the surface for several days to several weeks following large rainfalls. Periodic flooding plus the resistance of clayey soils to excavation eliminates many ant species as potential residents of these areas.

Alkali sacaton, burrograss-tobosa, and tobosa swales characteristically have few species and low densities of ants (table 6.3). On the Jornada del Muerto, the lowest species richness was found in alkali sacaton swales, where the clay soils have a high gypsum content. The only ant species we found was the crazy ant (*Conomyrma insana*), a small (worker length 2.5–3.8 mm) ant found in every grassland habitat we examined. The crazy ant colonies appear to be small (<500 workers) and exhibit rapid colony turnover. Crazy ants are dietary generalists that collect honeydew and cadavers of small arthropods, a characteristic that allows them to colonize extremely marginal habitats.

Of the low-elevation, clayey soil habitats we examined, the highest species richness was in the burrograss-tobosa basin, where microtopographic relief allows species to construct nests whose shallow chambers are above ponded floodwater levels (table 6.3). The nests of hairless honeypot ants (*Myrmecocystus depilis*) were in clumps of grass between 5 and 10 cm above the crusted ponding areas. In the low, crusted areas, several crazy ant colonies had constructed cemented mud chimneys 1–3 cm tall around the nest entrance holes to prevent water from inundating the nests. Because rainfalls in this region are usually less than 2.5 cm, a 3-cm-tall chimney will

Table 6.3. Densities of ant colonies per hectare in a variety of grassland habitats in the Jornada del Muerto Basin of the northern Chihuahuan Desert, Doña Ana County, N.M.

Ant Species	Grassland Habitats					
	AS	TS	BG	BT	BGDN	BGDS
<i>Aphaenogaster cockerelli</i>	0	0	6	0	0	0
<i>Conomyrma bicolor</i>	0	0	250	20	0	0
<i>Conomyrma insana</i>	71	50	117	340	1,639	1,282
<i>Crematogaster depilis</i>	0	0	267	0	0	0
<i>Iridomyrmex pruinosum</i>	0	50	150	0	0	0
<i>Myrmecocystus depilis</i>	0	0	2	20	0	0
<i>Pheidole desertorum</i>	0	0	333	0	0	0
<i>Pheidole xerophila</i>	0	0	33	0	0	0
<i>Pogonomyrmex desertorum</i>	0	0	33	0	181	100
<i>Pogonomyrmex rugosus</i>	0	17	2	0	0	0
<i>Pogonomyrmex texanum</i>	0	0	0	20	0	0
<i>Solenopsis krockowi</i>	0	0	0	100	0	0
<i>Solenopsis xyloni</i>	0	0	33	0	28	17

NOTE: AS = alkali sacaton swale, TS = tobosa swale, BG = bunchgrass grassland, BT = burrograss-tobosa basin, BGDN and BGDS = black grama-mesa dropseed grasslands.

prevent most flooding. The chimneys were found in areas surrounded by honey mesquite coppice sand dunes, which have little if any runoff.

The largest number of ant species (11) were in bunchgrass grassland on the lower slopes of a watershed (table 6.3), although the density of nests was not as high as in black grama grassland in the basin, where crazy ants were abundant. Most of the colonies in the bunchgrass grassland were seed-harvesting ants. In this habitat, seeds of a wide range of sizes and qualities from the abundant annual plants add significantly to the small seeds of grasses. Small seed-harvester ants (*Pheidole* spp.) and desert fire ants (*Solenopsis xyloni*) foraged primarily on small grass seeds, while harvester ants (*Pogonomyrmex* spp.) preferred the larger seeds of annual dicots and grasses (Whitford 1978a; Whitford et al. 1981). Species richness was low in the sandy soils of the basin black grama grasslands, where nests of only three species were recorded (table 6.3).

Comparisons of species richness among these habitats must be made with caution because the data were collected only in early summer, not over a full year, and the activities of ant species vary seasonally and within seasons (Whitford 1978b). Small seed-harvester species and desert harvester ants (*Pogonomyrmex desertorum*) are likely to be underrepresented in early-summer samples.

Seed-harvesting ants divide seed resources in a variety of ways. The black desert harvester ant (*Pogonomyrmex rugosus*) constructs large, permanent nests with several thousand workers per colony and forages primarily in groups or columns. Group foragers leave the nest and follow a discrete trail for some distance from the nest to collect seeds. Foraging trails are easily recognized by the stream of ants going toward and away from the nest. Other species, including desert harvester ants, are characterized by relatively small colonies (usually fewer than 500 workers), and individual workers search for seeds, apparently at random (Whitford and Ettershank 1975). Brown et al. (1979) suggested that these behavioral differences constrain species like the black harvester ant to forage in areas with dense seed accumulations while species that forage as individuals can exploit areas with scattered seeds.

Foraging behavior is an important variable that affects the activity time of the species and the impact of the species on seed reserves. Group foragers deplete seed resources more quickly than individual foragers (Whitford 1976). When such colonies have collected sufficient seeds to fill their granaries, they cease foraging (Whitford 1976). Satiated colonies of group foragers remain inactive aboveground for long periods even when climatic conditions are conducive to surface activity (Whitford and Ettershank 1975). Colonies of individual foragers initiate foraging activity in the spring before seed production occurs and continue to forage until weather conditions force cessation of activity in the autumn.

Ant colony entrances may be obscured in desert grasslands ungrazed by domestic livestock because the grass foliar cover may exceed 80 percent. Desert fire ants, for example, tend to build nests in the bases of grass clumps where they are difficult to detect unless a line of foragers can be traced back to the nest entrance. In these situations, species may be under-sampled if nests alone are recorded, as tests with bait showed. On the other hand, assessments of the composition and relative abundance of an assemblage of ants based on bait data must be treated with caution. The aggressive desert fire ant comes rapidly to baits and excludes other species. In our study of exclosures and grazed areas (table 6.4), the seed trays were in place

Table 6.4. Species of ants collected from seed trays in grazed and ungrazed paired plots.

Species	Ungrazed Plots				Grazed Plots			
	NW	N	S	W	NW	N	S	W
<i>Aphaenogaster cockerelli</i>	5	5	0	0	5	0	0	10
<i>Pheidole militicida</i>	10	20	0	0	10	5	25	0
<i>Pheidole xerophila</i>	0	0	0	0	0	0	5	0
<i>Pogonomyrmex desertorum</i>	5	20	0	15	20	0	0	55
<i>Pogonomyrmex rugosus</i>	10	0	0	0	5	0	5	0
<i>Solenopsis xyloni</i>	75	60	0	95	70	90	5	45

NOTES: Data are expressed as percentage of feeding stations at which a species was removing seeds (20 stations/plot). Multiple species were frequent at a single tray.

NW = northwest; N = north; S = south; and W = west.

at one location for several days before we began to record species at the trays. Desert fire ant colonies in the vicinity had collected so many seeds from the trays prior to our initial data recording that ants were no longer visiting the baits. Despite large differences in grass cover and plant species composition between grazed plots and ungrazed plots, we found no comparable differences in the ant faunas of those areas (table 6.4).

Ground-dwelling arthropods. Flightless arthropods and those with limited flying abilities make up the assemblage generally known as the ground-dwelling arthropod fauna. Most are nocturnal, especially the predatory arachnids. Grids of pitfall traps were used to sample this fauna at the Jornada del Muerto. Although a number of orders, families, and species of ground-dwelling arthropods inhabit desert grasslands, the diversity and abundance of these animals is greater in desert scrub vegetation.

A small darkling beetle (*Araeoschizus decipiens*) was the most abundant ground-dwelling beetle, but it made a relatively insignificant contribution to the ground-dwelling arthropod biomass (table 6.5). In general, tenebrionid beetle numbers decreased between 1988 and 1992, probably as a result of lower rainfall and higher temperatures in the last two years. The detritivore beetle genus *Eleodes*, which accounted for a large fraction of the biomass of ground-dwelling arthropods, has been the subject of numerous

Table 6.5. Abundances of ground-dwelling arthropods averaged for the growing season based on pitfall trap grids in two desert grasslands: black grama–dropseed basin grassland (I) and watershed bunchgrass grassland (II).

Taxon	1988		1989		1990	
	I	II	I	II	I	II
Arachnida						
Araneae	7.5	8.5	7.3	5.3	6.8	5.3
Scorpiones	6.5	5.0	7.1	6	5.6	5.3
Solifugae	5.3	5	1.3	1	0.8	1
Coleoptera						
Carabidae						
<i>Pasimachus duplicatus</i>	6	2	3	1.8	3.5	0
<i>Tetragonoderus pallidus</i>	1	2	0.5	0	0.2	0.2
Hymenoptera						
Mutilidae (3 species)	23.1	34.5	5.4	4.8	7.3	2.8
Orthoptera						
Gryllacrididae						
<i>Ceuthophilus</i> sp.	17.0	10.5	4.1	4.8	2.4	5.3
Gryllidae						
<i>Gryllus</i> sp.	2	1	6	2	1.4	5.5
Polyphagidae	5.3	3	2.4	1.3	4.6	0.5
Scarabaeidae						
<i>Canthon puncticollis</i>	0	0	0	0	0.5	1
<i>Diplotaxis</i> sp.	3.3	4	1.6	0	1.9	1
<i>Trox</i> sp.	0	0	0	0	0	1.5
Tenebrionidae						
<i>Araeoschizus decipiens</i>	165	165	33	9	15	3
<i>Eleodes extricatus</i>	14.8	23.0	6.8	1.8	3.6	0.3
<i>Eleodes gracilis</i>	4.8	4	1.1	4.3	1	2.5
<i>Eleodes hispilabrus</i>	6.5	2	2.1	0.5	0.1	0

NOTE: Numbers are average per 0.36-ha grid for each sampling season (May–October).

behavioral and physiological studies (Crawford 1981). In desert grasslands, *Eleodes* can frequently be seen feeding on the remains of seeds in the refuse piles of harvester ants. These stink beetles, or *pinacates*, often use head-standing defensive behavior when disturbed, and most individuals produce a noxious defensive secretion from their anal region.

Scarab beetles, which feed on dung, are not abundant in desert grasslands. Perhaps their scarcity is related to the virtual absence of large grazing mammals in the desert grasslands for the past 11,000 years (Parmenter and Van Devender, this volume; Van Devender, this volume). The low numbers of common dung beetles such as *Canthon* spp. may be related to climatic conditions or simply to domestic livestock management practices that shifted animals about in pastures adjacent to the ungrazed study areas. Other grassland dung beetles include *Copris* spp., *Onthophagus* spp., and *Phanaeus* spp., the latter a common bright metallic green Mexican dung beetle found in desert grasslands in Santa Cruz County, Arizona (pers. comm., T. R. Van Devender, Arizona–Sonora Desert Museum, 1993).

Members of the order Orthoptera make up the other major group of insect detritivores in the desert grasslands. These include camel crickets (Gryllacrididae; fig. 6.5), common crickets (Gryllidae), and desert cockroaches (*Arenivaga* spp.: Polyphagidae). Orthopteran populations appear to vary greatly from one habitat to the next and from year to year (table 6.5). Most burrow in the sand and are active at night. While there are no data on their food habits, most orthopterans probably feed on small plant fragments.

The remaining ground-dwelling arthropods are predators such as ground beetles (Carabidae), centipedes, scorpions, and spiders. Most predators decline in numbers during dry years (table 6.5), but the scorpions maintained a relatively constant abundance and biomass over the three years of our study, perhaps because they can reduce their metabolic rate when deprived of food (Crawford 1981) and thus are not likely to starve.

Grass canopy arthropods. Not much is known about the insects that live in or on the canopies of desert grasses, or their effects on the host plants. In a three-year study of a black grama–mesa dropseed (*Sporobolus flexuosus*) desert grassland, Ellstrom (1973) found that the peak densities of insects (78–99/m²) were 40 times lower than at a site in tall-grass prairie and 7.5 times lower than at a site in short-grass prairie in eastern Colorado. The biomass of arthropods in the desert grassland was also very low, with peaks ranging from 80 g/ha in a dry year to 3,330 g/ha in a wet year. The rela-



Figure 6.5. Camel cricket (Gryllacrididae). Photo courtesy of David Lightfoot.

tively low density and biomass of canopy-dwelling arthropods in desert grassland is a function of the variability in timing of growth and flowering of desert grasses in response to the relatively unpredictable wet season. The abbreviated growing season prevents many species of arthropods from attaining large population sizes.

Ellstrom (1973) found no consistent differences in canopy cover, arthropod densities, or biomass attributable to grazing by livestock. The lack of difference in vegetation cover and species composition probably accounted for the lack of differences in abundance and biomass of the canopy arthropods.

Populations of herbivorous arthropods increase when new vegetative biomass and flowering stalks are produced late in the growing season. The dominant herbivores in Ellstrom's study area included lace bugs (Tingidae), leafhoppers (Cicadellidae), seed bugs (Lygaeidae), and thrips (Thysanoptera) (Ellstrom 1973), but only lace bugs (*Corythucha morrilli*, *C. venusta*, and *Gargaphia opacula*) and the thrips (*Chirothrips simplex* and *Haplothrips haplophilus*) fed on black grama and other grasses. Ellstrom (1973) con-



Figure 6.7. The ground-dwelling bandwinged grasshopper (*Trimerotropis pallidipennis*) matches the soil. Photo courtesy of David Lightfoot.

foot 1985; table 6.7). The most abundant grasshopper was the bandwinged grasshopper (*Trimerotropis pallidipennis*), a widespread soil mimic found in both desert grassland and desert scrub vegetation.

Grass-dwelling grasshoppers generally feed on a variety of grasses but frequently exhibit preferences for certain species (Joern 1979a; Mulkern 1980; Mulkern et al. 1964; Ueckert and Hansen 1971). Ground-dwelling grasshoppers are generalists that feed on a variety of low-growing plants, including annual and perennial forbs, grasses (Joern 1979a; Scoggan and Brusven 1973; Sheldon and Rogers 1978), lichens, algae, and moss (Sheldon and Rogers 1978). Because these foods vary both in the time they are available and in distribution, terricoles tend to be generalist feeders.

The diversity and density of grasshoppers in arid grasslands (Uvarov 1977) primarily reflect the high diversity and the temporal and spatial distributions of their plant foods, but the long growing season and dense vegetation cover where grasshoppers can escape from predators are certainly important factors as well. Lightfoot (1985) presented evidence that predation is the major selective agent that has structured desert grassland grasshopper assemblages. He demonstrated that substrate selection for hiding was of greater or equal importance to the selection of food plants.

Table 6.8. Robber flies present in five grassland communities on the Jornada del Muerto Range, Doña Ana County, New Mexico.

Species	Grassland Community				
	Black Grama Grassland	Bunchgrass Grassland	Tobosa Playa	Isaacks Playa	College Playa
<i>Ablautus flavipes</i>	+	+			
<i>A. rufotibialis</i>		++		+	
<i>Cerotainiops abdominalis</i>		+			
<i>C. lucyae</i>				+	
<i>Dicropaltum mesae</i>			+		+
<i>Efferia apache</i>	+				
<i>E. benedicti</i>	++	++		+	+
<i>E. bicolor</i>		+			
<i>E. cressoni</i>	+	+		+	
<i>E. helenae</i>	+	+			
<i>E. kelloggi</i>		+	+	+	
<i>E. luna</i>		++		++	+
<i>E. mortensoni</i>		++			
<i>E. ordwayae</i>				+	
<i>E. pallidula</i>	++				
<i>E. pilosa</i>		++			
<i>E. subarida</i>		++			+
<i>E. tuberculata</i>				+	
<i>E. tucsoni</i>		++		++	
<i>E. varipes</i>	+				
<i>Heteropogon cazieri</i>			+	+	
<i>H. johnsoni</i>			++	+	
<i>Leptogaster hesperis</i>			+		
<i>L. patula</i>		+			
<i>Machimus nr. erythocenemius</i>					+
<i>Mallophora faultrix</i>					+
<i>Megaphorus lascrucensis</i>				++	
<i>M. prudens</i>		+			
<i>M. pulchrus</i>	+	++		+	++
<i>Metapogon punctipennis</i>		+			

Species	Grassland Community				
	Black Grama Grassland	Bunchgrass Grassland	Tobosa Playa	Isaacks Playa	College Playa
<i>Omninablautus arenosus</i>		+		+	
<i>Polacantha composita</i>				+	
<i>Proctacanathella leucopogon</i>	+	+	+	+	
<i>Proctacanthus nearno</i>	+	+		+	
<i>P. nigrofemoratus</i>	++		+		
<i>Promachus giganteus</i>		++		++	+
<i>P. nigrialbus</i>	++	++			++
<i>Psilocurus</i> sp.			+	+	
<i>Regasilus blantoni</i>				+	
<i>Saropogon coquillettii</i>	+	+			
<i>Scleropogon duncani</i>	+ ^a	++		+	+
<i>S. indistinctus</i>	++				
<i>S. picticornis</i>				+	
<i>Stichopogon fragilis</i>	+				
<i>Wilcoxia</i> nr. <i>martinorum</i>		++			
Total species	16	25	8	22	10

NOTE: ++ = common, 10 or more seen in a survey session; + = present, recorded at least once from site.

and one species (*E. benedicti*) also occur in a mesic grassland in British Columbia (Cannings 1989). The faunas are more similar than these comparisons suggest, however, because a species found in one grassland is frequently replaced by a closely related species elsewhere.

Robber fly species have characteristic and predictable flight periods. Although temperature and moisture may alter daily flight times, the adults of a given species are usually found at the same time and place each year (fig. 6.9). A few anomalous species are known; for example, *Ospricerus abdominalis*, a predator on meloid beetles, flies sporadically between May and October. *Heteropogon johnsoni* normally appears in late summer but briefly emerged following an unusually wet spring in June 1992. An undescribed species, *Psilocurus* sp., was found in the tobosa swales in June and again in

September, probably in response to rainfall.

There are three seasonal assemblages of robber flies in the desert grassland. The six species active from late winter through late spring are mostly ground perchers unable to tolerate hot summer soil surfaces; nearly all of these perch on shrubs or forbs and thermoregulate by moving between the soil surface and vegetation. Thirteen species are active from autumn through early winter. Ground-perching species—including three species of *Efferia*, *Omninablautus*, *Regasilus*, and *Wilcoxia*—are prominent in this assemblage. The greatest number of species is active in the summer, especially during the period of summer rains. These species have the largest numbers of individuals per unit area.

Shrubby grasslands have a richer robber fly fauna than grassland sites with little shrub cover. Sites with heavy clay soils usually have few flies. Clay soils are not conducive to robber fly larval success or to the growth of forbs and shrubs that attract potential prey and provide perching sites for the adults. A number of robber flies are restricted to specific areas, and some were absent from adjacent sites of seemingly identical habitat. For example, an obligate shrub-perching species, *Efferia bicolor*, was not found in the watershed bunchgrass habitat, which has little shrub cover, but was present further upslope where shrub cover was greater. The species apparently requires denser shrub cover than is present in most of the desert grasslands on the Jornada. Another species, *E. ordwayae*, seems to be restricted to tobosa grass swales with partial shrub cover. An especially localized genus comprised of three species, *Heteropogon cazieri*, *H. johnsoni*, and *H. patruelis*, was sporadically distributed through tobosa swales. The localized nature of robber fly populations in tarbush vegetation leads to distinct species assemblages in adjacent grassland sites, where these species are occasional visitors.

The reasons for the restricted distributions of robber fly populations are not understood. Perhaps a particular microhabitat provides more resources (e.g., more abundant prey, preferred prey species, and better perching sites) than an apparently similar adjacent area; or perhaps the population represents the result of a newly established (founder) or a declining relictual population. In addition, the suites of species present in an area may change along with plant composition and cover changes caused by climatic changes or livestock grazing. Interspecific interactions such as competition for prey, predation by other species of robber flies, and cannibalism may also determine the abundance or absence of a species at a site.

The diverse robber fly fauna of the desert grasslands exists because the

species partition the available resources temporally and spatially as well as behaviorally and morphologically. Intrafamily competition has been proposed as the driving force for niche separation in robber flies; it is known, for example, that differences in niche characteristics allow species to coexist in short-grass prairie (Rogers and Lavigne 1972). Fisher and Hespeneheide (1992) considered cannibalism to be a major cause of species replacements over time, although they cautioned that the overall role of adult competition in niche differentiation has not been adequately demonstrated. Most of the intraspecific competition and mortality may occur among the subterranean larvae. The larval biology is unknown for most species.

The structure of the robber fly assemblages reported here reflects the contemporary habitat. Dramatic changes have occurred in desert grasslands since the 1880s, though. Several of the dominant species, including *Efferia benedicti*, *E. pallidula*, *Promachus nigrialbus*, and *Scleropogon indistinctus*, were probably widespread and dominant members of the robber fly faunas of the desert grasslands before Europeans arrived but are not common in shrubland communities. Many desert scrub species that were formerly probably restricted to riparian areas or to shrubby bajadas have been able to colonize the grasslands because of the presence of shrubs there. The robber fly fauna of desert grasslands must be considered to be as dynamic as the plant species composition (Van Devender, this volume). Whatever the changes

that occur in plant species composition, however, robber flies will remain among the most important arthropod predators in desert grasslands.

Invertebrates of ephemeral aquatic environments. Ephemeral lake basins (playas) are common features in desert grasslands. Small playas and drainage channels are frequently modified into livestock watering tanks that capture and store runoff water. While these areas can flood at any time, flooding is most frequently the result of intense summer convectional storms that produce overland flow that fills arroyo channels. Playas can be virtually devoid of vegetation because of intense use by livestock.

A diverse invertebrate fauna populates playas and water tanks immediately after they are flooded. Loring et al. (1988) classified the aquatic invertebrates into two groups based on life history characteristics: fast onset with immediate development, including mosquitoes (*Aedes* spp.), clam shrimp (*Eulimnadia texana*: Conchostraca), and tadpole shrimp (*Triops longicaudatus*: Notostraca); and fast onset with prolonged development, including water fleas (*Moina wierzejskii*: Cladocera) and fairy shrimp (*Streptocephalus texanus*, *Thamnocephalus platyurus*: Anostraca). Clam shrimp and mos-

energy flow in ecosystems would seem to relegate invertebrates to an inconsequential status in ecosystem structure and dynamics. When the indirect effects of invertebrates on nutrient cycling processes and their direct and indirect effects on soil heterogeneity are considered, however, their importance becomes more evident. Indeed, ecosystem properties like resilience (the ability to recover following disturbance) are directly affected by the activities of key invertebrate species. Several groups of invertebrates found in desert grasslands produce nutrient-enriched, water-enhanced patches near their nests. Water infiltration, water storage, and rates of nutrient turnover are increased in such patches.

The limited data on the functional roles of invertebrates in their ecosystems are best interpreted by examining the species and species groups we know the most about. Data regarding these groups can be used to address a variety of questions about the functional roles of invertebrates in desert grasslands, including questions about the habitat specificity of the processes.

Soil invertebrates. Soil invertebrates play an essential role in decomposition and nutrient-cycling processes by feeding on bacteria and fungi. In order for microbes to grow on decomposing organic matter, most of which has a carbon:nitrogen ratio of 70–100:1, they must concentrate nutrients (especially nitrogen) in their biomass and create C:N ratios of 10–35:1 (Anderson et al. 1984). Microbes compete directly with plant roots for nitrogen and other nutrients. The accumulation of nutrients in microbial biomass, called immobilization, results in a very slow release of essential nutrients in mineral form—the form necessary for uptake by plant roots. Invertebrates that ingest microbes excrete mineral nutrients that are immediately available to plants. Additionally, invertebrates that have well-developed gut microfloras may process dead plant material rapidly and excrete minerals in a form usable by plants. Thus, by changing the relationship between immobilization and mineralization of nutrients, invertebrates have an important effect on nutrient cycling.

The population densities of nanorchestid and tydeid soil mites (fig. 6.1) vary seasonally, but not with the magnitude seen in other taxa (Cepeda-Pizarro and Whitford 1989; Steinberger and Whitford 1985). These mites are active even when the soils are dry, and they continuously graze on fungal hyphae and excrete mineral nitrogen and other elements. When mites were chemically excluded from decaying roots, significantly more nitrogen was immobilized by the fungi growing on the roots (Parker et al. 1984).



Figure 6.10. Bait roll showing surface galleries and paper eaten by subterranean termites.

Table 6.10. Organic material removed by termites versus mass lost in the absence of termites.

Material	Percentage Removed	
	Termites Present	Termites Absent
Annual plants (leaves & stems)	40–85	20–40
Annual plants (dead roots)	50–70	10–30
Perennial grass	40–80	15–25
Perennial grass roots	50–70	2–12
Creosotebush leaves	0–90	60–85
Dead wood	<1–5	—
Cattle dung	60–100	<1–4
Rabbit dung	15–50	—

SOURCES: Data from MacKay et al. 1987; Silva et al. 1989; Whitford et al. 1982, 1988; and unpublished data.

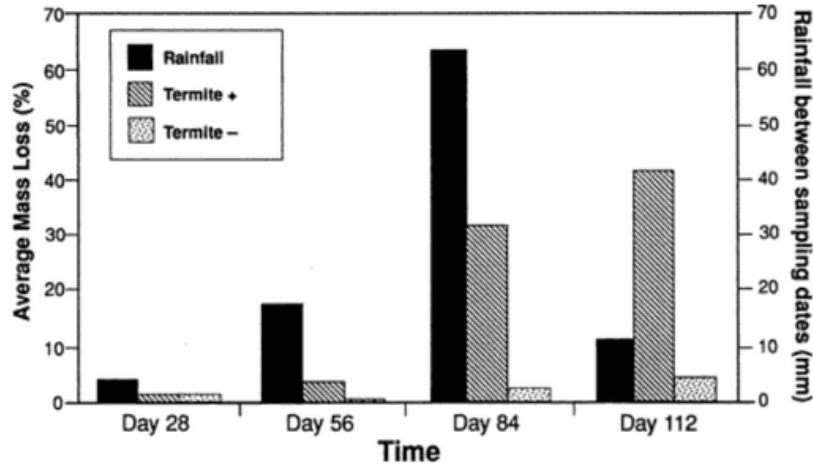


Figure 6.11. Comparison of cow dung decomposition on plots with termites present (Termite +) and excluded (Termite -).

decomposes very slowly (fig. 6.11). If subterranean termites were not present in desert grasslands grazed by domestic livestock, a considerable fraction of the soil surface would eventually be covered with dried dung (Par-

menter and Van Devender, this volume). Dried dung suppresses the growth of plants and, if a sufficiently large area is covered, reduces the productivity and carrying capacity of the ecosystem. Using Whitford et al.'s (1982) data on stocking rates and assumed defecation rates of cattle, we calculated that over a 50-year period approximately 20 percent of the soil surface would be covered by dried dung if it were not broken down by termites. A 20 percent reduction of the surface area would result in a significant loss of productivity.

When one takes into consideration all the plant litter, standing dead plant material, and feces consumed by termites, it becomes evident that 50 percent or more of all photosynthetically fixed carbon is consumed by termites (Whitford 1991). Thus, most of the cycling of carbon and other nutrients in desert grasslands is a function of subterranean termite activity. In fact, the organic matter content of soils on a desert watershed studied by Whitford (1991) was negatively correlated with the abundance and activity of subterranean termites.

Large quantities of dead plant material are consumed and broken down in the termite gut. The minerals released from that breakdown are either used by the insect or its gut microflora or are deposited as feces, often at depths below the root zone of desert grasses. Nutrients are returned to the soil via the feces, gallery sheeting, and predators. Nutting et al. (1987) found that soil brought to the surface by subterranean termites (*Gnathamitermes*

(table 6.3). Species such as the black harvester ant, the desert long-legged ant (*Aphaenogaster cockerelli*), and the hairless honeypot ant, which construct large, permanent nests, carry only small amounts of soil to the surface at the beginning of their activity period. Ants that move large quantities of soil include the crazy ant, the desert harvester ant, and the red piss ant (*Iridomyrmex pruinosum*). At the beginning of the growing season, the nest entrances of these species are easily identified by the cones of soil cleared from nest chambers (fig. 6.12). Soil movement by ants is an important factor in soil formation in several grassland habitats. An estimate of the amount of soil moved to the surface by ants in two black grama-dropseed habitats over 100 years was equal to a 1-cm layer of soil over the entire area (table 6.12). In the long term, grassland ants are cultivating the soils by transporting subsurface soil to the surface.

Nest-cone soils have a lower bulk density than intact soil and lack the surface crust that characterizes desert grassland soils, and are therefore readily eroded by wind and water. The redistribution of soils from ant nest cones by erosion has not been quantified. If there is significant wind erosion, the loss of clay-silt fractions may have a significant role in the development of the sandy soils characteristic of many desert grassland sites.

The seed-harvesting and consumption activities of desert ants have important implications for the area's vegetation, although there are few unequivocal data that demonstrate the impact of seed harvesting on the ecosystem. The exceptions are the studies by Brown et al. (1979), Davidson et al. (1984), and Inouye et al. (1981). Long-term studies showed that ants increase the plant species diversity by differentially harvesting the seeds of the dominant species. On plots where ants had been removed, ephemeral plants with small seeds dominated the community. Over the long term, however, the ephemeral plant assemblage exhibited density compensation, and this decline in the ephemerals shifted the assemblage back toward the original condition. Although seed harvesting by ants apparently affects the composition of the vegetation, especially ephemeral plants, harvesting does not result in the severe depletion of seeds that might be expected.

Yucca moths. Soap tree yucca, the tallest plant in many desert grasslands, is an important structural feature that provides nesting sites and perches for grassland birds (Kerley et al. 1992). The large masses of soap tree yucca flowers in early summer attract myriad insects. The pollination ecology of soap tree yucca was first described in 1872 and stands as a classic case of obligate mutualism. The plant and its insect pollinator are mutually depen-

lands, our knowledge of this fascinating fauna is scarce and fragmentary. In this chapter we have reviewed what is known about the biology of these animals, but our presentation also points out how much more remains to be learned.

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