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Chapter 4:

Biodiversity, Functional Processes, and the Ecological Consequences of Fragmentation in Southwestern Grasslands

What is Biodiversity?

Concern over accelerating extinction rates and loss of species diversity on a global scale was the subject of E.O. Wilson's seminal volume *Biodiversity* (Wilson 1988). This work essentially transformed the term "biodiversity" into a household word as a short-hand for species diversity—or more simply, the full array and variety of living organisms on Earth. But the term biodiversity means much more than the complement of plant and animal species that one expects to find in some given area. The term now encompasses not only the diversity of species, but their genetic structure, the interaction of the biotic and abiotic components of the environment at the ecosystem level, and at an even higher level the array of communities and ecosystem processes and functions that make up the landscape or regional level of biological diversity. Such a detailed exploration of biodiversity is beyond the scope of this section.

In the interest of (relative) brevity, the following discussion will focus on the more limited definition of biodiversity, concentrating on the variety of plant and animal species of the New Mexico and Arizona grasslands.

A few points of clarification on terminology: The most common indices of species diversity (such as Simpson index, Shannon-Weiner index) are a function of two parameters: (1) species richness, or quite simply the number of species that occur in a defined area; and (2) species evenness, a measure of the extent to which the individuals of the different species present are equally abundant. Diversity is thus a measure of species richness weighted by relative abundance. Technically the most highly diverse communities are those with the greatest species richness, each component species being equally abundant within the community. In reality, such a situation is unlikely to occur, as many species (such as top predators) are naturally less numerous in the community. Furthermore, from a management standpoint it is often the more rare species in the community that are of interest, rather than the common species that tend to dominate weighted indices of diversity. The term "biodiversity," then, as used by many biologists, most often refers to the more simple measure of species richness, and that is how the term is used in this discussion. Biodiversity as used here refers to *natural* or *native* biodiversity. The distinction is important because the introduction of exotic plants or animals may technically increase diversity (at least in the short term) by adding to the overall species richness of a given area. However, as discussed later, introduced species usually interfere with normal community and ecosystem functions at some level and often eventually replace the native species, thereby leading to a net loss of native biodiversity.

Why is Biodiversity Important?

There are two main schools of thought on this subject. One theory is commonly referred to as the "rivet hypothesis" (Ehrlich and Ehrlich 1981). This hypothesis proposes that each species plays some small but important role in the ecosystem – like the rivets that collectively hold an airplane together. After some number of species (rivets) are lost, a critical threshold is crossed and the system (plane) rapidly begins to disintegrate. The fundamental assumption is that greater diversity (more rivets) results in increased stability of the system.

The other theory may be called that of "functional redundancy." This idea holds that communities comprise a few functional groups of ecologically equivalent species, to the effect that several species may be lost with little impact because there are several "back-up" species in place that are capable of carrying out the same function in the ecosystem (Walker 1992).

Although sources of great debate, there is not a great deal of hard data to back up either theory. Studies in grasslands to date, however, tend to support the rivet hypothesis. Grassland plots with greater species diversity were found to be more resistant to drought and to recover more quickly than less diverse plots (Tilman and Downing 1994). Another grassland experiment showed that plant productivity and soil nitrogen utilization both increased significantly as a function of plant species diversity, leading the authors to conclude that "the establishment and functioning of these grassland ecosystems depended on their species richness" (Tilman and others 1996:720).

How, then, to manage for biodiversity in grassland ecosystems? With so little evidence, the assumption of functional redundancy seems somewhat reckless. Even if there is some degree of ecological overlap between species, we have no idea if the "backup" system is as efficient as the primary one (Odum 1992). The most prudent course of action in Southwestern grasslands – or any ecosystem—is to ensure the ecological integrity of the system by managing for the conservation of maximal native biodiversity, or, in the oft-quoted words of Aldo Leopold, "to save every cog and wheel"—or, to see the context of his remarks (Leopold 1953):

> The last word in ignorance is the man who says of an animal or plant: "What good is it?" If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.

Biodiversity in the Southwest

Although at first glance it might seem that the climatic extremes of the desert Southwest would prevent many species from being successful in this environment, in fact the opposite is true. The highly variable precipitation, temperature extremes, and elevational gradients created by the basin and range topography have provided numerous opportunities for adaptation and evolution. Small-scale variations in soils, aspect, and moisture all affect microclimate and resource conditions, and this variety of conditions in turn offers a diverse array of niches available for exploitation, resulting in increased floral and faunal species richness. Species diversity in the Southwest has been further enhanced by its biogeographic history. The flora and fauna of distinctive regions historically isolated during the Pleistocene (for example, Great Plains, Chihuahuan Desert, Sonoran Desert, Mojave Desert, and Great Basin Desert) have converged following glacial retreats, leading to the characterization of the desert Southwest as a "biological melting pot" (Parmenter and others 1995). For Southwestern grasslands in particular, biodiversity is further enhanced by the complex, mosaic nature of their distribution. Grasslands in this region are interspersed with shrubs, woodlands, and riparian areas, leading to high species diversity due to the presence not only of grassland specialists, but also more generalist species from adjacent habitats that may utilize the grasslands for other purposes (Parmenter and Van Devender 1995). Highly patchy interspersed habitats, such as sand dunes, playa lakes, and lava flows, add to biodiversity by the presence of specialized and/or endemic plant and animal species distinctive to these areas (such as fringe-toed lizards in sand dunes) (Parmenter and others 1995). Brown and Kodric-Brown (1995) argue that biodiversity along the Arizona and New Mexico borderlands may be among the greatest on the continent due to the biogeographic confluence in this region.

Underlying the considerable biodiversity of the Southwest at the level of species richness is a high degree of genetic variability. Rangeland plants as a group exhibit high levels of genetic diversity, probably due to a combination of adaptation to diverse ecological conditions and frequent hybridization between interfertile species (Nevo and Beiles 1989, Wayne and Bazzaz 1991). Modern grassland plants have survived historical cycles of great climatic variation; high levels of genetic variability have given these plants the ability to adapt and persist throughout such oscillations (Tausch and others 1993). Genetic diversity is also high in Southwestern animals, both vertebrates and invertebrates. Pocket gophers (Geomydiae), for example, are common mammals in Southwestern grasslands. Although the species often are difficult to distinguish visually, they are some of the most genetically variable mammals known; species may differ not only in terms of the alleles represented, but in the numbers of chromosomes carried as well (Parmenter and others 1995, Patton and Sherwood 1983). Despite the fact that Southwestern mammals are relatively well known, modern laboratory techniques continue to identify new species on the basis of genetic differences between populations. Within the last few decades several new species have been identified in New Mexico, including a grasshopper mouse (*Onychomys arenicola*), a meadow-jumping mouse (*Zapus hudsonius*), and a deer mouse (*Peromyscus gratis*) (Hafner and others 1981, Modi and Lee 1984). Similar patterns of high genetic variability have been documented in Southwestern invertebrate species as well, including fruit flies and grasshoppers (Dobzhansky 1944, Rentz and Weissman 1980).

Plant Diversity

Plant diversity in the Southwest is high relative to that elsewhere in the country (Brown 1982), due in large part to the factors discussed above (environmental variability, biogeographic history, and genetic mixing), as well as the convergence of temperate and subtropical species along the border with Mexico. In addition to representation of plants from different regions, the Southwest supports a high number of endemic species. In the grasslands of the Chihuahuan Desert, for example, two-thirds of the grass species may be considered endemics (Burquez and others 1998). The presence of not only grasses, but forbs, shrubs, and occasional trees as well, adds to the diversity of the grassland community (Burgess 1995, McClaran 1995). The richness of plant species present is considered to be one of the most important indicators of overall rangeland health (West 1993). Diversity in plant communities reflects much more than just the variety of species present; the array of cover values, patchiness, and densities of plants all contribute to vegetative diversity (Moir and Bonham 1995). Species composition is affected not only by factors such as soil characteristics, precipitation, and topography, but also by the frequency and intensity of disturbances such as fire or livestock (Burgess 1995). In general the identity of the plant species present tends to remain constant over time (not accounting for introductions of exotics), but the relative abundances of these component species may change dramatically, thereby leading to alterations in the physical structure of the grassland system (Westoby and others 1989). The vegetative architecture of the ecosystem is a particularly important consideration, as it is one of the key characteristics influencing the use of the habitat by both invertebrate and vertebrate animals (Parmenter and others 1995).

About 10,000 species of grasses exist worldwide, making the grass family Poaceae the fourth most speciose family in the plant kingdom (behind the asters, legumes, and orchids; Smith 1993, Watson 1990). If one considers grasses in terms of their contribution to range quality, Stubbendieck and others (1986) suggest 94 species of grasses in their list of the 200 most important range plants in North America. Some of the more common native grasses of the Southwest include several species of gramas (such as black grama [*Bouteloua eriopoda*], blue grama [*B. gracilis*], hairy grama [*B. hirsuta*]), bush muhly (*Muhlenbergia porteri*), mesa dropseed (*Sporobolus flexuosus*), tobosa (*Hilaria mutica*), and Arizona cottontop (*Digitaria californica*). Some native grasses have nearly been extirpated from their former ranges, such as the giant sacaton (*Sporobolus wrightii*), a bunchgrass that once grew 1 to 2 m high across the floodplains of the Southwest. In this climate characterized by low rainfall, high rates of evapotranspiration and shallow soils, more than 95 percent of the grass production in desert grasslands is from C_4 species (Sims and others 1978). Desert grasslands are typically composed of a mixture of perennial and some annual grasses, most of the dominants being perennial caespitose bunchgrasses such as blue grama interspersed with suffretescent grasses such as bush muhly. Some of the common desert grasses are sod forming, such as curly mesquite grass (*Hilaria belangeri*) (Burgess 1995). These may be interspersed with small trees or shrubs such as mesquite (*Prosopis* spp.), creosote (*Larrea tridentata*), sages (*Artemisia* spp.), saltbush (*Atriplex* spp.), or rabbitbrush (*Chrysothamnus* spp.), subshrubs such as snakeweed (*Gutierrezia* spp.), and succulents or cacti such as sotol (*Dasylirion* spp.) or prickly pear (*Opuntia* spp.). The diversity of plant life forms that typify desert grasslands today is different from the vast monotypic “grasslands” one associates with the prairies of the Midwest—so much so, that Burgess (1995:58) proposes that a more appropriate name for Southwestern desert grasslands would be “Apacherian mixed shrub savanna” (historical conditions may have differed, however, as will be discussed below).

Herbaceous plants provide much of the ecological and botanical diversity in Southwestern grasslands; legumes and asters are particularly prominent members of many grassland communities. Members of the legume genus *Astragalus* are common, amongst others, and numerous members of the sunflower family may be present (such as *Aster*, *Antennaria*, *Wyethia*, *Chrysopsis* spp.). Other familiar forbs in grassland communities include Rocky mountain beeplant (*Cleome serrulata*), various species of flax (*Linum* spp.), and penstemons (*Penstemon* spp.). Cacti and succulents are particularly distinctive features of desert grasslands. In New Mexico and Arizona, nearly 150 species of cacti contribute to the plant diversity of the Southwestern region. The prickly pear (*Opuntia* spp.) has been proposed as a “keystone resource species” in Southwestern grasslands, a species that provides resources during bottlenecks of availability, due to the dependence of a variety of animals on prickly pears for both food and water during times of drought (West and Whitford 1995). Cacti also demonstrate the importance of microclimate variation in providing for increased species diversity. The rare grama grass cactus (*Toumeya papyracantha*), for example, depends upon the favorable microclimate provided by black grama grass to survive (Fletcher and Moir 1992, as cited in Moir and Bonham 1995).

The variable climate and topography of the Southwest contribute to the plant diversity in the grasslands of this region. The plant species composition and distribution of Southwestern grasslands depends heavily upon soil depth and texture, which in turn control the water retention potential of the soil (Burgess 1995). The conservation of desert soils is particularly critical, as soils in arid Southwestern grasslands tend to be shallow, and more than 30 percent of the available nitrogen and organic matter is in the top 10 cm of soil (Charley 1977). This top layer is also highly susceptible to erosion, and loss of these soils may lead to a decrease in floral diversity and associated faunal diversity (Noss and Cooperrider 1994). Soil characteristics are also greatly influenced by the activities of invertebrate animals. Soil invertebrates play a critical role in decomposition of organic matter, soil development, and alteration of the physical characteristics of the soil leading to increased water holding capacity, thereby influencing the associated plant community as well (Abbott 1989, Hutson 1989, Whitford and others 1995). The importance of subterranean termites, for example, has been demonstrated by the experimental elimination of this group on study plots, resulting in dramatic changes in both the species composition and productivity of grasses, forbs, and shrubs (Whitford 1991). Herbivorous vertebrates also have a strong influence on plant community composition, structure, and productivity, particularly fossorial rodents such as kangaroo rats and prairie dogs. The activities of these burrowing rodents aerate the soil, modify soil nutrient levels, and enhance moisture retention (Parmenter and Van Devender 1995). As moisture availability is probably the single greatest factor limiting plant diversity in the Southwest (Burgess 1995), many of the vertebrate and invertebrate animals of grasslands are making a critical ecological contribution to maintaining the overall biodiversity of these systems through their impacts on soil characteristics.

Beyond aerating the soil, cycling nutrients, and creating pockets of moisture retention through their subterranean activities, grassland rodents such as kangaroo rats have yet another significant impact on plant diversity. Herbivores generally promote plant diversity by suppressing more vigorous species that might otherwise exclude other members of the community, thereby allowing less competitive species to persist in the system (Burgess 1995). In desert grasslands, the abundance of annual grasses and forbs increases in proximity to kangaroo rat mounds (Andersen and Kay 1999). Furthermore, kangaroo rats have been demonstrated to actually control vegetative species composition and structure through selective seed predation and soil disturbance. A Chihuahuan desert shrubland was converted to grassland following exclusion of kangaroo rats from the site; both annual and perennial grasses increased in density up to three-fold in the absence of these animals (Brown and Heske 1990).

Plant diversity is also strongly affected by the presence or absence of mycorrhizal fungi. Mycorrhizal fungi have been proposed as “critical link species” in Western grasslands (West and Whitford 1995). Critical link species are species that play an important role in ecosystem function, but are not necessarily considered keystone species (Westman 1990). Approximately 90 percent of vascular plants are believed to depend upon a mutualistic association with mycorrhizae for enhanced phosphorous uptake; plant establishment or growth may be severely inhibited in the absence of the appropriate fungus. Studies of sagebrush steppe invaded by the exotic cheatgrass (*Bromus tectorum*) found that the repeated fires carried by the cheatgrass led to the widespread elimination of soil mycorrhizae, thereby inhibiting the reestablishment of perennial grasses and shrubs (Wicklow-Howard 1989). Granivorous rodents again play an important role by dispersing mycorrhizal spores throughout the grassland system through seed transport (Parmenter and others 1995).

Invertebrate Diversity

When most people think of animal biodiversity, it is the larger, more conspicuous animals characteristic of the terrestrial ecosystem that come to mind—birds, mammals, reptiles, or amphibians. In virtually all ecological systems, however, it is the invertebrate animals that not only account for the vast majority of species diversity and animal biomass, but also make the greatest contribution to key ecosystem processes such as nutrient cycling. Grasslands are no exception to this rule. Referring to shortgrass prairie systems, Arenz and Joern (1996:91) dub invertebrates as “the most significant contributor to the diversity of the prairie system.” The contribution of invertebrates to biodiversity is hardly surprising, as insects alone compose approximately 90 percent of all terrestrial animal species, and fewer than 10 percent of these have even been identified and named (Gaston 1991). What invertebrates lack in size they make up for in sheer numbers; Lauenroth and Milchunas (1992) estimate the total biomass of arthropods on North American grasslands exceeds that of vertebrates if domestic livestock are excluded.

The invertebrate inhabitants of grasslands begin at the microscopic level in the soils with protozoans and nematodes. Protozoans are found in most any grassland with sufficient soil moisture. Although this requirement might seem to exclude them from the grasslands of the desert Southwest, this is hardly the case. Just a tiny amount of moisture trapped between soil particles is sufficient to sustain them. One study of the semiarid shortgrass prairie of Colorado found more than 20,000 protozoans in each gram of dry soil (Elliott and Coleman 1977). Soil protozoans feed on bacteria, yeasts, algae, and fungal mycelia (Curry 1994), and play an important role in the transformation of soil organic matter (Elliott and Coleman 1977). Nematodes are a highly diverse group of roundworms that also play a key ecological role in grasslands. Although their distribution and activity is also restricted to some degree by moisture availability, at temperate grassland sites a square meter of soil will yield an average of 9 million individuals of various nematode species (Sohlenius 1980). In terms of ecosystem function, nematodes are considered by some to be the most important consumers of energy (Scott and others 1979), and their habit of feeding on plant roots strongly affects net primary productivity in grassland systems (Smolik and Lewis 1982).

Arthropods form a more familiar component of the grassland invertebrate fauna and may include whip scorpions, crickets, grasshoppers, beetles, flies, bees, wasps, cicadas, centipedes, spiders, ants, and termites. Some grassland arthropods are less conspicuous due to their nocturnal or subterranean habits, a common strategy for coping with the heat stress of life in the desert (examples include sun spiders, scorpions, termites) (Whitford and others 1995). About 90 percent of grassland arthropods reside in either the soil or litter, including those that nest belowground or spend a significant portion of their life stage belowground (Arenz and Joern 1996). The presence of ephemeral wetlands in grassland systems provides for a more diverse array of arthropods, including mosquitoes, freshwater shrimp, and water fleas. If water is present long enough, dragonflies or damselflies may be added to the invertebrate fauna (Loring and others 1988).

The species diversity of most groups of grassland arthropods appears to be higher in the Southwestern United States than in the rest of the country (Danks 1994, Parmenter and others 1995), although data on arthropod diversity is relatively limited (Kosztarab and Schaefer 1990). Grasshoppers are one of the best known and highly diverse groups of grassland arthropods. The species diversity of grasshoppers in the Southwest is greater than all other Western States, with the exception of California (Parmenter and others 1995). For example, 30 species of the subfamily Gomphocerinae occur in the Southwest, as opposed to only five to 20 species in the rest of North America (Otte 1981, as cited in Parmenter and others 1995). Darkling beetles (Tenebrionidae) also reach the peak of species diversity in Western arid lands and are one of the major detritivores in Southwestern ecosystems (Crawford 1990). Other species rich arthropod groups in the Southwest include soil-dwelling mites and collembolans (Crawford 1990, Zak and Freckman 1991).

Termites (Isoptera) are considered keystone species in Southwestern grasslands (West and Whitford 1995). A keystone species is one whose ecological impact on the community is disproportionately large relative to its abundance (Power and others 1996). Although termites contribute relatively little to invertebrate diversity in the Southwestern grasslands (there are only about 12 species), they are widely considered to be one of the most important invertebrates in these grassland systems in terms of their contribution to ecosystem function. The biomass of subterranean termites in desert grasslands is estimated to exceed that of domestic livestock (Whitford and others 1995). The presence of termites has a strong influence on the abundance and species composition of soil microfauna, and they are important consumers of dead plant material and dung. This latter point is not to be taken lightly; dung decomposes so slowly in desert systems that without termites to decompose the dung from livestock and incorporate it into the soil, grazed desert grasslands would eventually be covered with dry dung, leading to reduced plant productivity and leading to an overall decrease in the carrying capacity of the grassland system (Whitford and others 1995). Termites also consume approximately 50 percent of all photosynthetically fixed carbon in desert grassland systems (Whitford and others 1995). Termites therefore play a critical role in carbon and nutrient cycling in desert soils, and their subterranean activities also have a strong effect on soil aeration and water infiltration, increasing the water storage capacity of the soil. The cumulative ecological impact of subterranean termites in grassland systems led Whitford and others (1995:181) to declare this group the “most abundant and functionally most important arthropods in desert grasslands.”

Ants (Formicidae) are one of the more familiar arthropods of Southwestern grasslands. Ants play an important role in maintaining the plant diversity of desert grassland systems by preferentially harvesting the seeds of dominant plant species (Whitford and others 1995). The subterranean nests of ants are important in grassland systems for concentrating nutrients and allowing for increased water infiltration; these properties lead to high density vegetation surrounding ant nests in the desert grassland environment (Whitford and others 1995). Ant nests may persist in grassland habitats for up to 80 years (Whitford and others 1995).

The local species richness of invertebrates in grasslands is largely dependent upon the species composition, productivity, and habitat structure of the plant community (Arenz and Joern 1996, Lawton 1983, Strong and others 1984). Herbivorous arthropods tend to dominate the invertebrate community in grasslands (French 1979). Each plant species tends to have its own specialized set of invertebrate herbivores, which in turn support an array of invertebrate predators and parasites, and so on. Herbivores make up approximately 85 percent of the arthropod biomass in shortgrass steppe (Lauenroth and Milchunas 1992), and spiders are significant secondary consumers in these systems (Schmidt and Kucera 1975). Even though most of the invertebrates in grasslands are herbivorous, invertebrates are estimated to consume less than 10 percent of the live biomass in grassland systems (Chew 1974). As many arthropods are associated with the early and midstages of vegetational succession (Usher and Jefferson 1991), the diversity of invertebrates is often greatest in areas with a diverse mixture of plant species and physiognomies, in conjunction with natural disturbances (Samways 1994).

Despite their largely inconspicuous nature, invertebrates form a critical component of Southwestern grasslands through their contribution to decomposition and nutrient cycling, increasing soil porosity and water infiltration, regulating the growth of soil bacteria and fungi, and controlling the availability of mineral nutrients for plants (Whitford and others 1995).

Vertebrate Diversity

The American Southwest has been called "one of the most biologically diverse regions in the United States" when it comes to vertebrate animals (Parmenter and Van Devender 1995:196). Many groups of animals reach their highest levels of species richness in the country along the border with Mexico in southern Arizona, New Mexico, and Western Texas. The species richness of mammals in the Southwest is rivaled only by that of central California; bird species richness reaches its peak in the Southwest, southern Texas, and California, and the numbers of species of reptiles are higher only in eastern Texas (Parmenter and others 1995 and references therein). The only group of vertebrates that are not richly represented in the arid Southwest is, not surprisingly, aquatic organisms; the species richness of amphibians and fishes reaches its peak in the Southeastern States (Parmenter and others 1995).

Once again it is environmental heterogeneity created through a combination of elevational variability, climate dynamics, and the natural mosaic pattern of desert grassland habitats, in conjunction with the biogeographic history of the region, that accounts for this faunal richness. The greatest diversity of animals is usually within the more temperate conditions found at intermediate elevations. Animals at high elevations tend to be limited by cold temperatures, while those at low elevations are limited by aridity (Parmenter and others 1995). Although how the merging of formerly isolated faunal regions has contributed to the present diversity of Southwestern animal species was mentioned briefly above, a more concrete example of this blending offered by Parmenter and others (1995) may help to clarify how this process has acted to enhance vertebrate diversity in the Southwest (table 4-1).

The vertebrate diversity of grasslands is enhanced by the collective representation of taxa from many convergent habitats. Not only are grassland specialists represented, but numerous other animals that may

Table 4-1. An example of how the rich assemblage of terrestrial vertebrate species present today in Southwestern grasslands is in part the result of biogeographic history. Formerly distinct faunas derived from several major geographic regions now coexist in this area due to range expansions and the removal of physical barriers following glacial retreats at the end of the Pleistocene. A few of these species are listed below (adapted from Parmenter and others 1995).

Biogeographic region	Vertebrate species contributed to Southwestern grasslands
Great Plains	Western box turtle Great Plains skink Black-tailed prairie dog Northern grasshopper mouse Swainson's hawk Lark sparrow
Sierra Madre (Mexico)	Yarrow's spiny lizard Rock rattlesnake Pygmy mouse Montezuma quail
Chihuahuan Desert	Texas horned lizard Trans-Pecos rat snake Silky pocket mouse Banner-tailed kangaroo rat Scaled quail Cassin's sparrow
Sonoran Desert	Collared lizard Sidewinder Desert kangaroo rat Southern grasshopper mouse Gila woodpecker Bendire's thrasher
Mojave/Great Basin Desert	Short-horned lizard Chisel-toothed kangaroo rat Sagebrush vole Sage thrasher Sage sparrow

dwell primarily in the surrounding mosaic of desert scrub, pinyon juniper, or riparian areas, and that use the grasslands for foraging, may add to the species richness; this is particularly true of more mobile, generalized species of mammals or birds (Parmenter and others 1995). Up to 18 species of bats, for example, may be found in Southwestern grasslands. While six of these species are commonly found in grasslands, most of them will utilize grasslands only if their other habitat requirements may be met within a reasonable distance, specifically the presence of appropriate roost sites and water (Chung-MacCoubrey 1996). The interspersion of Southwestern grasslands with habitats such as pinyon-juniper woodlands meets these requirements.

Reptiles and Amphibians

Herptiles—reptiles and amphibians—are important components of the grassland vertebrate community. In the Southwest, reptiles in particular make a significant contribution to overall diversity. Approximately 44 species of reptiles are associated with desert grasslands, with fewer (18 species) present in high elevation mountain meadows (Parmenter and Van Devender 1995). Although the arid Southwest is a challenging environment for many amphibians, certain toads are relatively common in desert grasslands (such as the Western spadefoot toad [*Scaphiopus hammondi*]), and true frogs (such as the Chiricahua leopard frog [*Rana chiricahuensis*]) and tiger salamanders (*Ambystoma tigrinum*) may be found near permanent water sources. Common grassland/desert specialists include various species of box turtles, spadefoot toads, earless lizards, whiptails, horned lizards, bullsnakes, and rattlesnakes. Many species associated with grassland habitats require specific habitat features, such as rock outcroppings to serve as dens for wintering snakes (Collins 1982, Hammerson 1986). Many reptiles and amphibians join a variety of other animals in taking advantage of the beneficial microclimate provided by prairie dog burrows. At least 12 species of amphibians and 17 species of reptiles have been reported as regularly associated with black-tailed prairie dog towns (Reading and others 1989, Sharps and Uresk 1990). Spadefoot toads (family Pelobatidae) require playas, temporary pools that fill with water during the summer monsoons, for breeding (Corn and Peterson 1996). Most Southwestern amphibians have short aquatic larval stages to take advantage of the ephemeral water sources for breeding. In fact, permanent water sources may be detrimental to amphibian populations by attracting predators such as raccoons (*Procyon lotor*), or by encouraging the establishment of exotic species such as bullfrogs (*Rana catesbiana)* and centrarchid fishes. These predators have been implicated in the disappearance of several native species of amphibians in various areas of the country (Collins and others 1989, Hayes and Jennings 1986).

Both reptiles and amphibians play functional roles in food webs both as predators on invertebrates and small vertebrates and as prey for larger animals (although some herps, such as the desert tortoise, are herbivores). Amphibians in particular are an important avenue for nutrient transport between aquatic and terrestrial systems. Amphibian and reptile populations are also particularly sensitive indicators of environmental stresses and may thus serve as a warning signal of problems such as pesticide contamination (Beiswenger 1986, Blaustein 1994). Like other grassland animals, herps are sensitive to changes in habitat composition and structure, and herp species richness is generally greatest in relatively heterogeneous habitats. In dense grasslands, for example, moderate grazing that increases the patchiness of the grass density and adds some variety to its structure enhances the habitat for a variety of snakes, lizards, and toads.

One of the more fascinating groups of grassland reptiles is the genus *Cnemidophorus*, the whiptail lizards. There are 10 unisexual species of whiptails in the Southwest that are made up entirely of female individuals. These lizards reproduce by an asexual autofertilization method known as parthenogenesis. All-female whiptail lines are polyploid (have more than one set of chromosomes), indicating that they were originally formed through the hybridization of two sexual species. Each individual in the species is genetically identical to the original hybrid (Cole 1984, Parmenter and Van Devender 1995). The desert grasslands of the Southwestern United States are the evolutionary center for this highly unusual group of vertebrates; seven of the 10 unisexual species are restricted almost entirely to this habitat. The desert grasslands of Texas and New Mexico are home to the New Mexican (*Cnemidophorus neomexicanus)*, checkered (*C. tesselatus*), and Chihuahuan (*C. exanguis*) whiptails; desert grassland (*C. uniparens*), Sonoran (*C. sonorae*), and Gila spotted (*C. flagellicaudus*) whiptails are found in Arizona; and the plateau whiptail (*C. velox*) is found in the grasslands of the Great Basin. Furthermore, several whiptail species (New Mexican whiptail, desert grassland whiptail, and the little striped whiptail *C. inornatus*—a nonparthenogenetic species) are believed to be dependent on native stands of grasses within these habitats.

Birds

Although birds are some of the most abundant vertebrates found in Southwestern grasslands (Parmenter and Van Devender 1995), the bird community tends to be the most simplistic in terms of species richness (Knopf 1996). As one example, Knopf (1996) cites his results from a series of 112 point count surveys in the Pawnee National Grasslands in Colorado, in which just three species (horned lark [*Eremophila alpestris*], McCown's longspur [*Calcarius mccownii*], and lark bunting [*Calamospiza melanocorys*]) accounted for 87 percent of all individuals recorded; only 14 species of native birds were recorded in total. Bird species commonly found in the grasslands of the Southwest include the horned lark, lark bunting, meadowlarks (both Eastern [*Sturnella magna*] and Western [*Sturnella neglecta*]), scaled quail (*Callipepla squamata*), mountain plover (*Charadrius montanus*), burrowing owl (*Athene cunicularia*), short-eared owl (*Asio flammeus*), prairie falcon (*Falco mexicanus*), ferruginous hawk (*Buteo regalis*), and various sparrows (such as vesper [*Pooecetes gramineus*], lark [*Chondestes grammacus*], Cassin's [*Aimophila cassinii*], and Botteri's [*A. botterii*]) (Knopf 1996, Parmenter and Van Devender 1995). Even some shorebirds, such as long-billed curlews (*Numenius americanus*), utilize Southwestern grasslands for breeding. At high elevations, rosy finches (*Leucosticte* spp.) and white-tailed ptarmigan (*Lagopus leucurus*) may be found in alpine meadows of the Southwest (Parmenter and others 1995).

Many of the typical avian residents of Southwestern grasslands nest on the ground, as the lack of vertical structure in grasslands offers little other choice. The burrowing owl, a common denizen of Southwest grasslands, nests below the ground in abandoned prairie dog burrows. Most members of the grassland bird community are granivores, and the dynamics of this community are closely tied to levels of seed production. As most desert grasses set seed in late summer or early fall following the monsoons (McClaran 1995), the peak in resident grassland bird numbers usually occurs in late summer in coincidence with maximum seed production (Maurer 1985). Avian species richness increases during the winter months, when the grasslands of the Southwest support a great concentration of migratory species such as Baird's sparrow (*Ammodramus bairdii*), white-crowned sparrow (*Zonotrichia leucophrys*), grasshopper sparrow (*Ammodramus savannarum*), sage sparrow (*Amphispiza belli*), Sprague's pipit (*Anthus spragueii)*, McCown's longspur, and chestnut-collared longspur (*Calcarius ornatus*).

Birds respond strongly to changes in habitat architecture, and the diversity of the grassland bird community will increase in the presence of shrubs, trees, cacti, or even human structures (Grinnell 1922, Knopf and Scott 1990, Parmenter and others 1995, Szaro 1981). The addition of vertical structure provides a far greater range of avian habitats and thereby adds a whole new component to the bird community. The maximum species richness is probably found along riparian corridors or near permanent wetlands in grasslands, where large numbers of migrants and transients concentrate (Parmenter and Van Devender 1995); here, various species of warblers, vireos, and other decidedly nongrassland species may be found. It is important to recognize, however, that even if species diversity is technically enhanced by the addition of vertical structure such as woody plants or human developments, grassland specialists are usually lost in the process. The enhanced bird diversity witnessed in such cases is most likely provided by an increase in relatively common generalist species and might mask any concomitant population declines or extirpations of narrow endemics that may occur (Knopf 1992).

In pure grasslands without significant vertical structure provided by shrubs or trees, different bird species demonstrate preferences for an array of grass heights and various patterns of patchiness. Mountain plovers and McCown's longspurs, for example, occur in short grasslands, often those that have been subjected to "heavy grazing pressure to the point of excessive surface disturbance" (Knopf 1996:141 and references therein). Lark buntings will use areas of shortgrass prairie but require that tufts of taller grasses be interspersed in the landscape to provide nest concealment (Finch and others 1987). Baird's sparrow can be found across a wide range of grassland types and grazing intensities (Kantrud 1981), and Cassin's sparrow requires grasslands that provide at least 6 percent shrub cover and may be lightly grazed (Bock and Webb 1984).

Grassland birds are a source of great conservation concern, as this group of birds has shown consistently steep population declines over the past few decades, on the order of 25 to 65 percent—more than any other guild of North American bird species (Askins 1993, Knopf 1992, 1996). Formerly widespread and common species such as the lark bunting and Cassin's sparrow are showing statistically significant declines, and the mountain plover has been proposed for Federal listing as a threatened species. Although some theorize that declines in populations of neotropical migratory birds are due to loss of wintering habitat in the tropics (see Briggs and Criswell 1979, Lovejoy 1983, Terborgh 1980), most of the grassland birds in question are short-distance migrants that spend their winters in the grasslands of the Southwest and Mexico, suggesting that alteration of Southwestern grassland habitats may be contributing to the decreases witnessed (DeSante and George 1994).

Mammals

The Southwestern grasslands owe much of their high vertebrate diversity to mammals, and more particularly to rodents. In a comparison of mammals found in six habitat types in a single region of New Mexico, desert grasslands had the greatest species richness of any major ecosystem type with 56 species, ahead of desert scrub, pinyon-juniper woodland, montane forest, montane meadow, and riparian zone (Parmenter and Van Devender 1995). The high species richness of the desert grassland is primarily due to the diversity of rodents in this system, especially ground squirrels (Sciuridae), kangaroo rats (*Dipodomys* spp.), and mice (Muridae). Rodents tend to be the dominant mammals in all desert grasslands, and are well represented by grassland specialists, including the bannertail (*D. spectabilis*) and Ord (*D. ordii*) kangaroo rats, black-tailed prairie dog (*Cynomys ludovicianus*), and spotted ground squirrel (*Spermophilus spilosoma*) (Parmenter and Van Devender 1995). As one indication of just how diverse the rodent community of the Southwestern grasslands is, Parmenter and others (1995) point out that just one 20 ha area of Chihuahuan Desert has the same number of native rodent species as the entire States of Michigan and Pennsylvania combined, and that's allowing those States two introduced species and two semiaquatic species.

Many other mammal species are also characteristic of Southwestern grasslands, including, amongst others, pronghorn (*Antilocapra americana*), white-sided jackrabbits (*Lepus callotis*), swift fox (*Vulpes velox*), badgers (*Taxidea taxus*), coyotes (*Canis latrans*), mule deer (*Odocoileus hemionus*), several species of bats, and—in high elevation grasslands—pikas (*Ochotona princeps*). Historically, bison (*Bison bison*) were found in the shortgrass prairie regions of eastern New Mexico, but probably did not occur regularly in the arid grasslands farther west (Berger and Cunningham 1994, Kay 1994, Mack and Thompson 1982). Many of these mammals have a strong impact on the overall diversity of the grassland system through various types of disturbance. Vegetation structure and species composition, for example, are affected by selective feeding of herbivores and by soil disturbance. By selectively grazing on dominant species, herbivorous mammals allow subdominant plant species to compete and persist in the community (Risser and others 1981). Digging by badgers, prairie dogs, kangaroo rats, and gophers creates soil disturbances that allow for the establishment of annual forbs and grasses, and also increases the porosity and water-holding capacity of the soil (Benedict and others 1996 and references therein). Wallowing by bison in areas where they formerly occurred, and small scrapes created by pronghorn, serve a similar function (Benedict and others 1996, Parmenter and Van Devender 1995). These small-scale natural disturbances add unique microhabitats available for colonization by other species, increasing vegetative diversity, enhancing the mosaic nature of the habitat, and leading to increased faunal diversity as well (both invertebrate and vertebrate) (Benedict and others 1996, Collins and Barber 1985). Overall, Collins and Barber (1985) found that diversity in a mixed-grass system was enhanced by moderate levels of natural disturbance (*sensu* the "intermediate disturbance hypothesis" of Connell 1978) and that small-scale disturbances have an additive effect that further enhances diversity.

Grassland biodiversity is also strongly impacted by the presence of keystone species. The power that kangaroo rats exert over the structure and dynamics of their habitat has led to their designation as a keystone species in the grassland systems of the Southwest (Brown and Heske 1990, West and Whitford 1995). Kangaroo rats exert their influence largely through selective seed predation and soil disturbance. In a long-term study on an Arizona desert shrubland, Brown and Heske (1990) demonstrated that the removal of kangaroo rats resulted in dramatic increases in grass densities, as well as a shift toward large-seeded winter annual plant species. Small-seeded winter annuals decreased, herbaceous vegetation increased (including both grass and forbs), litter accumulation increased, seed-eating birds decreased, and several new species of rodents colonized the plots where kangaroo rats were absent. The other native rodents on the plots where kangaroo rats were removed were not able to prevent the conversion of the habitat from shrubland to grassland, along with the associated changes in the resident fauna, thus supporting the keystone role of the kangaroo rats in this system. Furthermore, kangaroo rat burrows provide favorable microclimates for a diverse array of both invertebrate and vertebrate animals. Western box turtles, Great Plains skinks, and massasaugas use kangaroo rat mounds for shelter, and several species of roaches, crickets, and beetles are found almost exclusively in these mounds (Hawkins and Nicoletto 1992).

The black-tailed prairie dog is a critically important keystone species in Southwestern grassland systems whose presence greatly enhances local biodiversity (Kotliar and others 1999, Miller and others 1994, Whicker and Detling 1988). The burrowing and feeding behaviors of prairie dogs have drastic effects on the structure, species composition, and nutritive value of surrounding vegetation, create open areas to add to the heterogeneity of the habitat, modify the physical characteristics of soils, affect energy and nutrient cycles, and provide valuable microclimates utilized as shelters by a multitude of both invertebrate and vertebrate animals (Benedict and others 1996, Miller and others 1990, 1994, Whicker and Detling 1988 and references therein). The activities of prairie dogs, feeding on and clipping vegetation in the area of their colony, stimulates fresh plant growth and enhances the nutritional content of the vegetation, leading herbivores such as pronghorn to preferentially feed on prairie dog towns (Coppock and others 1983). Prairie dog towns are considered to be centers of animal diversity due to the great numbers of species that converge on the colonies to either use the old burrows, forage on the surrounding vegetation, or feed on the prairie dogs themselves (Miller and others 1990, 1994). Nearly 170 species of vertebrates have been reported using prairie dog towns, although this number is undoubtedly excessive due to the inclusion of birds flying over (Benedict and others 1996). A more critical recent review suggests that there is sufficient evidence for the strong dependence of nine vertebrates upon prairie dog colonies, 20 species appear to use the colonies opportunistically, and 117 species may have some relationship with the colonies, but data to support any solid conclusions are lacking (Kotliar and others 1999). However, of those animals that are closely associated with prairie dogs, several are of great conservation concern, including the black-footed ferret (*Mustela nigripes*), swift fox, ferruginous hawk, burrowing owl, and mountain plover (Kotliar and others 1999, Samson and Knopf 1994). This association does not bode well as eradication programs have resulted in eliminating the black-tailed prairie dog from 98 percent of its former range, reducing its numbers to the point that the species is now under consideration to be listed as endangered (Miller and others 1994, U.S. Fish and Wildlife Service 2001).

Threats to Grassland Biodiversity

The native biodiversity of Southwestern grasslands has been greatly altered through human activities. Numerous animal species have been extirpated or greatly reduced through direct persecution, including the black-tailed prairie dog, Mexican wolf, bison, and grizzly bear (Benedict and others 1996; table 4-2). Others have been reduced presumably due to their dependence on a keystone species that has been removed from the system. For example, the black-footed ferret (endangered) and mountain plover (proposed for listing) are strongly dependent upon prairie dog colonies for survival (Kotliar and others 1999), and the

Table 4-2. Terrestrial vertebrates of Southwestern grasslands that are now extinct or have been extirpated from the region. The following species are not necessarily restricted to grassland habitats; although many are grassland specialists, this list also includes those species that rely heavily on grasslands in some parts of their range or as one component of a mosaic of habitats utilized. Sources for the information presented here include Arizona Game and Fish Department (1988), Association for Biodiversity Information (2001), and New Mexico Department of Game and Fish (2000).

Common name	Scientific name	Federal status	Extirpated or extinct	Primary cause of extinction or extirpation	Notes
Western boreal toad	*Bufo boreas boreas*	CW	Extirpated	Unknown	Believed extirpated; formerly occurred in alpine meadows
New Mexico sharp-tailed grouse	*Tympanuchus phasianellus hueyi*		Extinct	Habitat loss or degradation due to overgrazing, agriculture, succession	
Sage grouse	*Centrocercus urophasianus*		Extirpated from NM & AZ	Overhunting, habitat loss or degradation from overgrazing	
New Mexican banner-tailed kangaroo rat	*Dipodomys spectabilis baileyi*		Extirpated from AZ	Habitat degradation from overgrazing	Inhabited Great Basin desertscrub
Black-tailed prairie dog	*Cynomys ludovicianus*	CW	Extirpated from AZ	Direct human persecution	Some small populations persist in NM
Black-footed ferret	*Mustela nigripes*	E	Extirpated	Elimination of prairie dogs (primary prey)	Currently attempting reintroduction in NM
Bison	*Bison bison*		Extirpated from NM and AZ	Overhunting	Now exist on private ranches
Merriam's elk	*Cervus elaphus merriami*		Extinct	Overhunting	Native AZ elk
Mexican wolf	*Canis lupus baileyi*	E	Extirpated	Direct human persecution	Experimental populations reintroduced in NM and AZ
Intermountain wolf	*Canis lupus youngi*		Extinct	Direct human persecution	
Grizzly bear	*Ursus arctos*	T	Extirpated from NM and AZ	Direct human persecution	Persist in Northwestern States (for example, Montana), Canada, and Alaska

E = endangered, T = threatened, CW = candidate with "warranted but precluded" determination declines in their populations have been linked to the extirpation of prairie dogs (Miller and others 1994). Not only does the disappearance of the prairie dog have dire consequences for the species dependent upon it, but the prairie dogs themselves are now threatened with deleterious genetic consequences as a result of the fragmentation and isolation of their remaining populations (Pizzimenti 1981).

A far more subtle factor has been responsible for most extinctions at the local level in Southwestern grasslands. Changes in the structure and function of grassland habitats have probably been responsible for more losses of native diversity than any other cause (Stacey 1995). "While losses of biological diversity at the local level are often the least noticed," Stacey (1995:34) points out, "they are extremely important because they change the functional dynamics of the local community and because if local extinctions continue long enough the species will be lost over wide areas and may not recover without human intervention." Changes in grassland habitat structure and function may come about in many ways, but some of the most important sources of these changes in Southwestern grasslands have been the loss of fire as a natural cyclical event, the elimination of prairie dog colonies, heavy grazing by livestock, the introduction of nonnative grasses, and shrub encroachment (Parmenter and Van Devender 1995, Risser 1988). The division of formerly expansive rural landscapes into increasingly fragmented "ranchettes" is the latest recognized threat to grassland biodiversity (Brown and McDonald 1995, Maestas and others 2002), and will be discussed separately under the section on habitat fragmentation.

Loss of Natural Fire Cycles

Fire plays a key role in the maintenance of most grassland systems. Without periodic fires, woody plants begin to encroach into grasslands, converting them to shrublands or woodlands. The grasslands of the Southwest are no exception. Many researchers agree that historically fires were both common and extensive in the desert grasslands, and that these fires were instrumental in maintaining the integrity of these systems (Bahre 1991, Humphrey 1958, McPherson 1995, McPherson and Weltzin 2000).

The exception to this rule may be grasslands dominated by black grama. The extreme difficulty black grama exhibits in recovering from a burn indicates that this species is not fire-adapted and probably did not evolve under a history of frequent burning (Buffington and Herbel 1965, Dick-Peddie 1993). More recently, however, it has been proposed that the negative effects witnessed may have been attributable to a coincident period of drought rather than to fire (Curtin and others 2002). Precipitation has a considerable impact on grassland productivity following fire, both in terms of timing and quantity.

The natural frequency and extent of grassland fires in the Southwest are believed to have declined dramatically since Euro-American settlement of the region in the late 1800s (Bahre 1991, 1995, Humphrey 1958). A review of the role of fire in desert grasslands reveals that the natural frequency of fire in these systems was probably on the order of every 7 to 10 years (McPherson 1995 and references therein). Fires occurring on this cycle are believed to be sufficient to prevent the establishment of woody plants, by killing seeds on the surface and preventing woody plants from reaching the age where resprouting is possible (McPherson 1995). Although fires eliminate grass cover in the short term, in the long term, grasses are rejuvenated by the occurrence of fire and benefit from the elimination of woody plants. The timing of fires is also important. Fire in the early summer, when the growth of many perennials is just beginning, can negatively impact warm season grasses, whereas these same grasses are tolerant of fire during the dormant season (McPherson 1995). The level of soil moisture at the time of ignition is also a consideration; for some plant species, burning on dry soils may be damaging (W. Moir, personal communication 2003).

Although many factors contribute to fire regimes, perhaps the most important change that has resulted in decreased fire frequency and intensity in the Southwest is the lack of fine fuels to carry the fires (Humphrey 1958, McPherson 1995). Historically, the timing of this change corresponded with the widespread increase in livestock grazing in the Southwest after 1880. At this time, stocking rates reached record levels, and overgrazing was actually encouraged to reduce the fire hazard and encourage the growth of trees (Bahre 1991, Leopold 1924 as cited in McPherson 1995). In addition, the use of wooden posts for livestock fencing provided the incentive for quickly suppressing rangeland wildfires that would compromise the integrity of the fences (Sayre 2002). Today, fragmentation from roads and suburban developments serve as a kind of artificial firebreak to contain the spread of extensive wildfires (Bahre 1995, McPherson 1995). The continuing growth of residences on formerly undeveloped lands has also led to a demand for active fire suppression in these areas (Hansen and others 2002). These changes in the frequency and intensity of natural fire regimes have doubtless contributed to the widespread conversion of Southwestern grasslands to shrublands (Archer 1989, Brown 1982, Humphrey 1958), thereby radically altering the nature of the habitat for native grassland species.

Prairie Dog Eradication

In the Southwestern grasslands, the prairie dog is considered a "keystone" species—a species that has a large overall effect on a community or ecosystem disproportionate to its abundance (Kotliar and others 1999, Power and others 1996). The activities of these burrowing animals have a dramatic impact on the patch dynamics and ecosystem function of the grasslands that they inhabit. Prairie dog disturbances impact the physical and chemical properties of the soil, alter vegetational structure, affect plant species composition, and improve the nutrient value of plants growing in the vicinity of their colonies (O'Meilia and others 1982 and references therein, Whicker and Detling 1988). The increased nutritional value of forage on colonies may act to offset any decrease in biomass as a result of clipping by prairie dogs (Holland and Detling 1990, O'Meilia and others 1982 and references therein). Bison, elk, pronghorn, and livestock all preferentially graze on prairie dog colonies, presumably because of the increased value and palatability of the herbage there (Coppock and others 1983, Knowles 1986, Krueger 1986, Wydeven and Dahlgren 1985).

Active prairie dog towns contribute to increased biological diversity by supporting a different complement of species compared to areas unoccupied by prairie dogs (Agnew and others 1986, Mellink and Madrigal 1993, O'Meilia and others 1982). Furthermore, several vertebrate species are considered highly dependent upon prairie dogs either as prey or for the habitat provided by their colonies, including the endangered black-footed ferret. Other animals considered true prairie dog associates are the mountain plover, burrowing owl, ferruginous hawk, golden eagle (*Aquila chrysateos*), horned lark, swift fox, deer mouse (*Peromyscus maniculatus*), and northern grasshopper mouse (*Onychomys leucogaster*) (Kotliar and others 1999).

Once a dominant force in the grasslands of the Western United States, the ecological impact of the prairie dog on these systems has nearly been extinguished. Up until the early 1900s, prairie dog colonies were estimated to cover hundreds of millions of acres of shortgrass prairie and desert grasslands west of the Great Plains (Anderson and others 1986). Today prairie dogs are estimated to persist on a mere 2 percent of their former range (Anderson and others 1986, Miller and others 1994). One species, the Utah prairie dog (*Cynomys parvidens*), is endangered, and the black-tailed prairie dog, formerly the most abundant and widespread of the five species of prairie dogs in North America, is a candidate for listing (USFWS 2000). The population numbers of the black-tailed prairie dog are estimated to have been reduced by 98 percent, and the species may occupy as little as 0.5 percent of its original range (Mac and others 1998 as cited in USFWS 2000). Although the conversion of native prairie habitat to other land uses may have contributed to some degree, undoubtedly the greatest single factor in the loss of prairie dogs has been the concerted effort by both Federal and State government agencies to exterminate these animals for the benefit of the livestock industry (Mulhern and Knowles 1996, Parmenter and Van Devender 1995).

The campaign to eradicate prairie dogs from Western grasslands began in earnest following the release of a Department of Agriculture report suggesting that the presence of prairie dogs may reduce range productivity by 50 to 75 percent (Merriam 1902). The U.S. Biological Survey responded with a massive poisoning campaign under the auspices of its Predator and Rodent Control program. Aiming to reduce competition with livestock, millions of acres of prairie dog colonies were poisoned, and shooting of prairie dogs was encouraged across their range (Bell 1921, Mulhern and Knowles 1996, Parmenter and Van Devender 1995, Van Pelt 1999). Fear of sylvatic plague buoyed these efforts after the bacterium was discovered in black-tailed prairie dogs in Texas in the 1940s (Cully 1989, Mulhern and Knowles 1996). In some States, annual extermination of prairie dogs on State and privately owned lands was a legal requirement. Nebraska, for example, only recently repealed this mandate in 1995 (Van Pelt 1999).

The black-tailed prairie dog and the Gunnison's prairie dog (*C. gunnisoni*) are the two species that inhabit the grasslands of Arizona and New Mexico. Described as occurring in "immense colonies" in Arizona in 1885 (Mearns 1907), the Arizona prairie dog (*C.l. arizonensis*), a subspecies of the black-tailed prairie dog, was largely extirpated from that State by 1938; one small single colony survived until 1960 (Van Pelt 1999). In New Mexico, the range of the black-tailed prairie dog has been reduced by at least 25 percent (Hubbard and Schmitt 1984). In the Animas Valley, for example, biologists from the Museum of Southwestern Biology did not observe one single prairie dog between the years 1955 and 1972 (Findley 1987). Yet in 1908 Vernon Bailey had described this same area as an almost continuous prairie dog town for its length and breadth, estimating that over 6 million prairie dogs inhabited the valley (Bailey 1932).

Notwithstanding the drastic declines already witnessed in prairie dog numbers and the evidence of a cascade effect on other species, prairie dogs today are still widely considered to be vermin and enjoy little in the way of legal safeguards from any states (Van Pelt 1999). This is in spite of more recent evidence that the level of competition between prairie dogs and livestock is more likely on the order of 4 to 7 percent (Uresk and Paulson 1988 as cited in Miller and others 1994) and that there is no significant difference in the market weight of steers whether they graze in conjunction with prairie dogs or not (O'Meilia and others 1982;

although it should be noted that the statistically insignificant weight difference did result in an economic loss). Following their comprehensive review, Kotliar and others (1999:186) concluded that prairie dogs are "crucial to the structure and function of native prairie systems." Not only are scientists today stressing the importance of preserving remaining prairie dog colonies to maintain biodiversity (for example, Miller and others 1994), some are going further and calling for the reintroduction of prairie dogs to restore ecosystem function (for example, Manzano-Fischer and others 1999).

Overgrazing by Livestock

Livestock grazing is the predominant land use in the Western States. More than 70 percent of the land area in the West (11 states, from Montana, Wyoming, Colorado, and New Mexico westward) is grazed by livestock, predominantly cattle, including wilderness areas, wildlife refuges, National Forests, and some National Parks (Fleischner 1994 and references therein). Some argue that overly heavy levels of livestock grazing are one of the greatest sources of habitat degradation in the West (for example, Noss and Cooperrider 1994), leading to widespread declines in the native wildlife of North American grasslands (Fleischner 1994). Others point out that most studies of grazing effects have suffered from poor experimental design (for example, Brown and McDonald 1995, Jones 2000), or have found the impact of grazing to be relatively negligible on factors such as native species richness (Stohlgren and others 1999). The issue of livestock grazing in the West is highly contentious. In all cases, it is important to remember that the impact of grazing will vary greatly depending upon any number of variables, including the season of use, stocking rate, environmental conditions, and the evolutionary history of grazing in the region (Fleischner 1994, Jones 2000, Milchunas and Lauenroth 1993), and may also differ according to geographic scale (Stohlgren and others 1999).

This discussion will focus primarily on how poorly managed grazing of livestock may impact grassland habitats in the Southwest.

Grazing by livestock has the potential to alter grassland habitats in many ways. Depending on the intensity and length of the grazing regime and environmental conditions, livestock activities may significantly alter plant species composition, extent of vegetative cover, and physical structure of the habitat (Bock and others 1984). As discussed above, any changes in these vegetative parameters exert a strong influence on the associated fauna, so that changes in plant diversity and structure result in changes in animal diversity. Most frequently, overgrazed sites result in a loss of specialized native fauna and may or may not exhibit an increase in more widespread, generalist species (Bock and others 1984, Bock and Webb 1984, Jones 1981). In an Arizona grassland, for example, heavily grazed pastures had an abundance of birds that are commonly found in disturbed areas, such as horned larks and scaled quail, while grassland specialists such as Cassin's, Botteri's, and grasshopper sparrows were the dominant species in ungrazed plots (Bock and Bock 1988). In an extensive review of the grazing literature, Jones (2000) found that a majority of the studies for which there were sufficient data reported a decrease in both rodent species richness and diversity in response to grazing.

Livestock grazing can have more indirect effects on the environment as well. Soil disturbances created by trampling and digging produce microsites ripe for the invasion of weedy plant species, and cattle tend to import propagules of nonnative plant species on their coats or through their feces (Hobbs and Huenneke 1992). The combination of selective grazing by livestock on more palatable species and the opportunities for invasion by exotic species through soil disturbance and increased nutrient input from dung results in the decline of native perennial grasses and an increase in nonnative annuals (Mack 1981, 1989, Moore 1970). Livestock grazing may also contribute to shrub encroachment by eliminating the grasses and reducing competition for the seedlings of woody plants (Humphrey 1958). Grazing had largely negative impacts on numerous soil and vegetation variables examined in the review by Jones (2000), including increased soil loss to erosion, decreased infiltration rates, and decreased litter cover. Although the results of her review suggest that grazing has an overall negative impact on arid ecosystems in North America, Jones also points out that it was not possible to control for important factors such as stocking rates, grazing intensity, or timing in her comparison.

Some would argue that moderate levels of grazing may benefit Southwestern grasslands because maximum biodiversity is achieved under intermediate levels of disturbance (Connell 1978). In a test of the intermediate disturbance hypothesis, Collins and Barber (1985) found that grassland vegetation diversity was high on light to moderately grazed mixed-grass prairie (as opposed to undisturbed or most severely disturbed treatments). They concluded that diversity in such systems may be increased by moderate levels of natural disturbance, and furthermore that such disturbances have additive effects that further increase diversity. Today, some practitioners promote the use of properly controlled livestock grazing as a key component of sustainable ecosystem management in Southwestern grasslands (Savory and Butterfield 1999).

The question of whether grazing is a natural disturbance in the grasslands of the Southwest has been the subject of some debate. In the shortgrass prairie, blue grama and buffalo grass *Buchloe dactyloides* coevolved with the bison and are apparently adapted to heavy grazing pressure; these grasses thrive under such conditions by reproducing both sexually and by tillering (Knopf 1994). By contrast, in more recent history the desert grasslands of the Southwest have been devoid of large herds of grazing ungulates. Most evidence points to an absence of large herds of bison west of the Rockies (Berger and Cunningham 1994, Durrant 1970, Gustafson 1972 as cited in Mack and Thompson 1982, Kay 1994). Although Southwestern grasses undoubtedly coevolved with grazing due to the presence of herbivorous megafauna in the Pleistocene, these grasses have now been released from selection for grazing defenses for at least 10,000 to 12,000 years (Jones 2000 and references therein). In their extensive review, Milchunas and Lauenroth (1993) report that the sensitivity of grasslands to grazing increases with increased aridity and/or the lack of an evolutionary history of grazing. If one accepts their results, it is hard to avoid the conclusion that the grasslands of the Southwest must be especially sensitive to potential grazing impacts.

The bunchgrasses of the arid Southwest are indeed highly susceptible to grazing by ungulates and respond in a manner quite distinctive from the grasses of the shortgrass prairie (Daubenmire 1970, Dyer 1979, Tisdale 1961). Whereas grazed areas in the shortgrass prairie tend to be recolonized by predominantly native plants (Mack and Thompson 1982 and references therein), the morphological and physiological features of bunch grasses render them incapable of recovering quickly from grazing. Continuous grazing in desert grasslands leads to changes in species composition, where bunch grasses are replaced by sod-forming grasses or annuals (Brown 1982), or invaded by Eurasian weeds (Mack and Thompson 1982; see also Milchunas and others 1988). Furthermore, the soils of these grasslands that evolved with few native grazers are protected by a cryptogamic crust of mosses, lichens, and liverworts; this crust can be permanently destroyed by the trampling of large ungulates, producing sites for the establishment of exotic species (Daubenmire 1970, Jones 2000, Mack and Thompson 1982). Uncontrolled livestock grazing also endangers riparian systems in grasslands, one of the greatest sources of local diversity, because livestock will eat the palatable woody species such as cottonwoods and willows, not only removing the bulk of the riparian plant community but also destabilizing the banks and potentially leading to a lowering of the water table (Kovalchik and Elmore 1992).

Grazing impacts in the Southwest remain a highly controversial and confusing issue. As Jones (2000) points out, the poor experimental design employed in the majority of grazing studies has left us with a dearth of solid information about the impacts of grazing on arid rangelands. Furthermore, results are contradictory. Although Jones (2000) found that grazing had negative impacts in the majority of studies reviewed, Stohlgren and others (1999) suggest that factors such as soil fertility or water availability may overshadow the impacts of grazing on variables such as native plant species richness. There is little question that the astronomical stocking rates of livestock in the late 1800s did great environmental damage to the grasslands of the American Southwest; what is not well known is how current grazing practices are impacting the system (Curtin and others 2002). From a management standpoint, one important point to keep in mind is that restoration of degraded rangelands will require much more than merely removing cattle. Ecosystem function must be restored, which demands the incorporation of dynamic processes such as fire and precipitation to affect grassland condition, and furthermore may require mechanical removal or chemical treatment to turn the clock back on woody invaders (Curtin and others 2002, McPherson and Weltzin 2000). Today there is a generally greater awareness of the importance of maintaining ecosystem function for long-term sustainability, and a growing emphasis on the proper management of livestock grazing to ensure the ecological integrity of Southwestern grasslands (Brown and McDonald 1995, Curtin 2002, Savory and Butterfield 1999, Sayre and Ruyle 2001), as witnessed by the recent evolution of sustainable ranching organizations such as the Malpai Borderlands Group and The Quivira Coalition. More well-designed scientific studies of various grazing practices and their effects on the biodiversity of Southwestern grasslands are clearly needed to eliminate the confusion surrounding this issue and to develop sound management guidelines.

Exotic Grasses

A mounting problem in the West is the spread of exotic grasses. Grasses such as cheatgrass and crested wheatgrass (*Agropyron cristatum*) may be intentionally introduced as livestock forage or invade following disturbance, soon displacing native grasses (Mack 1981, Marlette and Anderson 1986). Although exotics such as lovegrasses (*Eragrostis* spp.) are planted as cattle forage, these grasses actually increase in response to grazing, as the livestock tend to preferentially forage on the native grasses and reduce competition for the lovegrasses (Bahre 1995 and references therein).

From a biodiversity standpoint, one of the problems with at least some exotic grasses is that they do not appear to provide adequate habitat for native grassland species. In Arizona, grasslands that have been seeded with Lehmann and Boer lovegrass (*Eragrostis lehmanniana* and *E. curvula* var. *conferta*) have been described as "biologically sterile" (Bock and others 1986:462). Twenty-six native species (10 plants, five birds, three rodents, and eight grasshoppers) were found to be significantly more abundant in native grasslands; only three native species (one bird, one rodent, and one grasshopper) were more common in the grasslands dominated by the African lovegrasses. Bock and others (1986:462) explain: "Indigenous animals appear to have evolved specific dependencies on the native flora and/or its associated fauna, insofar as most find the exotic grasslands far less inhabitable."

The increase of exotic grasses in the Southwest may have further ramifications as well, as they alter the natural fire regimes and lead to further ecological changes in the system (Anable and others 1992, Cox and others 1990). Some exotics such as Lehmann lovegrass increase after fire, and such grasses provide more fine fuel to carry fires than native species of grasses (Cox and others 1984). This may result in a positive feedback loop, in which introduced grasses play a beneficial role in terms of increasing fire frequency, yet simultaneously have the negative consequences of extending the coverage of the less-desirable exotic grasses as well as increasing the intensity of fire (Anable and others 1992).

Shrub Encroachment

The landscape of the Southwest has been inexorably altered over the past century by an extensive invasion of woody plants into areas that were formerly grasslands. Numerous authors have documented this transition from grassland to shrubland (for example, Bahre 1991, Buffington and Herbel 1965, Glendening 1952, Humphrey 1987) using a variety of techniques including early survey records (York and Dick-Peddie 1969) and photo points (Hastings and Turner 1965). The evidence suggests that although about 75 percent of southern New Mexico was covered in grasslands prior to the late 1800s, by the late 1960s only 5 percent grassland coverage remained (York and Dick-Peddie 1969). In another study of the Chihuahuan Desert, an estimated 25 to 50 percent of the area that is currently covered by shrublands was actually grassland less than 200 years ago (Dinerstein and others 2000). Such a conversion represents a significant loss of habitat for both plant and animal species that are grassland specialists.

Many factors appear to have played a role in this transformation. The conversion of grasslands to shrublands is a common result of overgrazing (Risser 1988). As livestock preferentially consume the more palatable species, initially the perennial grasses, competition is reduced and unpalatable woody species have the opportunity to become established (Humphrey 1958). Furthermore, heavy grazing reduces the fuel loads provided by grasses to the point that fire frequency and intensity become reduced, thereby removing the natural source of control for woody shrubs in grassland systems (Archer 1989).

Increases in woody plants such as mesquite following active fire suppression were recognized early on by Griffiths (1910). Since that time, the critical role of periodic fires in restricting woody plant establishment has been clearly demonstrated (for example, McPherson 1995 and references therein). Humphrey (1958:37) argued that the grasslands of the Southwest are a "fire-caused subclimax," but many other factors—such as soil type and herbivory by native animals—are now believed to interact with fire to maintain the grasslands of the Southwest (Curtin and others 2002). Although fire alone is not considered sufficient to prevent shrub encroachment and maintain the grassland condition indefinitely (McPherson 1995), it is a critically important element, and human alteration of natural fire cycles through suppression efforts has undoubtedly facilitated the spread of woody plants into these grassland systems.

Another explanation for the shift from grassland to shrubland in the Southwest is climate change. It has long been recognized that shrubs will increase in grassland systems in response to drought (for example, Schlesinger and others 1990). However, Brown and others (1997) found evidence for shrub increases not in response to drought, but rather in response to increased levels of winter rainfall in recent years. Furthermore, through the observation of livestock exclosures they were able to document that these increases in woody plants occurred in spite of protection from grazing. The authors argue that under conditions of high winter precipitation, the establishment of cool-season C_3 woody shrubs is favored over that of the warm-season C_4 grasses that normally dominate the landscape (Brown and others 1997 and references therein).

Prairie dogs are believed to be instrumental in retarding the growth of woody invaders such as mesquite (Koford 1958, Weltzin and others 1997), and some authors have suggested that the elimination of prairie dogs may be partially responsible for the widespread encroachment of mesquite into Southwestern grasslands observed in recent years (Parmenter and Van Devender 1995). Other authors have also found that small mammals play an important role in maintaining grassland systems by restricting the establishment of woody plants (for example, Curtin and others 2000).

Whatever the mechanism(s), there is little doubt that the continuing expansion of woody plants and cacti into Southwestern grasslands is one of the greatest sources of habitat degradation or loss threatening grassland specialists today.

Table 4-3. Threatened and endangered terrestrial animal species of Southwestern grasslands. The following species are not necessarily restricted to grassland habitats; although many are grassland specialists, this list also includes those species that rely heavily on grasslands in some parts of their range or as one component of a mosaic of habitats utilized. Sources for the information presented here include Arizona Game and Fish Department (1988), Association for Biodiversity Information (2001), New Mexico Department of Game and Fish (2000), and U.S. Fish and Wildlife Service (2001).

Common name/ Scientific name	Federal status	New Mexico status	Arizona status	NM	AZ	Primary threats	Types of grassland habitat utilized	Note
Amphibians								
Great Plains narrowmouth toad *Gastrophryne olivacea*		E	C	●	●	Water developments, water table draw-down, overgrazing, road development	Flooded desert grasslands	
Northern leopard frog *Rana pipiens*			C		●	unknown	High elevation wet meadows	
Plains leopard frog *Rana blairi*			E	●	●	Habitat loss, bullfrog predation	Low elevation wetlands	
Northern casque-headed frog *Pternohyla fodiens*			C		●	Vegetation clearing, overgrazing, water table draw-down, roads	Desert grasslands and scrub	AKA lowland burrowing treefrog
Reptiles								
Bunchgrass lizard *Sceloporus slevini*		T		●	●	Habitat loss and degradation due to overgrazing, drought, shrub invasion	Dense grass cover at mid-elevations; alkali sacaton in NM	Now restricted primarily to montane grasslands
Desert tortoise *Gopherus agassizii*	T		C	●	●	Habitat fragmentation, habitat loss, overgrazing, off-road vehicles	Semi-desert grassland	
Massasauga *Sistrurus catenatus*			E	●	●	Agricultural development, road kills	Desert grasslands	
Arizona ridgenose rattlesnake *Crotalus willardi willardi*			C		●	Mining, woodcutting, road development, collecting	Ecotonal montane grasslands	
New Mexico ridgenose rattlesnake *Crotalus willardi obscurus*	T	E		●		Collecting, habitat degradation due to overgrazing	Ecotonal montane grasslands	
Birds								
Crested caracara *Caracara cheriway*	T		C		●	Human disturbance at nest sites	Desert grasslands	Small breeding population in Arizona (Pima Co.)
Northern aplomado falcon *Falco femoralis septentrionalis*	E	E	E	●		Collecting, pesticides, loss of grasslands to shrub invasion	Desert grasslands, savannah	Now primarily in Mexico
Ferruginous hawk *Buteo regalis*			T	●	●	Loss of prairie dogs, human disturbance at nest sites	Desert, plains grasslands & shrubsteppe	
California condor *Gymnogyps californianus*	E		E		●	Direct and indirect human persecution (shooting, lead poisoning, and so forth)	Forages in grasslands	Experimental population reintroduced in Arizona
Lesser prairie chicken *Tympanuchus pallidicinctus*	C			●		Habitat loss, fragmentation due to overgrazing, agriculture	Shortgrass steppe (in NM, shinnery oak-bluestem association)	
Masked bobwhite *Colinus virginianus ridgwayi*	E				●	Habitat loss and degradation due to overgrazing	Desert grasslands and scrub	
Mountain plover *Charadrius montanus*	PT			●	●	Loss of prairie dog towns (early declines due to market hunting)	Shortgrass steppe	

White-tailed ptarmigan *Lagopus leucuras altipetens*		E		•		Grazing of tundra habitats, human disturbance	Alpine tundra, montane grassland	
Gray vireo *Vireo vicinior*		T		•	•	Unknown – possibly clearing of shrubs	Juniper grassland	
(Arizona) grasshopper sparrow *Ammodramus savannarum ammolegus*		T		•	•	Habitat loss and degradation due to overgrazing	Arid grasslands, desert scrub	
Baird's sparrow *Ammodramus bairdii*		T	T	•	•	Urban development, overgrazing on wintering grounds; loss of native prairies on breeding grounds	Shortgrass steppe, plains, desert grasslands	Wintering migrant in Southwest
Bobolink *Dolichonyx oryzivorus*			E	•	•	Agricultural and urban development, overgrazing	Plains grasslands, agricultural fields	Local breeder in Arizona (Apache and Navajo counties)
Sprague's pipit *Anthus spragueii*			C	•	•	Agricultural and urban development, overgrazing	Winters in Sonoita and San Rafael grasslands (Cochise and Santa Cruz Co., Arizona)	Wintering migrant in Southwest
Mammals								
Black-tailed prairie dog *Cynomys ludovicianus*	C		E	•		Direct human persecution, canine distemper	Shortgrass steppe, desert and plains grasslands	Extirpated in AZ; remnant populations in NM
Hualapai Mogollon vole *Microtus mogollonensis hualpaiensis*	E		E		•	Loss of habitat due to overgrazing, recreational development	High elevation grassy areas near springs assoc. with ponderosa pine/mixed conifer forest	Listed as Hualapai mexican vole; distribution highly restricted
Navajo Mexican vole *Microtus mogollensis navaho*			T		•	Loss of habitat due to overgrazing, mining, recreational development	Mid-elevation montane grasslands	
(Arizona) montane vole *Microtus montanus arizonensis*		E		•	•	Loss of habitat due to water diversions, livestock impacts	High elevation mesic grasslands and marshes	
Least shrew *Cryptotis parva*		T		•		Loss of habitat due to water diversions, livestock impacts, agriculture	Mesic grasslands and marshes	
Meadow jumping mouse *Zapus hudsonius*		T	T	•	•	Loss of habitat due to overgrazing, urban encroachment	Montane meadows	
White-sided jackrabbit *Lepus callotis*		T		•		Loss and degradation of habitat due to overgrazing, agriculture	Desert grasslands	Found in Hidalgo County, NM (and Mexico)
Black-footed ferret *Mustela nigripes*	E		E	•	•	Elimination of prairie dogs (primary prey source)	Desert and plains grasslands in association with prairie dog towns	Extirpated; experimental reintroductions in NM and AZ
Mexican gray wolf *Canis lupus baileyi*	E	E	E	•	•	Direct human persecution	Desert grasslands	Extirpated; experimental reintroductions in NM & AZ
Sonoran pronghorn *Antilocapra americana sonoriensis*	E		E		•	Loss of habitat due to grazing, agriculture; in Mexico, poaching	Desert grasslands, galleta grasslands of SW Arizona	
Chihuahuan pronghorn *Antilocapra americana mexicana*			T		•	Overhunting, habitat loss and fragmentation	Southern Arizona grasslands	Extirpated; present populations reintroduced
(Desert) bighorn sheep *Ovis canadensis mexicana*		E		•	•	Overhunting, habitat loss and fragmentation	Desert grasslands, montane grasslands	Reintroduction programs under way

E = endangered, T = threatened, P = proposed, C = candidate

Summary of Threats to Biodiversity in Southwest Grasslands

Unfortunately the native biodiversity of Southwestern grasslands is threatened by multiple sources, as are the native flora and fauna of all major ecosystems today. The alteration of natural fire cycles, inappropriate grazing regimes, eradication of keystone species, exotic grasses, habitat loss to shrub encroachment—these are just a few of the many factors believed responsible for the plant and animal species of Southwestern grasslands that have declined to the point of being listed as threatened or endangered (tables 4-3 and 4-4). Human activities such as urban development, mining, water diversions, and collecting have all contributed to declines in biodiversity, as has the purposeful elimination of certain species in several cases. Given the vast array of potential factors impacting the biodiversity of Southwestern grasslands, the discussion here of threats is not meant to be comprehensive, but only to touch on some of the major sources of declines in native species richness. Habitat fragmentation, a major potential threat to myriad grassland species in the Southwest, is discussed separately in the following section.

Ecological Consequences of Habitat Fragmentation

Introduction and Theoretical Background

Human use of the environment has led to a condition in which large areas of formerly continuous landscapes

Table 4-4. Threatened and endangered plants of Southwestern grasslands. The following species are not necessarily restricted to grassland habitats; although many occur primarily in grasslands, this list also includes those species that are found in grasslands in some parts of their range or as one component of a mosaic of habitats utilized. Sources for the information presented here include Association for Biodiversity Information (2001), New Mexico Native Plants Protection Advisory Committee (1984), New Mexico Rare Plant Technical Council (2001), and U.S. Fish and Wildlife Service (2001).

Common name/ ***Scientific name***	**Federal status**	**NM**	**AZ**	**Primary threats**	**Grassland habitat**	**Notes**
Arizona agave *Agave arizonica*	E		•	Collecting, overgrazing	Juniper grasslands 1100-2750 m	Endemic to central AZ
Cochise pincushion cactus *Coryphantha robbinsorum*	T		•	Collecting, pesticides, mining	Limestone hills in desert grasslands 1280 m	Only two populations, one in SE AZ and one in Mexico
Pima pineapple cactus *Coryphantha scheeri* var. *robustispina*	E		•	Collecting, livestock impacts, ORVs, habitat loss due to development	Open, flat alluvial basins of semi-desert grasslands and Sonoran desert-scrub 700-1400 m	Pima and Santa Cruz Co., Arizona and Sonora, Mexico
Kuenzler's hedgehog cactus *Echinocereus fendleri* var. *kuenzleri*	E	•		Collecting, livestock impacts	Great Plains grassland 1600 – 2000 m	Southcentral New Mexico
Fickeisen pincushion cactus *Pediocactus peeblesianus* var. *fickeiseniae*	C		•	Collecting, livestock impacts, ORVs	Limestone soils in Great Plains grasslands ~1500m	Coconino and Mohave Co., Arizona
San Francisco Peaks groundsel *Senecio franciscanus*	T		•	Recreational: off-trail hiking and climbing	Alpine tundra 3350-3750 m	Isolated mountain endemic
Sacramento Mountains Thistle *Cirsium vinaceum*	T	•		Water development, livestock impacts	Wet meadows ~2440 m	Endemic; persists only in areas too steep for livestock
Canelo hills ladies' tresses *Spiranthes delitescens*	E		•	Water diversions, livestock impacts, exotic species, mining	Permanently wet meadows (cienegas) ~1525 m	Limited to four cienegas in southern Arizona
Gypsum wild-buckwheat *Eriogonum gypsophilum*	T	•		Gypsum mining, recreational development	Open gypsum in grama grasslands ~1500m	Isolated population in Eddy County, NM

E = endangered, T = threatened, P = proposed, C = candidate have become increasingly fragmented and isolated. Urban development, agriculture, power lines, road construction, and other such activities have accelerated over the past century, subdividing the natural world into disjunct remnants of native ecosystems embedded in a matrix of anthropogenic land uses (Saunders and others 1991). The negative ecological impacts of such fragmentation on natural systems has led many conservation biologists to identify habitat fragmentation as one of the greatest threats to biodiversity today (Harris 1984, Noss and Cooperrider 1994, Wilcox and Murphy 1985).

Under the traditional definition, there are two fundamental components to habitat fragmentation. First, the activity that leads to fragmentation usually leads to an outright loss of some area of the original habitat; this component can be considered habitat loss or destruction. The second component is fragmentation per se, in which the remaining natural areas are relegated to patches of reduced size isolated from one another across the landscape (Wilcove and others 1986). A common analogy is that these fragments now exist essentially as habitat islands in a sea of altered or degraded lands; thus, this effect is also referred to as insularization (Wilcox 1980). The introduction of "edge effects" might be considered a third fundamental component of fragmentation. Edge effects are manifested in the form of altered physical processes and biotic interactions along habitat edges. The amount of edge habitat may increase dramatically through the process of fragmentation because reducing the size of the habitat patches results in a proportional increase in the amount of edge (Janzen 1983, Williamson 1975, Yahner 1988); altering the shape of fragments may also have this effect (Diamond 1975, Wilson and Willis 1975).

Many of the negative impacts of fragmentation are based on the principles of island biogeography, a classic model in conservation biology that predicts the number of species that will be found on an island as a function of species colonization and extinction rates, the size of the island, and its degree of isolation (MacArthur and Wilson 1967; fig. 4-1). Large islands near a potential source of immigrants have the greatest rates of colonization because individuals can traverse a short distance more easily, and the size of the island makes it more likely that dispersing individuals will happen upon it. Small islands far from the source have the least chance of intercepting potential colonists; it is less likely that individuals will be capable of traveling the greater distance required, and the small size of the island makes it less likely to be discovered. Balanced against the effect of colonization is that of extinction. Large islands support large populations of different

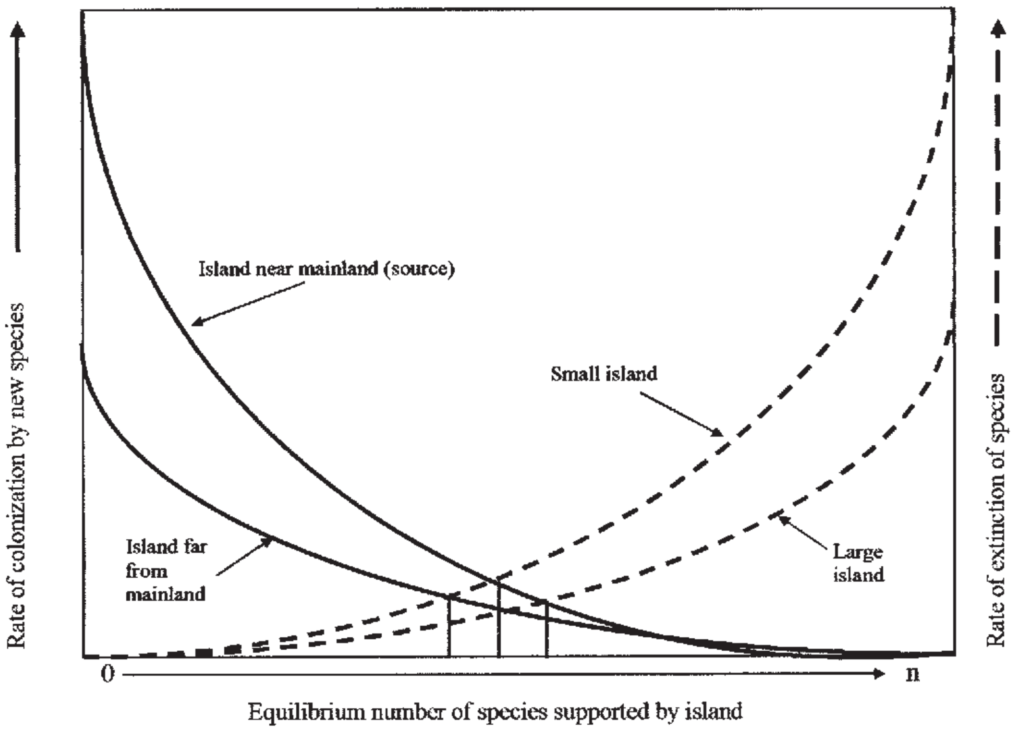

Figure 4-1. Graphic representation of island biogeography theory. Large islands located near a potential source of colonists should support a greater equilibrium number of species due to high immigration rates and low extinction rates. Small, isolated islands are predicted to have the least number of species due to lower colonization rates and greater extinction rates (after MacArthur and Wilson 1967).

species, and as large populations are more resilient in the face of potential extinction events, extinction rates should be relatively low. Small islands would support small populations of different species, and as small populations are particularly vulnerable to extinction (Harris 1984, Saunders and others 1991), extinction rates would be high. Based on the interaction between extinction rates and colonization rates, the model thus predicts that large islands located near a potential source of immigrants will support the greatest equilibrium number of species, while small, isolated islands will support the lowest number of species.

Although the theory of island biogeography was based on the species-area relationships observed on oceanic islands, this model has been widely applied to habitat fragments ("islands") in continental terrestrial systems as the basis for conservation planning (for example, Shafer 1990) and has largely formed the foundation of scientific inquiry into the effects of habitat fragmentation. Closely aligned with the theory of island biogeography and often applied to fragmented systems as well is the idea of metapopulation biology. The metapopulation concept holds that a population may be composed of a number of scattered subpopulations that are subject to repeated colonizations and extinctions, but that as a whole generally persists at some equilibrium level of abundance over time (Levins 1969, 1970). Metapopulations are typically characterized by one or more core or source populations and several fluctuating satellite populations. Satellite populations may occasionally go extinct when conditions are not favorable, but are replaced by new colonists dispersing from the core population when conditions improve (Bleich and others 1990). The viability of a metapopulation thus depends on the persistence of the core subpopulation and the ability of dispersing individuals to balance local extinction events by successfully recolonizing vacant patches (Gilpin and Hanski 1991); such recolonization events have been deemed the "rescue effect" (Brown and Kodric-Brown 1977).

Much of applied conservation biology rests on the precepts of island biogeography theory, the metapopulation concept, and the avoidance of edge effects. Basic principles of conservation design in fragmented landscapes include maximizing the size of habitat fragments to preserve species diversity and reduce extinction risk, minimizing the distance between fragments to facilitate dispersal, and controlling the shape of fragments to minimize the amount of edge relative to core habitat (Diamond 1975, Shafer 1990). In recent years, the major hypotheses stemming from the application of these theories (for example, that small fragments will support fewer species than large fragments) have been tested repeatedly and with largely variable results (discussed below; also see Bierregaard and others 1992, Debinski and Holt 2000 for a review). The vast majority of studies on the effects of fragmentation have centered on forested landscapes, particularly those in the tropics (for example, Lovejoy and others 1984) and the Central or Eastern United States (for example, Askins and others 1990, Robbins 1980, Robinson and others 1995, Whitcomb and others 1981, Wilcove and Robinson 1990). Few studies have focused on the impacts of fragmentation in North American grasslands (for example, Collinge 1998, 2000, Quinn and Robinson 1987, Robinson and Quinn 1988), and many of these have concentrated primarily on birds of the tallgrass prairie in the Midwest (for example, Johnson and Temple 1990, Winter and Faaborg 1999). As the effects of fragmentation in Western grasslands have gone largely unstudied, the discussion of the ecological impacts of habitat fragmentation that follows here is of necessity derived from studies conducted primarily in other ecosystems. On an ecological level grasslands suffer many of the same consequences of habitat fragmentation as do forested areas, although the contrast between the natural and altered conditions may not appear as abrupt. Data from grassland systems are utilized whenever they are available.

Edge Effects

Habitat edges exhibit a marked contrast in the structure and species composition of the vegetation between two adjacent elements in the landscape. Although natural edges occur in nature, as when blowdowns create openings in forests, the most common edge in a fragmented landscape is the product of human activity—an "induced" edge (Yahner 1988). Such edges have been associated with numerous negative impacts on the organisms originally inhabiting the remaining fragment, including increased levels of parasitism and predation, changes in species composition, and physical alterations in environmental conditions; these impacts are collectively known as edge effects (Lovejoy and others 1986, Yahner 1988). In forest systems, it is the removal of trees that results in fragmentation and the creation of habitat edges. Clearing for logging, development, agriculture, road construction, and other purposes all contribute to this process. In grassland ecosystems, it is just the opposite: the *introduction* of trees or shrubs is one of the primary causes of fragmentation and edge effects. Such seemingly innocuous human constructs as treelines planted for windbreaks or fencerows, stringers of trees along irrigation ditches, and trees along roadsides create long, linear stretches of edge habitat that can negatively impact the native species of the surrounding grasslands (O'Leary and Nyberg 2000).

Trees and shrubs create vertical structure in the grassland landscape, providing cover and perches for predators and leading to increased levels of predation along the edge habitat created by the interface between the grassland and the treeline (Burger and others 1994, Gates and Gysel 1978, Johnson and Temple 1990, Møller 1989, Ratti and Reese 1988, Winter and others 2000). Nest predators such as jays, raccoons, skunks and opossums hunt preferentially along the perimeter of agricultural fields or not far from a wooded edge, and prairie raccoons are known to use shelterbelts as travel lanes (Bider 1968, Fritzell 1978, Gates and Gysel 1978, Wilcove 1985). Structures such as fences, telephone poles, or rooftops provide perches for predators as well, and any human developments also tend to serve as a source of "urban predators" such as cats (Wilcove 1985). Perches that provide a good view to scan for potential host nests are also considered a critical habitat feature for brown-headed cowbirds, a nest parasite (Norman and Robertson 1975). In grassland systems, the introduction of trees, shrubs, or human structures provides these lookout sites, leading to significant increases in parasitism levels along such edges and resulting in reduced nest productivity or even nest failure in grassland breeding birds (Best 1978, Johnson and Temple 1986, 1990, Wray and others 1982). These effects have been found to extend into grasslands up to 75 m in from a woody edge (Burger and others 1994, Helzer 1996, Paton 1994), and many grassland breeding birds appear to avoid nesting or foraging within this zone (Delisle and Savidge 1996, Johnson and Temple 1990). In addition, grassland birds that do not tend to fly toward shrubs for cover when disturbed have been found to actively avoid woody edges, and the density of these birds tends to decrease as the amount of woody cover increases (Lima and Valone 1991). Such impacts are of particular concern because most species of grassland breeding birds have been exhibiting consistent and often striking population declines over the past few decades (Herkert 1994, Peterjohn and Sauer 1999, Samson and Knopf 1994), and many of these declines are believed to be linked with the loss and fragmentation of native grassland habitats (Herkert 1994, Johnson and Temple 1986, 1990, Peterjohn and Sauer 1999, Samson 1980, Vickery and others 1994).

The creation of edges, whether through increased woody vegetation or clearing, opens up avenues for incursion by opportunistic "edge" species and invasive exotics. The disturbance of native plant communities facilitates invasion by weedy and/or exotic plants, and such disturbance events typically accompany the activities that lead to fragmentation, such as road construction (Ewel 1986, Hobbs 1989, 1991, Rejmanek 1989, Saunders and others 1991, Schowalter 1988). Such increases in edge species or habitat generalists have also been found in such diverse taxa as insects (for example, Suarez and others 1998, Webb and Hopkins 1984), frogs (Laurance and Bierregaard 1996) and birds (for example, Herkert 1994, Samson 1980). Fragmentation and edge effects have been found to have a dramatic impact on the diversity of native ant species, for example. Suarez and others (1998) found that habitat fragments were characterized by high numbers of introduced ant species along the edges, and that unfragmented control plots supported three times as many native ant species as did habitat fragments. Furthermore, there was a negative correlation between the number of native ant species and time since fragmentation, suggesting that the native ants were incapable of recolonizing patches in the fragmented landscape once local extinctions had occurred.

Changes in the vegetative structure or species composition of the plant community may effect some changes in the animal community as well, typically leading to increased numbers of opportunistic species or habitat generalists (Saunders and others 1991). In grassland communities, the introduction of woody vegetation is correlated with increased species diversity of birds and lizards due to greater representation by generalists or species that normally utilize shrubby vegetation, while grassland specialists that formerly occupied the area tend to be lost (Germano and Hungerford 1981, Saunders and others 1991, Schmiegelow and others 1997). Changes in the faunal composition of habitat fragments may also impact the remainder of the community. In California grasslands, there was a significant correlation between the loss of native mammal species richness and the numbers of exotic birds and mammals occupying habitat fragments (Smallwood 1994). The loss of native species, it is proposed, leads to unstable population dynamics and lowers the "biotic resistance" (Simberloff 1986) of the community, leaving it vulnerable to invasion by exotics. Edges allow for the infiltration of formerly inaccessible interior habitats by a diverse array of invasives, but while fragments tend to support increased numbers of exotic or opportunistic species, habitat specialists tend to consistently decline within these patches (for example, Harris and Scheck 1991, Herkert 1994, Robinson and Quinn 1988, Samson 1980, Suarez and others 1998, Verner 1986, Webb 1989).

Impacts on the physical environment and ecological processes—The reduction in area of the original habitat and concurrent increase in the amount of edge can provoke physical changes in the fragment microclimate. Studies of forest systems have found that habitat fragments experience increased solar radiation along edges, altering plant species composition and leading to higher soil temperatures, in turn potentially affecting nutrient cycling (Lovejoy and others 1986, Saunders and others 1991). Increased soil temperatures may impact the numbers and activities of soil-dwelling organisms involved in decomposition as well as decrease the moisture retention capacity of the soil (Klein 1989, Parker 1989, Saunders and others 1991). Whether increased solar radiation effects such changes in grassland systems is largely unknown, although one study reports that nutrient cycling was not affected in studies of fragmented old fields (Debinski and Holt 2000). Another physical edge effect in forest fragments is the increased penetration of wind, which may result in direct physical damage to the vegetation or act to increase evapotranspiration and hence desiccation (Lovejoy and others 1986). Although grassland systems probably do not experience the same impacts due to their naturally short stature, winds do have increased accessibility to grasslands along cleared edges, resulting in the potential for increased transport of seeds, insects, and disease organisms into grassland fragments (Hobbs and Atkins 1988, Saunders and others 1991). Fragmentation can lead to changes in water regimes, as cleared areas contribute to increased runoff and erosion and lowered absorption of water into the soil (Kapos 1989, Saunders and others 1991). Replacement of deep-rooted native perennial grasses with introduced annuals can also contribute to reduced evapotranspiration rates, increased runoff, and increased temperatures at the soil surface. Such changes in the moisture levels of soils and runoff patterns can lead to the creation of new substrates for invasion by exotic or weedy plant species, impact seedbed characteristics, and result in the displacement of organisms that are unable to survive the altered environmental conditions (Hobbs and Huenneke 1992, Jones 1981, Saunders and others 1991).

Fire regimes may also be affected by habitat fragmentation. Most grasslands are considered fire-dependent ecosystems, requiring frequent fires to set back succession and maintain the natural distribution, productivity, and diversity of the grassland (McPherson 1995). As discussed above, habitat fragments are vulnerable to invasion by exotic species, and increased numbers of exotic grasses may seriously disrupt normal fire cycles. Introduced species such as lovegrasses (genus *Eragrostis*) are common throughout Southwestern rangelands (Loftin and others 2000). Sites dominated by lovegrasses may exhibit biomasses up to four times that of native grasslands, resulting in abnormally high fire frequencies and intensities that tend to kill the native plants but that lead to even greater abundances of the lovegrass (Anable and others 1992, Cox and others 1990). Fragments of native grasslands, on the other hand, may face the problem of decreased fire frequency. As fragments diminish in size, it becomes increasingly unlikely that they will be struck by lightning frequently enough to maintain the grasslands. A study of small prairie fragments in Wisconsin showed that the absence of fire over 32 to 52 years resulted in a loss of between 8 and 60 percent of the original plant species (Leach and Givnish 1996). Rare plants showed the greatest losses from these grassland fragments in the absence of fire. Roads and other agents of fragmentation may also act as firebreaks, restricting the spread of what would otherwise be extensive range fires. Finally, fragmentation due to human habitation also provides an incentive for active suppression of fires that could potentially threaten structures (Hansen and others 2002).

Area-Sensitive Species: Interaction of Edge Effects and Habitat Reduction

That species richness will decrease as a function of reduced geographic area is the most basic prediction of island biogeography theory. Studies of grassland birds show that this guild closely follows this prediction, as species richness is significantly correlated with the size of habitat fragments (Herkert 1994, Samson 1980). However, several species of grassland birds drop out of the community even in fragments that appear large enough to support them. These species simply will not utilize habitat fragments below a certain threshold size for nesting, even if the fragment is large enough to hold several average-sized territories and the habitat appears to be suitable; such species have been termed “area-sensitive” (see for example Herkert 1994, O’Leary and Nyberg 2000, Samson 1980, Vickery and others 1994; for forest birds, see Blake and Karr 1987, Robbins 1980, Robbins and others 1989, Winter and Faaborg 1999). The minimum area required by area-sensitive species varies widely: Eastern meadowlarks require only 5 ha, whereas Henslow’s sparrow will not nest in a fragment of less than 55 ha. Grasshopper sparrows and savannah sparrows fall toward the larger end of the range at 30 and 40 ha, respectively (Herkert 1994). Greater prairie chickens and upland sandpipers are well known for their avoidance of small grassland fragments and are found regularly breeding in fragments of 160 ha or more (Cannon and Christisen 1984, Samson 1980, Westemeier 1985). Furthermore, not only does nest density and nest success decrease with fragment size (Burger and others 1994, Johnson and Temple 1986, 1990, Samson 1980, Winter and Faaborg 1999; but see Delisle and Savidge 1996), but the simple distribution and density of several species of grassland birds is also positively correlated with fragment size (Helzer 1996, Herkert 1994, Winter and Faaborg 1999).

Exactly why these birds avoid small fragments, even when adequate suitable habitat appears to be available, is unclear. Most likely it is not the amount of available habitat per se that is important, but rather the amount of core habitat—that is, the amount

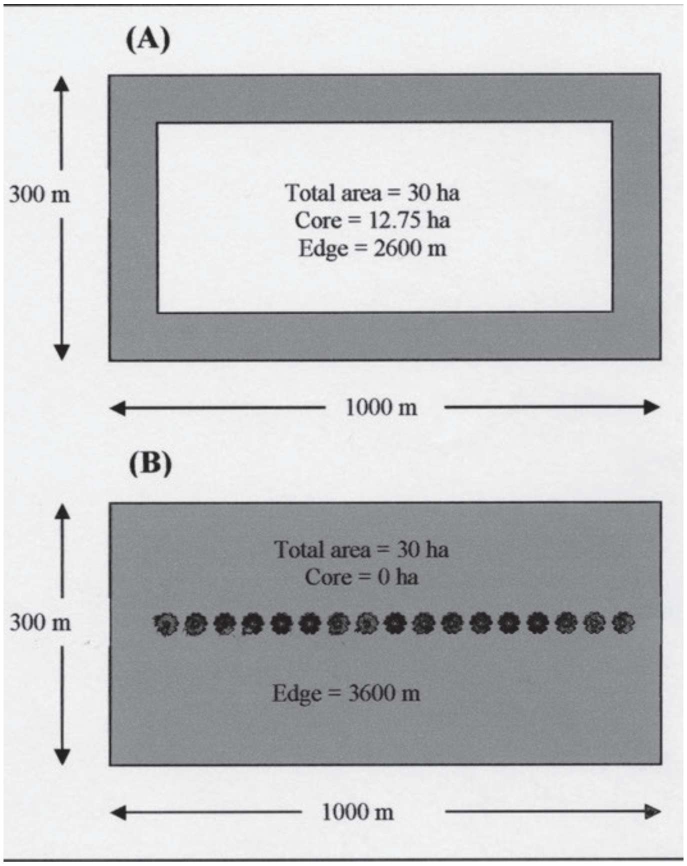

Figure 4-2. An example of how fragmentation and edge effects may render what appears to be an adequate area of quality habitat unsuitable for nesting or other activities for grassland birds. (A) Assuming edge effects extend a distance of 75 m into the interior from any edge (the shaded area), an area of 30 ha would offer 12.75 ha of potential core habitat. (B) Bisecting this area with a treeline (an induced edge) effectively places the entire area within the zone of edge effects and eliminates all potential core habitat, even though the total area is essentially unchanged.

of habitat that is far enough into the interior of the fragment to escape the edge effects of increased predation and parasitism—that is the critical factor (Brittingham and Temple 1983, Burger and others 1994, Gates and Gysel 1978, Johnson and Temple 1986, Winter and others 2000; see "Edge Effects" section above). Grassland birds clearly avoid nesting close to edges in habitat fragments (Delisle and Savidge 1996; Johnson and Temple 1990; O'Leary and Nyberg 2000; Warner 1994; Winter and others 2000); small fragments, particularly if they are somewhat linear in shape, may simply not provide any core area for nesting (fig. 4-2). Avoidance of edge for other activities, such as foraging, may also be a reaction to increased predator activity along edges (Andrén and Angelstam 1988, Fritzell 1978, Gates and Gysel 1978, Johnson and Temple 1986, 1990, Wilcove 1985, Yahner and Scott 1988). Several studies have found that the edge:area ratio of fragments has a greater influence on the presence and richness of grassland birds, and on the presence and success of nesting species, than does fragment area (Burger and others 1994, Helzer and Jelinski 1999, Temple 1986, Winter and others 2000). Area-sensitivity has been attributed only to birds thus far, but may possibly occur in other taxa as well.

Loss of Grassland Habitats and Fragmentation in the Southwest

In the Midwest, as little as 4 percent of the original native tallgrass prairie is estimated to remain; in some states, that figure may drop as low as 1 percent (Samson and Knopf 1994). Most of the Midwestern grasslands have been cleared for agriculture, particularly rowcropping for products such as wheat and corn. Destruction of Southwestern grasslands due to clearing for rowcrop agriculture has been relatively minimal, since such crops are few (for example, chile, cotton) and cover only a small portion of the land area of New Mexico and Arizona. Nonetheless, clearing for such purposes has contributed to the outright loss of native Southwestern grasslands, as has clearing for urban development (Bahre 1995). Grazing is the predominant use of Southwestern rangelands, and improper grazing practices can lead to loss of grasslands not through clearing per se, but through degradation of the grasslands to the point that they no longer function as suitable habitat for native species (for example, Bahre 1995, Bock and others 1984, Bock and Webb 1984, Noss and Cooperrider 1994). Uncontrolled heavy use of native arid grasslands by domestic livestock can lead to the loss of native grasses, the introduction of invasive exotic grasses and other weedy species, the destruction of cryptogamic crusts, altered grassland structure, and contribute to the conversion of grasslands to shrub-dominated desert scrub or pinyon-juniper (Bahre and Shelton 1993, Hobbs and Huenneke 1992, Humphrey 1958, Mack 1981, 1989, Martin 1975, Moore 1970, Wright and others 1979). Most grassland systems are maintained by periodic fires that set back succession, but a history of fire suppression has allowed the widespread encroachment of shrubs and trees into such systems (Humphrey 1958, McPherson 1995). The increased invasion of grasslands by exotic plants facilitated by grazing, road construction, and other forms of disturbance also contribute to altered fuel structure and fire regimes, leading to the eventual conversion of the native grassland to some other habitat type (Loftin and others 2000, MacDonald and others 1989, Panetta and Hopkins 1991, Saunders and others 1991). Whether lost through outright clearing, degradation, or gradual conversion, the end result of such habitat loss is twofold: first, there is an overall reduction in the area of extant native grassland, and second, those grasslands that do remain are relegated to disjunct fragments of relatively small size.

A new term for one particular source of fragmentation is becoming increasingly prevalent in the Western United States: exurban development (Knight 1999). Exurban development refers to low-density residential development that occurs beyond the limits of incorporated towns and cities. Expanses of land that were once devoted to agriculture or ranching are subdivided and sold for the development of "ranchettes" (single houses generally situated on from 10 to 40 acres of land) which contribute to this new trend of rural sprawl (Brown and McDonald 1995, Hansen and others 2002, Theobald 2000). Between 1994 and 1997, nearly 80 percent of the new home construction in the United States was in nonmetropolitan areas, and 57 percent of the houses were built on lots equal to or greater than 10 acres (Heimlich and Anderson 2001). This conversion of private ranching and farming lands to rural residential developments has been called "the most profound land use change in the New West" (Maestas and others 2002).

Although much of the land surrounding these homes remains in a relatively natural state, these low-density rural developments still introduce the negative effects of fragmentation into the environment with the associated predictable negative impacts on native biodiversity. The construction of buildings, roads, fences, and other structures associated with these rural subdivisions result in a dramatic increase in habitat fragmentation (Knight and others 1995). Knight (2003) reports that approximately one-fifth of the land area of a subdivided ranch is affected by houses and roads. The native species community composition changes in a predictable fashion, as specialized native species, such as dusky flycatchers, tend to be replaced by generalist, human-adapted species, such as black-billed magpies (Maestas and others 2002; see also Hansen and others 2002, Odell and Knight 2001). These changes are apparently little affected by the density of the housing development; that is, these effects are seen whether houses are densely clustered or spread more widely across the landscape (Odell and Knight 2001).

Predation and parasitism on native birds and mammals increases as residential development brings a concurrent increase in predators, both in the form of family pets and through associated increases in human-adapted species such as brown-headed cowbirds or jays (Hansen and others 2002, Maestas and others 2002). Nonnative plant species also tend to increase in association with exurban developments (Knight and others 1995, Maestas and others 2002), and natural disturbance regimes (such as fire) are disrupted (Bahre 1995, Hansen and others 2002). Furthermore, people tend to settle in the same areas that are most favored by wildlife, and outdoor recreationists moving into these rural areas both disturb and displace native wildlife (Hansen and others 2002). Although there has been little discussion of this issue until relatively recently, conservation biologists and land managers are becoming increasingly concerned about this newest threat to the biodiversity of the Western United States, apparently with good reason (see for example, Bahre 1991, 1995, Brown and McDonald 1995, Hansen and others 2002, Knight and others 2002, Odell and Knight 2001).

Changes in Species Richness and Species Composition

The reduced size and increased isolation of areas of native habitat have numerous theoretical repercussions for the native species that depend upon them, such as reduced species richness in the remaining fragments, interference with dispersal and colonization abilities, interruption of metapopulation dynamics, and increased risk of extinction (Meffe and others 1997, Noss and Cooperrider 1994, Wilcove and others 1986). Examination of these hypotheses in studies of habitat fragmentation has yielded mixed results. Although some habitats reduced in size do exhibit decreased species richness as predicted by island biogeography theory (Baur and Erhardt 1995, Bierregaard and others 1992, Collinge and Forman 1998), many either maintain the same number of species as prior to fragmentation, or actually exhibit an increase in species richness (Quinn and Robinson 1987, Simberloff and Abele 1982, Simberloff and Gottelli 1984). This is one of the key problems in applying island biogeography theory to continental systems: real islands are surrounded by a habitat matrix that is truly inhospitable to terrestrial species, whereas habitat "islands" are often encompassed by a matrix of habitats that, although hostile, may be habitable to some extent (Andrén 1994). In continental systems this matrix may serve as a source of potential colonists, allowing for the invasion of habitat fragments by weedy edge species, habitat generalists, or exotics (Doak and Mills 1994, Noss and Cooperrider 1994, Zimmerman and Bierregaard 1986). In such cases, fragmentation may actually result in an increase in species richness. However, the key point that is often overlooked is that while the overall number of species may rise, the *species composition* of the fragment may be irretrievably altered. Sensitive species of habitat interiors, endemic species, or habitat specialists may be lost, while numbers of common opportunistic species increase (for example, Harris and Scheck 1991, Lynch 1987, Noss 1983, Samson 1980, Verner 1986, Webb 1989, Webb and Hopkins 1984; see also discussion in the "Edge Effects" section above).

Although the number of species found in a habitat fragment may initially be high, one theory holds that over time the number of species the reduced fragment can now support will eventually drop—a process known as "relaxation" (Diamond 1972). A common criticism of contemporary studies of habitat fragmentation is that the time frame is too short—often on the order of just a few years—to document the relatively slow process of extinction following fragmentation (for example, Andrén 1994, Gonzalez 2000, Schmiegelow and others 1997, Tilman and others 1994). The process of species relaxation has been observed to some degree in birds (Schmiegelow and others 1997), small mammals, and insects (Debinski and Holt 2000), but perhaps the most thorough documentation of this phenomenon comes from a study of a microarthropod community in a bryophyte-based microlandscape (Gonzalez 2000). The reduced spatial and temporal scale of the dynamics in this community enabled the investigator to observe the effects of habitat fragmentation over many generations, which did in fact finally result in substantial numbers of local extinctions. Fragmentation thus has two effects on species richness operating on two time scales: first, immediately following fragmentation there is an "instantaneous sampling effect," in which species richness is a sample of the richness at a larger scale; second, there is the long-term process of community relaxation, resulting in a decrease in species richness to a new steady state value (Gonzalez 2000). This difference between the initial postfragmentation level of species richness and the eventual lowered steady state value has been termed "the extinction debt," because although the extinctions do not occur until many generations following fragmentation, they are bound to occur and are thus a debt that will come due in future years (Tilman and others 1994). The model upon which the extinction debt is based showed a 50 to 400 year or more time lag between habitat destruction and species extinctions; it also predicted that even those species initially most abundant in undisturbed habitat fragments can be the same species that are most susceptible to eventual extinction (Tilman and others 1994).

Vulnerability to Local Extinction

Habitat fragments may lose species for many reasons. Those species generally considered most susceptible to local extinctions are naturally rare species, species of habitat interiors or "area-sensitive species" (see discussion above), sedentary species, species with limited dispersal capabilities, species with specialized habitat requirements (especially if the resources required are patchy or unpredictable in occurrence) and animals with large home ranges or wide-ranging animals (Meffe and others 1997, Saunders and others 1991, Wilcove and others 1986). For naturally rare species, or those that occur at low densities in the environment, extinction due to fragmentation is largely a matter of chance. Being widely distributed across the landscape, the initial persistence of such a species would depend upon the likelihood that any remnant habitat patches just happen to capture some individuals of the population. The long-term maintenance of the larger population would depend upon the ability of these surviving individuals to successfully interact and reproduce in the fragmented landscape.

For other organisms, survival in a fragmented landscape may depend on the size of the remaining fragments. For each species, there is some "critical threshold" size of habitat area below which the species cannot persist. A generic threshold of 10 to 30 percent of the remaining habitat has been reported for birds and mammals (Andrén 1994), but the exact value of any such threshold ultimately depends upon the scale at which an organism interacts with its environment. In other words, it depends upon whether or not individuals of the species in question perceive the landscape as connected or fragmented (With and Crist 1995). For example, a wide-ranging species that is a habitat generalist, such as a robin, might essentially be able to experience a fragmented landscape as functionally connected, because the robin can easily utilize several disjunct fragments by flying between them and would be able to make use of the resources in most any fragment it happens upon. However, an animal with limited mobility and specialized habitat requirements such as a frog, might be incapable of crossing the surrounding landscape matrix and would therefore experience the same landscape as fragmented and restrictive. Furthermore, even if the frog managed to travel to another habitat patch, it would have to depend upon the presence of water in the new patch to persist there. The degree of fragmentation, then, as well as the value of a critical threshold, is a matter not only of the area of habitat remaining and its spatial arrangement, but also the habitat requirements and dispersal ability of the species in question (O'Neill and others 1988, Plotnik and Gardner 1993, With and Crist 1995). Even for relatively wide-ranging species, however, fragmentation can have significant impacts. Grassland raptors such as prairie falcons, ferruginous hawks, and rough-legged hawks have been found to decline in numbers if as little as 5 to 7 percent of the landscape becomes urbanized (Berry and others 1998).

Despite their excellent dispersal abilities, large animals are often the first to be lost from small fragments. For many of these, the remnant habitat patches may simply be smaller than their minimum home range or territory sizes. Some species of Midwestern raptors are thought to be declining because there are few tracts of habitat left that are extensive enough to meet their needs during the breeding season (Robinson 1991). Large carnivores typically maintain extensive home ranges; the home ranges of male mountain lions may exceed 400 km^2 (Seidensticker and others 1973). Mountain lions and other large carnivores such as grizzly bears are decreasing in numbers as the large tracts of habitat they require continue to shrink in size and become increasingly isolated from one another (Picton 1979, Wilcove and others 1986). Even many of our National Parks do not provide areas of habitat extensive enough to sustain populations of large animals over time without active management (Meffe and others 1997). Although larger parks are more likely to maintain their native animal communities, nonetheless nearly 30 species of mammals have experienced local extinctions from National Parks, including many smaller species such as rabbits (Newmark 1987, 1995). Overall, the current system of nature reserves in the world is considered to be too small to support viable populations of large carnivores and herbivores over the long term (Belovsky 1987, Grumbine 1990).

Animals with large area requirements face the problem of inadequate fragment size, but in addition these and all species face the problem of barriers to dispersal. Even for animals that have the ability to travel long distances, the terrain that must be traversed to move from one fragment to another is often so vast and hostile in nature that they stand little chance of surviving the trip. Roads are one potential barrier to dispersal and are a major cause of habitat fragmentation. One obvious consequence of roads is direct mortality. It is estimated that one million vertebrate animals are killed on roads in the United States every day (Lalo 1987). For the Florida panther, a wide-ranging species whose endangered status stems largely from habitat fragmentation, roadkill is the single greatest source of mortality (Meffe and others 1997). Roads also serve to block the movement of animals, both small and large, effectively isolating populations within habitat fragments. Many species of small mammals have been found to cross roadways only rarely, if ever (Adams and Geis 1983, Garland and Bradley 1984, Mader 1984, Oxley and others 1974). The same has been found for some carabid beetles (Mader 1984), and animals as large as black bears may find roads a barrier to movement (Brody and Pelton 1989). Even a 3-m dirt track was found to deter the movement of prairie voles and cotton rats in a Kansas grassland (Swihart and Slade 1984). Fencing of rangelands may also serve as a barrier to movement for large grassland species. Pronghorn, for example, normally travel across wide ranges but are restricted in their movements by their inability or reluctance to jump fences, potentially leading to death in cases where the animals are unable to escape particularly severe winter weather (White 1969, Wilson and Ruff 1999, Yoakum 1978). Although fences have now been designed to allow passage of pronghorn (Yoakum and others 1996 and references therein), they are not widely used, and recent studies demonstrate that fencing still serves as a barrier to natural pronghorn movements in the Southwest (van Riper and others 2001).

The inability of individuals to move freely between habitat patches may interrupt the stability of metapopulations, leading to their eventual decline and local extinctions. Key source populations may be eradicated in the process of fragmentation, or barriers such as roads, agricultural fields, or other inhospitable altered habitat may simply impede the dispersal of individuals to the point that the potential colonists required to shore up satellite populations are eliminated. Real world metapopulations in fragmented landscapes, such as that of the endangered bay checkerspot butterfly, closely follow the predictions of the theory of island biogeography: the probability of extinction of satellite populations increases with isolation from the source population and declines with increasing patch area (Thomas and Jones 1993).

Problem of Small, Isolated Populations

Long-lived species in particular may persist for many years following fragmentation due simply to the longevity of the individuals making up the population. Unless successful reproduction and recruitment is taking place, however, this species will disappear from the fragment as these individuals die out. For small populations in a fragmented landscape, the impediments to reproduction and recruitment are many. Simply by chance, the demographics of the population may not be conducive to successful reproduction; the age structure and sex ratio of the remaining few individuals are critical. A classic example of demographic misfortune is the dusky seaside sparrow: this endangered species was eventually reduced to a population of only six individuals, all of whom were male, thus dooming the species to extinction (Kale 1983). Successfully locating a mate is key to reproduction for most species, but fragmentation of the habitat may make it difficult for potential mates to find each other. Several studies have found a greater percentage of unmated male birds in small habitat fragments, indicating that females may not be able to locate them in isolated patches (Gibbs and Faaborg 1990, Robinson 1988, Simberloff and Gotelli 1984, Van Horn and others 1995, Villard and others 1993). Predation or parasitism may occur at greater levels in habitat fragments, thus reducing the reproductive success of individuals residing there (see discussion in the "Edge Effects" section). This last point underscores the importance of productivity data for estimating the viability of populations; numerous studies have shown that the abundance and/or density of individuals or nests are not reliable indicators of habitat quality (Maurer 1986, Van Horne 1983, Vickery and others 1992, Zimmerman 1992) or of nest success (Johnson and Temple 1990, Vickery and others 1992, Zimmerman 1984). Simply because large numbers of individuals of a particular species are found in a habitat fragment does not necessarily mean that the fragment is capable of supporting that species over the long term.

In addition to these problems, the small size and isolated nature of fragmented populations makes them vulnerable to other random processes. Natural catastrophes such as floods or fires may eliminate the few remaining individuals of a small population purely by chance. Random environmental changes may prove disastrous for such a population; a prolonged drought, for example, might lead to the extinction of a population of pupfish when the spring that they live in dries up. The genetic structure of populations may be profoundly affected by isolation. The interruption of gene flow among individuals in subpopulations may result in increased genetic drift, population bottlenecks, and inbreeding, all of which could lead to the fixation of deleterious alleles and decreased genetic diversity (Falconer 1981, Lerner 1954, Ralls and Ballou 1983, Wright 1977). Any of these factors—catastrophes, environmental variations, altered gene flow—as well as changes in demographic structure, might potentially lead to the extinction of a small, isolated population (Shaffer 1981). In reality, however, it is more likely a synergistic interaction between two or more of these factors that ultimately leads to the extinction of such populations in a process that is called an "extinction vortex" (Gilpin and Soulé 1986).

Of all these processes, the genetic consequences of isolation and interrupted gene flow in particular have received a great deal of attention by conservation biologists. In general, population bottlenecks, inbreeding, and the loss of genetic diversity are all believed to have a negative impact on the fitness of individuals through decreased fecundity and survivorship, a condition known as inbreeding depression (Falconer 1981, Lerner 1954, Ralls and Ballou 1983). The negative effects of inbreeding depression have been witnessed primarily in captive animal populations, but such impacts have also been documented in small wild populations that have become isolated, such as the lions of the Ngorongoro Crater in Africa that exhibit high levels of sperm abnormalities and low reproductive success (Packer and others 1991). However, there are also examples of small, isolated populations that have either retained relatively high levels of genetic variability (for example, one-horned rhinos; Dinerstein and McCracken 1990) and/or have survived severe population bottlenecks with no apparent problems stemming from inbreeding (for example, elephant seals; Bonnell and Selander 1974). Plants in particular seem to be resistant to the negative effects of inbreeding, most likely an adaptation to the limited dispersal ability of many species and self-fertilization (Barrett and Kohn 1991), although reductions in genetic diversity have been correlated with decreased fecundity in some plants found in isolated patches (Baur and Erhardt 1995). Although the impacts may be variable, the changes in gene flow and reduced number of individuals resulting from habitat fragmentation have the potential to significantly impact both the demographic and genetic structure of remnant populations (Fahrig and Merriam 1994). In the short-term, such alterations may be reflected in the reduced reproductive capacity and survivorship of individuals, possibly leading to localized extinctions for some species. On an evolutionary time scale, the reduced genetic variability stemming from processes such as fragmentation impedes the ability of individuals to respond to selection pressures, possibly leading to the extinction of the species (Frankel and Soulé 1981).

Corridors and Connectivity in Fragmented Landscapes

A central tenet of applied conservation biology has been the maintenance or reconstruction of habitat corridors to achieve connectivity between fragments (Meffe and others 1997, Preston 1962, Saunders and others 1991, Shafer 1990). In theory such corridors would essentially reconnect an otherwise fragmented landscape, facilitating the movement of individuals between patches, enabling continued gene flow, maintaining metapopulation dynamics, and reducing mortality of animals attempting to disperse through hostile terrain. In practice such corridors have produced mixed results. Most experiments have found that corridors do enhance movement, although this has been true primarily for small, less-mobile animals (Debinski and Holt 2000; but see Haas 1995). Small mammals such as chipmunks may use treelines to successfully colonize wooded patches in a fragmented forest landscape (Henderson and others 1985), and a few species of invertebrates have been found to preferentially utilize corridors in grassland fragments (Collinge 1998, 2000). In arid grasslands, movements of beetles in the genus *Eleodes* are strongly affected by vegetation structure (Crist and others 1992, Wiens and Milne 1989), and these beetles are one of the few species known to use corridors (Collinge 2000). Neotropical migratory birds, on the other hand, decrease in habitat fragments regardless of the degree of connectivity (Debinski and

Holt 2000). In the case of highly mobile organisms, the ability to move between fragments is most likely not the factor limiting populations. Corridors also do not appear to assist organisms with limited mobility; the habitat corridors provided by roadsides or ditches did not prove effective for colonization of habitat fragments by plants with short-range dispersal mechanisms (Van Dorp and others 1997). In general, many questions remain regarding the efficacy of corridors, particularly as they can serve not only for dispersal but also as conduits for predators, parasites, and disease transmission (see Noss 1987).

Impacts of Fragmentation on Grassland Plants

Due to their small area requirements, plants are often proposed to be relatively immune to habitat fragmentation (Noss and Cooperrider 1994). Some short-term studies have found that small fragments support just as many plant species as large fragments and that rare species appear to persist in such small fragments (Simberloff and Gottelli 1984). However, studies of fragmented grasslands in Europe using historical records have documented high levels of extinctions of plants when followed over the long term (Fischer and Stöcklin 1997). Although the total numbers of species at each site were essentially unchanged, there were significant increases in habitat generalists, while habitat specialists that formerly occupied the sites had disappeared. The interruption of plant-pollinator interactions, leading to reduced viability of plant populations in fragments, may be one factor contributing to local extinctions. Isolation of patches has been found to diminish both the abundance and species richness of bees, butterflies, and other pollinators (Debinski and Holt 2000, Jennersten 1988, Steffan-Dewenter and Tscharntke 1999). Fewer visits by pollinators can lead to reduced fecundity, viability, and decreased genetic diversity in plants isolated in habitat remnants (Aizen and Feinsinger 1994, Baur and Erhardt 1995, Jennersten 1988). The small population size and isolation of plants in habitat fragments may also result in inbreeding depression and loss of genetic diversity through founder effects, random genetic drift, and inbreeding (Rajmann and others 1994, Templeton and others 1990, van Treuren and others 1991, Young and others 1996, 1999). In some cases genetic variation continues to remain high in isolated plant populations, although even in these cases rare alleles may be lost from smaller fragments (Young and others 1999). In terms of negative genetic impacts, wind-pollinated species appear to be much more resilient to the effects of fragmentation (Fore and others 1992, Young and others 1993).

Summary of Habitat Fragmentation Effects

Not all organisms respond in the same manner to habitat fragmentation; persistence in habitat fragments, impacts on dispersal abilities, and use of corridors are highly species specific (Debinski and Holt 2000). Nor are all habitat fragments created equal; the size of the fragment, shape, amount of edge, and nature of the surrounding matrix will all influence the nature of the impacts on the individuals residing in the remnant patch (Helzer and Jelinski 1999). Taken as a whole, however, the majority of evidence from studies of habitat fragmentation indicates that the loss and isolation of natural habitats pose a strong threat to both regional and global biodiversity. Fragmentation greatly increases the risk of extinction for the native species of the original habitat through several mechanisms, including:

- Loss of habitat area for interior species.
- Barriers to dispersal, colonization, and maintenance of metapopulation dynamics.
- Random alteration of demographic and genetic structure resulting from isolation and small population size.
- "Edge effects" such as increased predation and parasitism, and invasion by exotic species or habitat generalists.
- Interference with biotic relationships, such as plant-pollinator interactions.
- Alteration of the physical environment, ecological processes, and natural disturbance regimes.

Strategies for counteracting the effects of habitat fragmentation include:

- Preventing or minimizing further fragmentation.
- Managing lands to restore natural disturbance regimes.
- Maintaining or restoring large natural areas to act as avenues for dispersal and genetic mixing of populations.
- Restoring habitat to increase the size of remaining habitat patches or buffer existing patches (Meffe and others 1997, Shaffer 1990).

Some basic design principles to counteract the effects of habitat fragmentation are summarized in figure 4-3. In an already fragmented landscape, it may be necessary to strive for protection of the largest possible area through strategies such as creating corridors by restoring connections between natural areas (Gatewood 1998). However, the importance of preserving extensive landscapes in order to maintain ecosystem processes cannot be overemphasized; wherever possible, such a strategy should be the first line of defense.

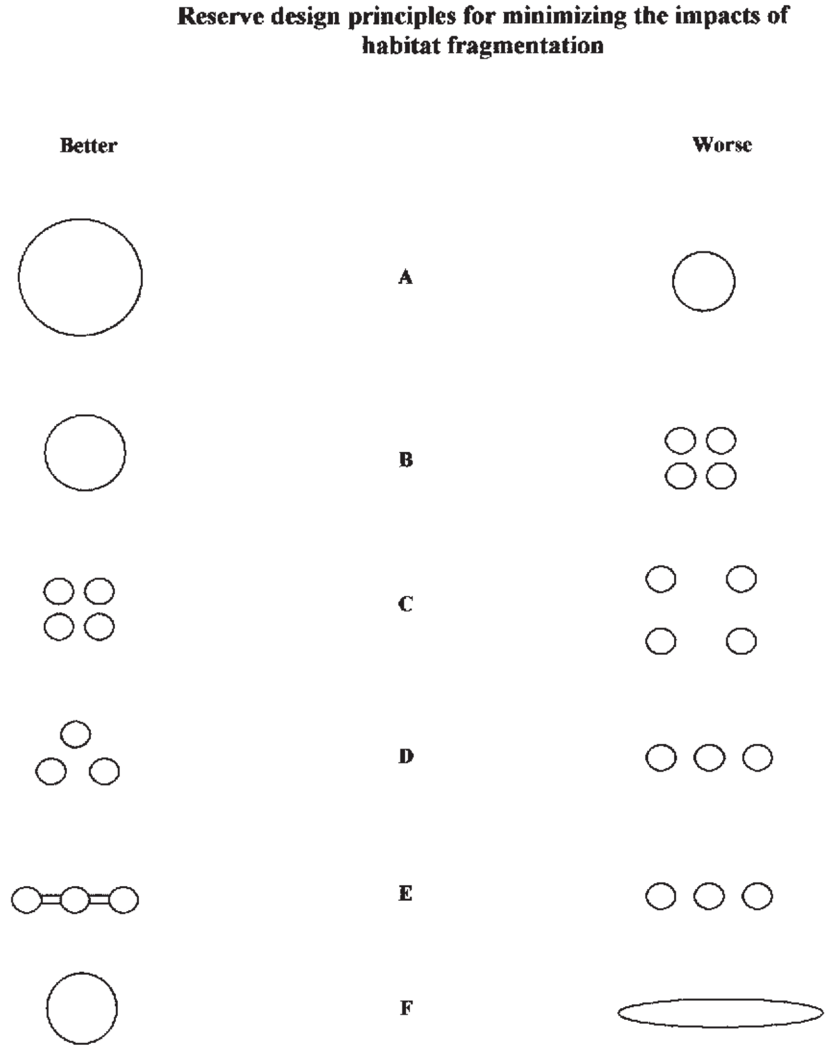

Figure 4-3. All areas of habitat are circular to minimize the amount of edge relative to area. These principles are based upon the theory that, in general: (A) large reserves are better than small to maximize number of species and individuals supported; (B) one large fragment is better than several small fragments, even if total area is equal; (C) fragments close together are better than fragments more widely separated to enhance movement between fragments; (D) fragments clustered are better than fragments strung out in a linear fashion to allow for easier movement between fragments; (E) fragments connected by corridors are better than fragments that are entirely disjunct to enhance movement between fragments; (F) fragments that are circular are better than fragments that are long and thin to minimize edge effects. Based on Diamond (1975). As discussed in the text, the basic theories behind these principles are not without controversy, yet they remain the primary foundation upon which contemporary conservation design is based.

The vast majority of information that we have on the consequences of habitat fragmentation is based on studies of forested ecosystems or tallgrass prairie. One of the greatest needs for research in the grasslands of the Southwest is the need to study the impacts of fragmentation in these arid grassland systems.

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