

Wildlife of Eastside Shrubland and Grassland Habitats

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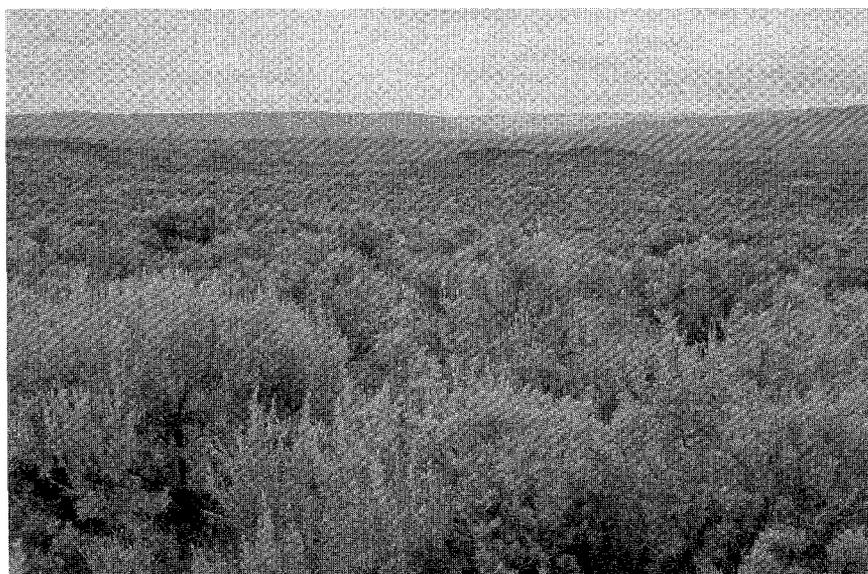
Introduction

The rain shadow of the Cascade Mountains gives rise to a suite of arid and semi-arid habitats that differ substantially from those of the surrounding forest. O'Neil and Johnson¹⁰⁰ have classified these habitats into 6 different types: shrub-steppe, dwarf shrub-steppe, desert playa and salt scrub, western juniper and mountain mahogany woodlands, eastside canyon shrublands, and eastside grasslands. Most of these communities are dominated by shrubs and herbaceous vegetation (grasses and forbs) and typically have a microbiotic crust of lichens and mosses binding the upper surface of the soil. With the exception of the western juniper and mountain mahogany woodlands habitat type, trees in these communities are limited mainly to riparian zones and ecotones with forested habitats and are entirely absent from extensive areas. Much of the historical vegetation in these habitat types, particularly in Washington and north central Oregon, has been converted to agricultural crops.^{27, 113} In some areas, the only remaining native communities are on rocky soils or steep slopes unfit for agriculture. The dominant land use in these shrubland and grassland habitats is livestock grazing, and few examples of undisturbed stands exist, limited primarily to sites where topography or remoteness from water has made access for livestock grazing impractical.²²

Although pristine climax communities do exist for eastside grassland and shrubland habitats, the majority of sites have been shaped by a legacy of past land uses that includes continuous grazing by livestock and range improvements to increase livestock forage and that in turn has facilitated invasion by exotic vegetation. This legacy has modified the vegetation community in many areas, with some changes occurring so long ago that they are not apparent to the present day observer.²² Changes in the herb community brought about by excessive grazing and exotic invaders are particularly damaging in these arid habitats where the herb layer often contains the most vegetation biomass. Moreover, the successional trajectory of vegetation communities in arid habitats can be modified by influences such as grazing and fire, resulting in present day "zootic" climax communities that differ greatly from those which occurred historically.^{22, 128} Sites in southcentral Washington that were dominated by exotic annuals in the 1950s still have not been colonized by native plants some four decades later.¹¹⁵

The low vertical structural diversity inherent in these habitats provides fewer habitat layers for wildlife, resulting in lower diversity in some taxa. There are, for example, no arboreal mammals or canopy nesting birds.

Photograph 1. Shrub-steppe habitats dominate the landscape in much of eastern Oregon and Washington. Moses Coulee, Douglas County, Washington. (M. Vander Haegen, WDFW).



Habitats with a shrub component tend to have more diverse wildlife communities than grass dominated habitats, a function of increased nesting and foraging strata. For example, the shrub-steppe habitat has 49 closely associated species, whereas eastside grassland has only 34. Sites dominated by native plants have more closely associated species than sites dominated by exotics (34 species closely associated with eastside grasslands vs. 2 with modified grasslands).

Available water is a defining factor in these arid and semi-arid habitats, and this strongly shapes the composition of plant communities²² and influences the ecology and behavior of associated wildlife. In Washington, precipitation occurs primarily during late autumn and winter with annual totals ranging from 5.9 inches (150 mm) in the lowest parts of the Columbia Basin to 21.7 inches (550 mm) in the higher elevations near the forest ecotone. Annual snowfall can be substantial at higher elevations and snow can remain in colder areas into spring. Growth of vegetation in spring is affected by available soil moisture, a result of "bioyear" precipitation—water that falls as rain or snow from October-April and is stored in the soil.²² Bioyear precipitation varies widely from year to year, affecting plant growth⁶⁹ and influencing both forage for herbivorous wildlife and populations of herbivorous insects that form the food base for many reptiles and breeding birds. The marked seasonality in precipitation creates a flush of available food in spring and early summer that is capitalized on by breeding birds. In the lower rainfall zones most vegetative growth is completed by early summer and many plants senesce in preparation for the dry, hot months ahead.

Adaptations to Arid, Seasonally Hot and Cold Environments

Hot and arid conditions that prevail in many of these habitat types in summer play a part in determining the animal life that can persist there. Daytime temperatures can exceed 113°F (45°C) and free water can be scarce. Some species are physiologically adapted to survive in such an environment, whereas others modify their behavior—some survive by a combination of both strategies (Table 1). Species that require daily access to free water (e.g., bats, elk) must restrict their daily use areas to include open water. Mourning doves must drink daily and frequently fly great distances to reach free water.⁷⁸ Other species drink infrequently and conserve body water by minimizing water lost through evaporation, respiration, and excretion. These species meet their daily water requirement through moisture contained in food and from metabolic water produced from oxidation as part of digestion.¹⁷ The grasshopper mouse and the sage sparrow are examples of species that spend considerable time far from free water. Black-throated sparrows are particularly well adapted to life in arid environments; experiments have shown that they can survive on a diet of dry seeds without access to free water and without restricting their activity.⁷⁸

Birds and reptiles have some physiological characteristics that allow them to tolerate arid conditions. Birds excrete nitrogenous waste as uric acid, a characteristic that they share with reptiles and that uses <10% of the water required by mammals excreting urea.⁷⁸ Birds also operate at a higher body temperature than do most other animals, allowing them to cool themselves by convection at most ambient air temperatures. Some arid-land birds (e.g., black-throated sparrow) can drink and process water with a high saline content.⁷⁸ Reptiles are particularly well adapted to arid environments. Their dry, scaly integument and lack of exocrine glands reduces water loss to the environment¹⁷ and, unlike amphibians, they can reproduce independent of standing water.

Many arid-land species modulate their activities to avoid temperature extremes, seeking shade during the heat of the day or, in the case of the rock wren, seeking the cooler environment offered by rock crevices.⁷⁸ Fossorial species find cooler temperatures and reduced water loss underground. Seeking milder conditions in underground

Table 1. Living and breeding in arid and semi-arid environments: constraints, consequences, and animal adaptations.

A. Environmental Constraints

- High and low temperature extremes
- High winds
- Open habitats
- Aridity
- Strong temporal resource gradients
- Fragmented habitats
- High annual variability in rainfall

B. Ecological Consequences

- Cooling and warming adaptations required
- Increased variability in annual reproductive output
- Need to disperse across unsuitable habitats
- Water conservation required

C. Adaptations

- Physiological
 - Facultative breeding
 - Flexible reproductive timing
 - Ability to process hypersaline water
 - Ability to survive without free water
 - Large ears for cooling (jackrabbits)
 - Speed for eluding prey (pronghorn)
- Behavioral
 - Cryptic behavior
 - Shade-seeking
 - Burrow into soil to avoid heat extremes
 - Daily trips to available water

D. Life History Adaptations

- Cryptic plumage/pelage
- Strong seasonality in habitat use
- Colonial living
- Accelerated larval development
- Hibernation or migration during winter
- Estivation during summer

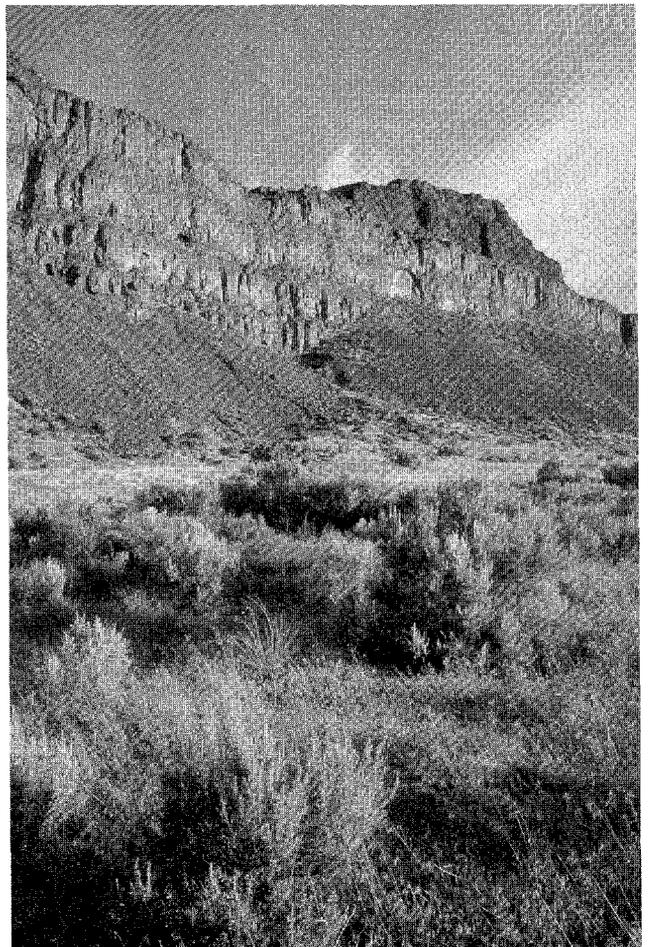
burrows can be a temporary tactic used during the heat of the day, or it can be a way to escape harsh conditions for much longer periods. Some fossorial mammals, including ground squirrels and pocket mice, may estivate during the driest months and emerge from their burrows when the winter rains renew vegetation growth. Great Basin spadefoot toads are one of few amphibians to live in arid habitats, surviving the arid summer months by estivating underground. Members of this genus minimize water loss by burrowing underground and by allowing urea levels in the blood to rise as the soil around them dries. Sufficiently high internal osmotic pressures create water potentials that should allow spadefoot toads to absorb water from even very dry soil.¹¹¹ Spadefoot toads are also capable of tolerating considerable loss of body water (up to nearly 50%).¹³⁸

Spadefoot toads may spend many months burrowed deep in the soil, emerging to feed or to breed on rainy nights. Their facultative breeding system is well adapted to arid habitats, allowing them to track local conditions and breed after rain events or, in more recent times, after irrigation has wetted the soil.⁹⁸ They are adapted to temporary breeding ponds by needing only 2-3 days for egg hatching and only a few weeks for development to metamorphosis. Some tadpoles may feed on carrion as well as vegetation, which also may result in more rapid development. Tadpoles of some other species of spadefoot toads are known to be cannibalistic.⁹⁸

Cold conditions may limit the activity times of ectotherms daily and seasonally; however, their low energetic requirements (typically <10% of those of similar sized endotherms) allow amphibians and reptiles to survive for extended periods of time without eating. For example, an adult rubber boa, maintained in captivity under simulated field thermal gradients, voluntarily fasted for 23 months before eating, with no apparent long-term ill effects (Michael E. Dorcas, Davidson College, pers. comm.). Such fasting abilities enable these animals to survive conditions such as droughts when food availability may be low. The low metabolic rates of amphibians and reptiles also result in low rates of respiratory water loss.¹¹¹

Habitat Elements— Special Habitat Features

Some wildlife species of eastside grassland and shrubland habitats are strongly associated with special features (habitat elements) on the landscape and are unlikely to be found in their absence. Many species are associated with geological formations such as rock outcrops, cliffs, and talus slopes. Peregrine falcons, cliff swallows, and golden eagles nest on cliffs and rock faces and are among the 35 species associated with these structures. All of the snake species and about half of the lizard species in shrub-steppe habitats are associated with rocky features (individual rocks, talus slopes, outcrops, cliffs, ridges, caves, crevices, etc.) that serve a variety of functions including providing foraging locations (e.g., side-blotched lizards), retreat sites from predators (e.g., western fence lizards), vantage points



Photograph 2. Cliffs provide valuable roost sites for bats as well as nest sites for numerous species of shrub-steppe wildlife. Grand Coulee, Douglas County, Washington. (M. Vander Haegen, WDFW).

within territories (e.g., Mojave black-collared lizards), nesting sites (e.g., ringneck snakes), and gestation sites (e.g., western rattlesnakes). Rocky features are often needed to provide the temperature gradients required for effective behavioral thermoregulation.⁵⁶ Rocky features such as talus slopes and crevices within lava flows are especially important as overwintering sites for snakes, and their availability may limit the distribution of some species.⁴³ Often, overwintering sites are used by multiple species (e.g., striped whipsnakes, gopher snakes, western terrestrial garter snakes, and western rattlesnakes). Talus slopes and talus-like structures (rock piles, lava stringers) are associated with 22 species and provide refuge for small mammals like the least chipmunk, and hibernacula for a variety of snakes including the western rattlesnake. Some amphibians (e.g., long-toed salamanders and Pacific treefrogs) may be associated with talus. Rocky outcrops provide nest sites for ferruginous hawks and habitat for rock wrens, yellow-bellied marmots, and 42 other species. Caves are used by 18 species, including bobcats and common ravens, and are critical habitats for bats for roosting and hibernation.

Burrowing owls and fossorial mammals like the Columbian ground squirrel and badger require deep soils for constructing nests and dens. Washington ground squirrels used sites where soils were deeper, weaker, and contained less clay than adjacent, unoccupied sites.⁴ Soil type also can affect the persistence of underground burrows. In an Oregon study, nest burrows of burrowing owls were more likely to be reused in subsequent years when constructed in silty-loam soil; burrows in loamy-sand soils were often silted in and thus unusable by the next breeding season.³⁸ Loose soils are important to burrowing species like Great Basin spadefoot toads, sagebrush lizards, and horned lizards. Several species of reptiles (e.g., long-nosed leopard lizards) bury their eggs in loose soils.

The burrows of other animals are often used by burrowing owls, many species of lizards and snakes,¹³⁴ and some species of amphibians (e.g., tiger salamanders and western toads). Burrows may serve a variety of functions, including providing retreats from predators (e.g., long-nosed leopard lizards), foraging sites (e.g., rubber boas), egg deposition sites (e.g., collared lizards), and thermal gradients for regulating body temperature. The use of burrows by reptiles and amphibians in dry shrub-steppe habitats is particularly important for minimizing evaporative water loss.

All amphibians in eastside shrubland and grassland communities are associated with standing or slow-moving water sometime during their life cycle, because it is required for breeding and larval development. Several species of reptiles also are associated with water (i.e., marshes, pools, ponds, lakes, streams, or rivers). Western skinks and rubber boas are often found near moist areas. Garter snakes often forage in the water or along shorelines. Painted turtles overwinter, breed, and forage in water. Human-made stock ponds have probably increased the amount of suitable habitat for some of these water associated species.

Anthropogenic structures are frequently used for nesting sites or as shelter by a variety of wildlife. Common ravens, American crows, and several buteonid hawks nest on power transmission towers. Construction of such towers was responsible for an increase in the number of breeding ferruginous hawks on the Hanford Site in southcentral Washington in the 1980s.³² Cement road culverts and bridges are used as shelter or as nest sites by cliff swallows and 13 other species; they provide appropriate nesting structure previously missing in many areas. Garter snakes often use the foundations of bridges and buildings for nocturnal retreat sites and overwintering sites. Western fence lizards and racers use stone walls for retreat sites and foraging areas.

Abandoned homesteads and farm buildings provide unique vertical structure in many areas of shrubland and grassland habitat. Old buildings are used as nest sites by kestrels, barn owls, deer mice, and numerous other species. Abandoned buildings and trash piles may attract small mammals and thus reptiles that prey on them (e.g., western rattlesnakes). Gopher snakes may use wells for estivation sites (C.R. Peterson, Idaho State University, pers. obs.). Trees planted as windbreaks around homesteads and orchards provide nesting structure for red-tailed hawks, black-billed magpies, orioles, and numerous other birds. Abandoned farm equipment serves as nesting sites for European starlings, domestic pigeons, western kingbirds, and other birds as well as various small mammals.

Bird Communities in Shrub-steppe

The following wildlife community profiles focus on shrub-steppe habitat, with references to other eastside shrubland and grassland habitats where appropriate. We selected shrub-steppe as a focal habitat based on its dominance in eastside landscapes and because of the severe management issues that this habitat currently faces.

Shrub-steppe bird communities are characterized by a relatively small number of breeding species. The



Photograph 3. Talus slopes and talus-like structures provide hibernacula for western rattlesnakes. Grant County, Washington. (M. Vander Haegen, WDFW).

assemblage of passerines, for example, typically totals 4-8 birds and often is dominated by a single species.¹⁵⁶ Extensive surveys including many sites may generate a much larger species list;²⁷ however, many species on these longer lists occur infrequently or breed in other habitats and are tallied on surveys as they forage or migrate through the shrub-steppe. For example, three years of surveys on one site in the shrub-steppe of eastern Washington produced a list totaling 28 species; however, only 5 species were documented to nest on the site (Washington Department of Fish and Wildlife [WDFW] unpubl. data). Fragmentation of formally extensive shrub-steppe and new habitats associated with agriculture and irrigation contribute species that are not typical of the shrub-steppe community type.

What the shrub-steppe bird community may lack in variety, it makes up for in specificity. Several species associated with shrub-steppe are so dependent on sage cover that they are termed sagebrush obligates. Sage and Brewer's sparrows, sage thrashers, and sage grouse are considered obligates, whereas vesper sparrows and green-tailed towhees are classified as near-obligates.⁸ These species often characterize the big sagebrush (*Artemisia tridentata*) shrub-steppe community, although other shrub-steppe or grassland-associated species may dominate at specific sites. In big sagebrush communities in northcentral Oregon and southcentral Washington, the breeding bird community was dominated by sage sparrows and western meadowlarks^{54, 146} (WDFW unpubl. data). In northcentral Washington, the breeding bird community was dominated by Brewer's sparrows and vesper sparrows (WDFW unpubl. data). Disturbed sites with few shrubs frequently are dominated by western meadowlarks, horned larks, grasshopper sparrows, and long-billed curlews.^{54, 146}

Most passerines that breed in shrub-steppe eat insects and other arthropods at some period during the year. Some birds are primarily insectivorous, consuming a variety of invertebrates that they capture on the wing, or glean from shrubs or herbaceous vegetation. Even granivorous birds that feed mostly on seeds and plant material as adults feed invertebrates to their young to supply critical nutrients. Total precipitation during the biowater affects primary and secondary production and varies widely among years in this ecosystem.²² This yearly variation in rainfall can affect reproductive success of shrub-steppe nesting birds, probably through its influence on availability of arthropod prey.¹²¹

The community of breeding birds in shrub-steppe is largely comprised of migrants, many ($n = 16$) wintering south of the United States and therefore termed *Neotropical migrants*. Spring migrants that pass through the shrub-steppe on their way to more northern breeding grounds and that spend time in the sagebrush communities include the white-crowned sparrow and ruby-crowned kinglet. Resident species are largely gallinaceous birds (e.g., greater sage-grouse and sharp-tail grouse) and corvids (e.g., common raven and black-billed magpie). The winter bird community is supplemented by species that breed in more

northern sites but spend all or part of the winter in the shrub-steppe, including rough-legged hawks and northern shrikes.

Two native galliforms, greater sage-grouse and sharp-tailed grouse, live in shrub-steppe communities of Oregon and Washington. Both are ground nesters and require large areas for their annual home ranges, including open areas for leks in the spring. Both grouse are listed as threatened in Washington, and the sharp-tailed grouse was only recently reintroduced to Oregon after having been extirpated in the 1960s.⁹⁹ Loss of habitat and fragmentation by agriculture are believed to be primary causes for the decline of these species.^{16, 124} Exotic galliforms that frequently can be found nesting in shrub-steppe include the chukar, gray partridge, and ring-necked pheasant.

Numerous raptors use shrub-steppe for nesting and foraging, preying on a variety of small mammals, reptiles, birds, and insects. Burrowing owls and short-eared owls nest on the ground in shrub-steppe and can be found nesting in stands of big sage, antelope bitterbrush (*Purshia tridentata*), or open, low grasslands. Northern harriers often forage in shrub-steppe, especially along edges with agriculture, but they require wetlands or similar areas of thick reeds or grasses for their ground nests. Most raptors require elevated nesting sites and historically nested on buttes, cliffs, and in riparian-associated trees. In northcentral Oregon, juniper trees were important nesting platforms for ferruginous and Swainson's hawks, and long-eared owls.^{39, 54} Juniper trees also were important as nest sites for ferruginous hawks in southcentral Washington.³¹ Artificial planting of trees and the proliferation of power transmission lines during the last century have increased the availability of suitable nest sites and likely have boosted raptor populations in some areas.¹¹⁹

A recent analysis of population trends using the Breeding Bird Survey (BBS)¹²² identified 8 shrub-steppe-associated species that are declining in the interior Columbia River Basin. Four of these species, the Brewer's sparrow, lark sparrow, loggerhead shrike, and western meadowlark, are closely associated with shrub-steppe. Numerous other birds, including the sage sparrow, grasshopper sparrow, and burrowing owl, likely are not monitored adequately by the BBS and will require specialized monitoring to detect changes in their populations.¹²²

Organizing Principles: Birds

Shrub-steppe communities extend from the northern border of Washington to the southern border of Oregon. Although some shrub-steppe-associated birds are common to much of this area, there are differences in avian species assemblages across this latitudinal gradient. For example, black-throated sparrows and green-tailed towhees reach the northern extent of their range near Oregon's northern border and occur only sporadically in Washington. Sharp-tailed grouse occur in several locations in northcentral and eastern Washington, but were extirpated from Oregon and have only recently been



Photograph 4. Sage sparrows are sagebrush obligates and nest in extensive tracts of shrub-steppe. Moses Coulee, Douglas County, Washington. (M. Vander Haegen, WDFW).

reintroduced.⁹⁹ Bird communities also may change along an elevational gradient in shrub-steppe, as rainfall increases with elevation and changes the vegetation community. Vesper and Brewer's sparrows occur rarely in sage communities on the low elevation Columbia River Plain, whereas they are regularly found on ridges only a few kilometers to the west in sage communities above 5,900 feet (1,800 m).¹⁴⁶ As one proceeds north in the Columbia Basin, elevation increases and these species become common at all elevations. In fact, these two sparrows, along with the sage thrasher, typify sage communities in northcentral Washington (WDFW unpubl. data).

Presence and abundance of individual bird species vary with a range of local and landscape variables. On a gross scale, vegetation structure determines what species can breed in a community through presence of suitable nesting and foraging strata. A suite of grassland-associated birds that breed in shrub-steppe includes the grasshopper sparrow, horned lark, western meadowlark, and long-billed curlew. These birds nest on the ground and depend on grasses and forbs to conceal their nests. Native perennial grasses generally dominate the ground layer in undisturbed shrub-steppe communities, and presence of several ground-nesting species, including the grasshopper sparrow and horned lark, increased with percent cover of these grasses.¹⁴⁷ In contrast, long-billed curlews in northcentral Oregon¹⁰⁴ and southeast Washington² seemed to prefer short-statured annual grasslands for nesting and foraging, an apparent adaptation to this recent, disturbance-related vegetation community.

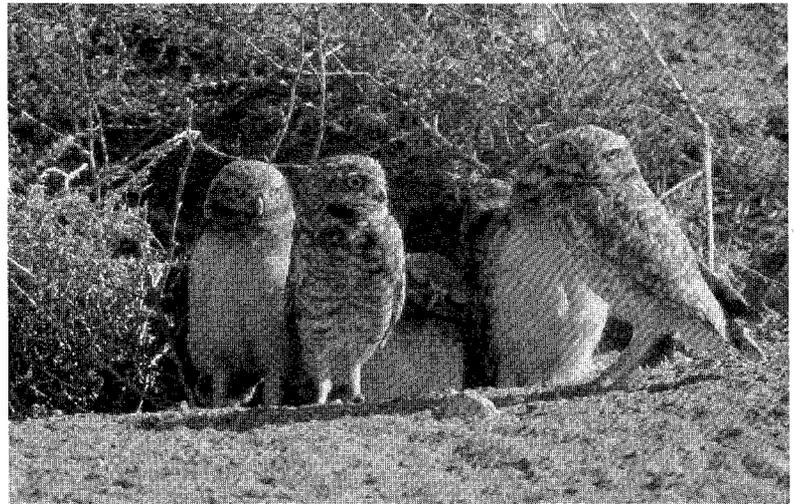
Shrub cover is a requirement for the suite of shrub-nesting birds that nest in Washington and Oregon's shrub-steppe. Sage, Brewer's, and lark sparrows, along with sage thrashers, and loggerhead shrikes, nest in or immediately beneath shrubs. They also use shrubs for singing and foraging perches, and Brewer's sparrows forage extensively within the foliage of shrubs.¹⁶² Presence of trees, either along riparian areas or planted as windbreaks or near homesteads, provides nesting platforms for black-

billed magpies and a host of raptors, including red-tailed and Swainson's hawks, and long-eared owls. Without the vegetation structure to support nests and foraging activities, these species are unlikely to establish territories and breed successfully.

Floristics also play a part in determining the composition of the avian community in shrub-steppe. In their extensive study of shrub-steppe birds that included sites in Washington, Oregon, and Nevada, Wiens and Rotenberry¹⁵⁸ found that whereas habitat structure played a part in determining species occurrence at a biogeographic scale, presence of particular plant species was important to some birds at a regional scale. Sage sparrows, true to their name, prefer a shrub community dominated by sagebrush over other species of shrub.¹⁵⁸ Even within the sagebrush family, sage sparrows show a preference for stands of big sagebrush. Recent work in Washington has shown that both sage sparrows and Brewer's sparrows occur at greater abundance in communities of big sagebrush than in stiff sagebrush (*A. rigida*) communities typical of rocky soils.¹⁴⁷ Wiens and Rotenberry¹⁵⁸ found abundance of Brewer's sparrows to be negatively correlated with cover of spinescent shrubs such as hopsage and budsage. These authors suggested that some shrub-steppe birds key on particular shrubs to take advantage of arthropod foods particular to those shrub species.

Although we have only recently begun to examine spatial components of community structure, there is evidence that landscape characteristics influence the occurrence of some shrub-steppe species. In Idaho, the probability of finding sage sparrows and Brewer's sparrows in patches of sagebrush increased with size of the patch.⁶³ Recent work in Washington has shown patch size to be very important to sage sparrows, with males establishing territories and nesting only on sites many times larger than an average territory (WDFW unpubl. data). The landscape context in which these spatial effects are examined also may have a bearing on how species react. In extensive shrub-steppe in Idaho, where sagebrush

Photograph 5. Young burrowing owls near their nest burrow. Burrowing owls in the Columbia Basin depend on fossorial mammals both for nest sites and for much of their diet. Grant County, Washington. (D. Hoyt, WDFW).



communities were fragmented by fire and subsequent cheatgrass (*Bromus tectorum*) invasion, sage thrashers occurred more frequently in spatially similar sites with low fragmentation of sage.⁶³ However, in Washington, where sagebrush stands are fragmented by agriculture, thrashers were regularly found in small fragments of sage and were more likely to occur in fragmented than extensive sites.¹⁴⁷ For some species, these landscape features likely interact with local vegetation characteristics to determine suitability of a site. Landscape characteristics such as patch size and spatial similarity seem to have little effect on occurrence of some of the more generalist birds such as western meadowlarks and horned larks, at least at the scales studied.^{63, 147}

Another physical variable that influences the bird community in shrub-steppe is soil type. Texture and depth of the soil can affect its suitability for foraging and nesting, and composition of the vegetation community is influenced by soil characteristics. Burrowing owls nest in underground burrows and require deep, friable soils. Sage and Brewer's sparrows in Washington were more abundant in deep soil communities characterized by big sagebrush than in shallow soil communities dominated by low-growing stiff sagebrush.¹⁴⁷ Size of the sage shrubs affects their suitability as nest sites and perhaps also determines availability of insect prey. In this same analysis, loggerhead shrikes occurred in greatest numbers, and western meadowlarks in lowest numbers, in sandy soil communities typical of the Columbia River Plain. Mourning doves were the only species that occurred at greater abundance in shallow soil communities.

Occurrence of some shrub-steppe birds may be related to the presence of other animal species. Burrowing owls in the West are closely tied to populations of fossorial mammals and the vegetation communities and soil types that support them.^{38, 49} Burrowing owls may depend on badgers for nest sites in the Columbia Basin.³⁸ Although burrowing owls eat a variety of prey, small mammals are a key component and western populations often are associated with colonies of ground squirrels and other small, burrowing mammals. In the Columbia Basin of Washington and Oregon, small mammals, particularly

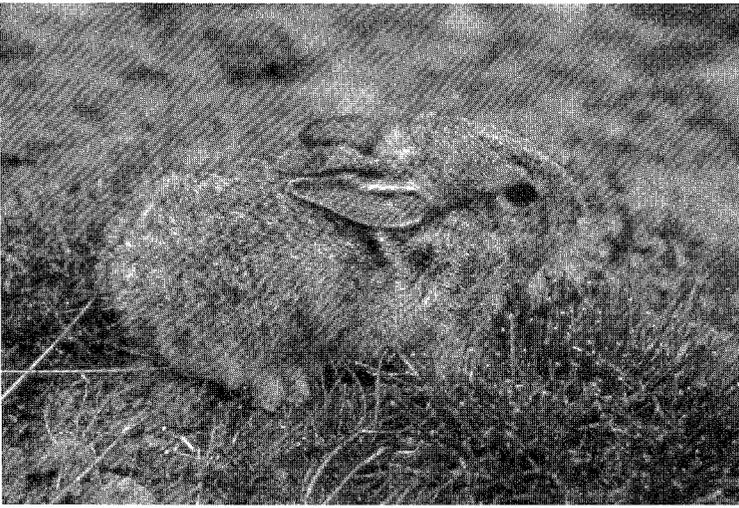
Great Basin pocket mice, comprised the majority of the biomass in pellets collected at nest sites.⁴⁰

Brown-headed cowbirds may use different habitats for feeding and for breeding and selection of both may be driven by the presence of other species. Cowbirds likely evolved with large, grazing animals (i.e., bison) of the short-grass prairies of the Midwest, following the animals as they grazed and eating seeds and insects exposed by trampling hooves.⁷⁴ In the shrub-steppe of Oregon and Washington, cowbirds are typically associated with livestock and can be found foraging among cattle and horses in pastures and feedlots. Cowbirds are "nest parasites" who lay their eggs in the nests of other birds, and therefore require suitable populations of "host" species to reproduce successfully. In big sagebrush communities in eastern Washington, cowbirds typically parasitized sage, Brewer's, and vesper sparrows, although rates of parasitism were low compared to other communities.¹⁴⁸ Cowbirds also parasitize birds that nest in riparian communities within shrub-steppe,^{33, 102} and their distribution likely is tied to that of suitable hosts in these communities as well.

Mammal Communities in Shrub-steppe

Species richness is typically related to the structural complexity of dominant vegetation.^{18, 116} Not surprisingly, the diversity of mammals in the shrub-steppe of western North America is lower than that typical of structurally more complex habitats of the region. For example, 40 small mammal species are closely associated with forested habitats of Oregon and Washington, whereas only 20 are closely associated with shrub-steppe habitat. Ten carnivore species are closely associated with forested habitats compared to 2 in shrub-steppe. Because of low precipitation, high incident solar radiation and wide fluctuations in seasonal temperatures, the shrub-steppe is a challenging environment for homeotherms. Not surprisingly, many shrub-steppe mammals are relatively specialized for life in this arid region.

In addition to the relatively few mammals that are



Photograph 6. Pygmy rabbits are sagebrush obligates, building their burrows in deep soils beneath sagebrush plants and feeding on sagebrush foliage. Douglas County, Washington. (WDFW).

clearly associated with true shrub-steppe vegetation, numerous species may be associated with very specialized habitats that occur as minor components of shrub-steppe systems. For example, black bears, beavers, and muskrats are not considered shrub-steppe species, but all may occur in larger riparian corridors that extend from forested communities into shrub-steppe.

Small and Meso-sized Mammals

Small mammals of the shrub-steppe include ubiquitous species such as the white-footed deer mouse and several species that are relatively restricted to shrub-steppe and other arid biotic associations. Hedlund and Rogers⁵⁰ trapped Great Basin pocket mice, northern grasshopper mice, sagebrush voles, western harvest mice, and deer mice in shrub-steppe habitat of the Hanford Site of southcentral Washington. Marr et al.,⁷⁹ trapping another area of the Hanford Site, caught deer mice, western harvest mice, grasshopper mice, montane voles, Great Basin pocket mice, and northern pocket gophers. Rogers and Rickard¹²⁰ also listed vagrant shrews as occurring in shrub-steppe habitat of southcentral Washington. Although small mammal communities of the shrub-steppe commonly contain several of these species, a few species, notably Great Basin pocket mice and deer mice, numerically dominate most assemblages in eastern Washington.^{36, 50, 79} Although uncommon in Washington, kangaroo rats, such as Ord's kangaroo rat and the less common chisel-toothed kangaroo rat, inhabit shrub-steppe in eastern Oregon.¹⁹ The least chipmunk and dark kangaroo mouse also occur in some areas of shrub-steppe.¹⁹

Meso-sized mammals of the shrub-steppe include several lagomorphs, such as white-tailed and black-tailed jackrabbits, mountain cottontails, and pygmy rabbits. The 2 jackrabbit species are sympatric; however, white-tailed jackrabbits are generally less common and tend to be distributed in smaller, isolated populations, at least in recent years.^{19, 80} Both species are prone to cyclic population growth,^{44, 64, 97} and variation between high and low population levels in black-tailed jackrabbits can be dramatic.³ When the 2 jackrabbit species occur together, white-tailed jackrabbits tend to occupy more open, grass-

dominated areas and black-tailed jackrabbits predominate in areas with a strong shrub component.^{19, 143} Areas occupied by jackrabbits are obvious due to their practice of clipping vegetation to make runways, which they travel repeatedly.⁹⁷ Pygmy rabbits are uncommon and typically occur only in areas dominated by tall, dense stands of Great Basin or big sagebrush, which provide preferred forage.^{19, 41, 153} Pygmy rabbits also excavate burrows in which they den, and therefore also require areas with friable soil. Mountain cottontails often are associated with distinct microhabitats such as riparian areas or rocky ravines and also occur in areas developed by humans.¹⁹ Yellow-bellied marmots are not associated with shrub-steppe associations except where rock piles occur as special, localized habitat features. Bushy-tailed wood rats, Columbian ground squirrels, Belding's ground squirrels, and a complex of smaller ground squirrels (discussed below) also occur in shrub-steppe habitats of eastern Oregon and Washington.

Carnivores of the Shrub-Steppe

Because diversity and biomass tend to decline with increasingly higher order consumers,¹¹⁶ the diversity and abundance of shrub-steppe carnivores is a fraction of that of small and meso-sized mammals. Among the common carnivores are the ubiquitous coyote, the more habitat restricted badger, and the widespread long-tailed weasel. The kit fox reaches its northern range limit in arid plant associations of southeastern Oregon.¹⁹

Coyotes, badgers, and weasels consume a diverse array of small mammals, insects, birds, and reptiles. Carnivore densities are related not only to densities of their prey but also to complex social factors.^{92, 126, 130} Coyote, weasel, and badger occupancy of shrub-steppe habitats is probably linked to vegetation indirectly via effects of vegetation on prey diversity and abundance. The bobcat, another widespread species, occurs in shrub-steppe where rock outcrops, ravines, or lava formations are available for suitable den sites.⁶² Mountain lions are the largest carnivores that use shrub-steppe habitat and typically occur only where mountainous terrain and shrub-steppe vegetation are contiguous.^{19, 20} Bobcats and mountain lions

prefer prey at least as large as a hare, and are found only where suitable prey biomass is relatively high. Not surprisingly, bobcat and mountain lion reproductive success and spatial use of the landscape varies with cyclic changes in densities of primary prey, whether lagomorphs or ungulates.⁶² Mountain lions tend to be found only where large mammal prey also are available.

Large Herbivores

Native species of large herbivores in the shrub-steppe include generalists such as the mule deer and elk, as well as more specialized ungulates such as the pronghorn antelope. Bighorn sheep are not a true shrub-steppe species and have been historically rare in arid mountain ranges of eastern Oregon and Washington, but bighorns did occur prehistorically in some mountainous areas adjacent to shrub-steppe habitats and have been reintroduced to several locations in Oregon¹⁰¹ and Washington.¹⁵¹ All of these large herbivores require free water and therefore are not found in extensive tracts of shrub-steppe that lack surface water such as springs or ponds. Large mammal ecology in the shrub-steppe is discussed in greater detail in a later section.

Organizing Principles: Mammals

The determinants of habitat suitability for mammals in the shrub-steppe undoubtedly varies across species. For example, floristics may be important for some species because of diet specialization. For some species, however, the vegetative structure of the association is probably more important than the specific assemblage of plant species that comprise the association.

Secondary and tertiary consumers are usually linked to vegetation associations indirectly via habitat affinities of their prey species. But because most predators in the shrub-steppe will consume a variety of prey organisms,⁶² their generalized affinities for plant communities reflect the diversity of habitats used by their smaller mammalian prey. However, as noted, several shrub-steppe carnivores directly select structural and geological habitat features because of their importance to other life history needs (e.g., den availability). Accordingly, these important structural

habitat features seem to be strong determinants of habitat suitability for some shrub-steppe carnivores.

Occurrence and density of primary consumers would normally be expected to be directly linked to community floristics. However, generalists such as the larger herbivores seem to have broad tolerances for plant associations as long as acceptable forage biomass is above critical limits that relate to foraging efficiency thresholds. Primary consumers with specialized diets, such as pygmy rabbits, may be very selective of plant associations.⁴¹ Black-tailed jackrabbits are seasonally selective of forage type, but will consume a variety of plant species¹⁴³ and therefore display more generalized affinities for plant associations than pygmy rabbits. Black-tailed jackrabbits will generally not consume cheatgrass, and therefore largely avoids pure cheatgrass swards.¹⁴³ Where cheatgrass invasion is occurring, jackrabbits foraging on native bunchgrasses can convey a competitive advantage to cheatgrass and facilitate further conversion towards an annual grassland.¹³²

Mammal species vary considerably in their affinity to associations with a strong sagebrush component. Pygmy rabbits are strongly associated with sagebrush, rarely occurring where sagebrush is a minor component or lacking from the plant community. Sagebrush voles have a strong affinity for sagebrush but occur in stands lacking a sagebrush overstory if grass understories are thick enough to provide cover.¹⁹ Pronghorns are the only large herbivore in the shrub-steppe that frequently forage on sagebrush. Pronghorns often show an affinity for sagebrush^{81, 135} and are most successful where sagebrush species are available for winter forage, although they can occupy areas without sagebrush if other acceptable forage is available.¹²⁵

The Role of Ground Squirrels in Shrub-Steppe Communities

In pre-European times, shrub-steppe habitats in eastern Oregon and Washington and adjacent states were

Photograph 7. Badgers feed extensively on ground squirrels and are ecologically linked to another ground squirrel predator, the burrowing owl, that uses badger dens for nest sites. Morrow County, Oregon. (G. Green, Foster Wheeler Environmental Corporation).



inhabited by the smaller ground squirrels of the genus *Spermophilus*. Like other ground squirrels they were sedentary, and rivers and other barriers were significant obstacles to gene flow.^{24, 37} Consequently, they diverged into a complex of 7 species, each with a separate range but all with similar ecological roles. Larger species of this genus, such as Columbian and Belding's ground squirrels, also inhabited shrub-steppe habitats, but were generally in deeper soils, and frequently in more mesic habitats, and are not considered here. Each species occupied a separate geographic area. In Washington, Townsend's ground squirrel lived between the Cascade Mountains and the Yakima River,^{47, 52} whereas a similar, but chromosomally distinct form occurred between the Yakima and Columbia Rivers.⁴⁶ The Washington ground squirrel formerly occupied the Columbia Basin between the Columbia River and the range of the Columbian ground squirrel to the east, and extended south into the Columbia Basin of Oregon.⁴ Merriam's ground squirrel (*S. canus canus*) occupied the shrub-steppe communities in central Oregon, except in Malheur County where it was replaced by the similar *S. c. vigilis*.^{47, 55, 149} These small ground squirrels remain poorly studied, but available information indicates that they prefer deep, well-drained sandy to loamy soils^{4, 55} but otherwise occur in a variety of native vegetation types.^{129, 149, 167}

There is little information available on the abundance of ground squirrels in pre-European times. It is likely that their distribution was patchy, with subpopulations acting as sources and sinks. Their distribution may have been driven by foraging needs, as small herbivores have a low digestive capacity and therefore depend on increasingly higher quality forage as body size decreases.²⁵ Ground squirrels depend upon high quality forage and an abundant supply of seeds in order to store the fat necessary to survive 8 months of hibernation. High quality forage in turn depends on wildfire and disturbance providing young, succulent, productive growth. In presettlement times, wildfires were patchy and post-burn succession generally maintained a mosaic of patches in various successional stages¹⁶⁵ that would have allowed ground squirrels to move about the landscape monopolizing new growth as it appeared.

Ground squirrels are important as a prey base for many of the predators in their ecosystems. In Idaho, Paiute ground squirrels are a keystone species, providing a critical food source for prairie falcons and an important prey source for red-tailed and ferruginous hawks, badgers, western rattlesnakes, and gopher snakes. They also are prey for long-tailed weasels, ravens, and others.¹⁶⁷

As burrowers, ground squirrels are important in mixing soils.^{1, 53, 137} For example, arctic ground squirrels were documented to move 19 tons of soil/acre/yr.¹¹² They are important in soil aeration,⁵⁷ and fertilize the soil with their feces and urine,^{42, 112, 136, 137, 141} resulting in significantly greener vegetation in the vicinity of their burrows.¹¹² The burrows significantly increase water infiltration into the soil, which increases plant productivity. In an Idaho study, ground squirrel burrows increased productivity of

bunchgrasses by about 20%.^{67, 68} In shrub-steppe environments, ground squirrels are important to the very plants they eat.

Badgers feed extensively on ground squirrels, and areas with high ground squirrel densities usually have high densities of badger digs.¹⁶⁷ These badger digs also increase water infiltration and aeration of the soil⁵³ and provide nest sites and shelter for a variety of wildlife. Thus, the presence of ground squirrels has positive effects on other animal species, as well as on soil and vegetation.

Invasion of exotic annuals has changed both the fire regimes and successional patterns in shrub-steppe habitats. Range fires burn much hotter in exotic annual infested rangelands, killing shrubs and allowing exotic annuals to out-compete native species. In many areas, native communities of shrubs, bunch grasses, and forbs have been replaced by annual grasses (especially cheatgrass) and dicots (particularly mustards). Ground squirrels will eat exotic plants,¹⁶⁶ but the productivity of these invasive plants varies annually with precipitation, providing an unstable food base for ground squirrels. In southwestern Idaho, ground squirrel populations are unstable in areas dominated by exotic annuals and are prone to extinction.¹⁶⁷ This instability is compounded by the large amounts of indigestible silica in cheatgrass and especially in medusahead (*Taeniatherium asperum*) seeds, making them a poor food source regardless of the quantity.¹²³

Fire also affects ground squirrels by reducing shrub cover. Although ground squirrels can survive in areas without shrubs as long as the herbaceous layer remains unchanged,¹⁰⁶ in the long term their density decreases when shrub cover drops below 11%, probably due to loss of protective cover, moisture changes, or other factors. Ground squirrel density also drops when shrub cover exceeds 20%, apparently due to reduced productivity in the herbaceous layer.⁵⁹

Agricultural conversion has had an even more drastic effect than exotic annuals on ground squirrel populations. In the Columbia Basin, agricultural conversion has reduced the Washington ground squirrel to a handful of isolated populations with low probability of long-term survival⁵ (E. Yensen, Albertson College, pers. obs.). Agricultural conversion likely has had similar effects on the Townsend's ground squirrel.⁴⁵ No systematic survey has been done on Merriam's ground squirrel, but it seems to be extirpated over much of its range (E. Yensen, Albertson College, unpubl. data). In this case, vegetation changes favoring the larger Belding's ground squirrel may be responsible.

Despite their importance in shrub-steppe ecosystems, ground squirrels generally have not been appreciated by humans. Ground squirrels do invade agricultural fields, eat alfalfa, grain and other produce, and dig holes in irrigation ditches. In return, ground squirrels have been poisoned, trapped, used for target practice, and reviled for over a century with little understanding of, or interest in, their ecological roles. Ironically, their demise has unfortunate ecological consequences for shrub-steppe

ecosystems that may portend economic losses as well. The decline of ground squirrels in some areas implies reduced productivity of the rangeland and, thus, lower value to grazing cattle.

Ecology of Large Herbivores in Shrub-Steppe

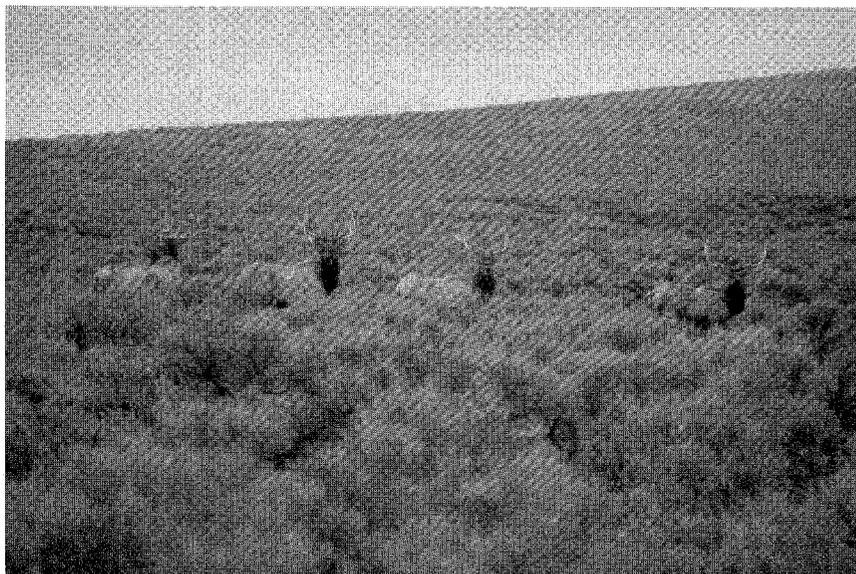
Living in warm, arid climates presents unique challenges to large mammals in terms of water conservation and maintenance of homeothermy.⁹⁴ As previously noted, the availability of drinking water is an important component of suitable habitat for large herbivores in the shrub-steppe.^{30, 86} Large herbivores also have relatively high forage intake demands; this intake rate is strongly correlated with the biomass of acceptable forage.^{15, 155} Accordingly, minimum forage biomass would also be expected to limit the types of arid environments that large herbivores can effectively exploit.⁸⁴ Among ruminant herbivores, smaller animals tend to have lower intake demands, but because of morphological and digestive constraints, require higher quality forage relative to larger ruminants.^{48, 58} Smaller ruminants can afford the costs of selective herbivory typically required to obtain high quality diets. Larger ruminants have high intake demands and must maintain high intake rates in order to meet these demands within the amount of time they invest in foraging. Therefore, it has generally been theorized that smaller ruminants are typically forage-quality limited, in contrast with larger ruminants that are expected to be constrained more by forage quantity.⁵⁸

Because of low primary productivity in the shrub-steppe relative to more mesic habitats of the region, it would seem that the shrub-steppe would be a more suitable environment for small ruminant herbivores. However, many shrub-steppe associations are dominated by bunchgrasses and nonpalatable shrubs such as big sagebrush. Because of high silica content and relatively thick cell walls, grasses are not easily digested by small herbivores.

Contemporary shrub-steppe habitats are exploited by 3 large ruminant herbivores: pronghorn antelope, mule deer, and elk. Bison occurred historically in the shrub-steppe of southeast Oregon,¹⁴⁵ and there is archaeological evidence that they once occurred in the shrub-steppe of the Columbia Plateau.¹⁰³ Of the 3 contemporary shrub-steppe ruminants, only the pronghorn is a steppe specialist. Pronghorns are widespread in steppe-like habitats of western and midwestern North America,¹³⁵ but the shrub-steppe of eastern Washington and Oregon represents the fringe of their distribution. The pronghorn is well suited for occupation of open steppe-like country.¹² As previously noted, pronghorns have a pronounced affinity for plant associations with a strong sagebrush component,¹³⁵ and their distribution conforms relatively well to the distribution of areas occupied by *Artemisia* species. Pronghorns are the only ruminant herbivore in North America that forages heavily on sagebrush, a relatively unpalatable and poorly digested shrub. Pronghorns also seasonally consume a diverse array of forbs, although they generally consume little grass.^{135, 168, 169} Pronghorns are relatively common in eastern Oregon but have been extirpated in eastern Washington.¹³⁵ The factors relating to their disappearance in Washington are not well understood, but competition with livestock for palatable forb species and the generally large-scale conversion of sagebrush-dominated rangelands to other uses are implicated.

Mule deer are generalists and occur in a relatively broad array of habitats of western North America from densely forested coastal areas to arid deserts of the southwest.¹⁵⁰ Mule deer are relatively common in the shrub-steppe of eastern Oregon and Washington, although their distribution is far from uniform.⁷⁰ On the Hanford Site of southcentral Washington, mule deer densities are highest near riparian areas such as the Columbia River shoreline, waste ponds, and perennial springs.^{29, 144} Individual Hanford Site mule deer also make disproportionate use of areas near water.³⁰ Carson and Peek¹³ found that mule

Photograph 8. The Rattlesnake Hills elk herd resides entirely in shrub-steppe habitat in eastern Washington. Elsewhere, shrub-steppe serves as winter habitat for some migratory populations of elk. Arid lands ecology reserve, Benton County, Washington. (S. McCorquodale, Yakama Nation).



I: The Rattlesnake Hills Elk Herd

Until recently, shrub-steppe communities were not thought to be year-round habitat for elk.^{10, 95} Although elk were known to use shrub-steppe habitat contiguous with forested habitats during severe winters, elk were generally thought to be precluded from year-round occupation of shrub-steppe due to low forage productivity and the inability to tolerate high thermal loads. In 1972, however, a small group of elk colonized the shrub-steppe habitat of the Hanford Site in southcentral Washington.¹¹⁴ This group, commonly known as the Rattlesnake Hills elk herd, has been studied extensively. The original colonizing group of 4-7 elk grew rapidly because of high reproductive output and extremely high first-year survival.⁸⁸ Despite the fact that shrub-steppe had been considered unsuitable year-round habitat for elk, individual fitness, indexed by reproductive success in females and age-specific antler growth in males, has been exceptional in the Rattlesnake Hills elk population.^{86, 87, 88} Currently this population numbers >700 individuals (B. Tiller, Battelle Memorial Institute unpubl. data).

Although primary production is low in shrub-steppe relative to forested environments, energetic modeling has indicated that shrub-steppe communities may rival or exceed more productive environments in terms of forage energy availability because all production occurs in the herbaceous and shrub layers.⁸⁴ Grass-dominated associations typical of eastern Oregon and

Washington shrub-steppe seem to be well suited to exploitation by elk; forage biomass typical of many shrub-steppe communities is above that considered minimum for elk.^{84, 155} In grass-dominated communities, elk seem to be competitively superior to mule deer.

Elk in the shrub-steppe use a broad array of plant associations. Telemetry data indicate that stands with a sagebrush overstory are used heavily by elk for bedding, particularly during the heat of summer.⁸⁹ Foraging elk, however, have shown an affinity for grass swards where historical fires have eliminated sagebrush.⁸³ Elk diets are diverse in the shrub-steppe, with grasses dominating spring and winter diets, and forbs dominating summer and fall diets.^{82, 85}

The Rattlesnake Hills elk population has shown little dependence on shrub forage, even during winter, but the predominant shrubs in the herd range, sagebrush, greasewood (*Sarcobatus vermiculatus*), and spiny hopsage (*Atriplex spinosa*) are not considered good elk forage.

Other factors have contributed to the success of the Rattlesnake Hills elk population. The portion of the Hanford Site occupied by elk is topographically diverse,⁸² and access restrictions associated with Hanford Site security are believed to limit harassment to levels tolerable to elk.⁸⁹ The presence of perennial springs in the southern portion of the Hanford Site are probably essential to the thermoregulatory strategy of elk in high thermal loading environments.^{89, 105}

deer in northcentral Washington preferred riparian cover types and areas with some topographic diversity as opposed to flat expanses of shrub-steppe vegetation. Mule deer in the shrub-steppe consume diverse diets typical of a generalist herbivore, but forbs and the early growth of shrubs are particularly important,¹⁴⁴ consistent with energetic predictions. Large areas dominated by bunchgrasses and lacking palatable shrubs do not seem to be vegetation types exploited effectively by mule deer.⁷⁰

Although mule deer and elk may be residents of the shrub-steppe region (see Box 1), some migratory populations also use shrub-steppe exclusively as winter habitat. Where shrub-steppe occurs adjacent to low-elevation xeric forest, suitable arrays of forage species and biomass and favorable climatological features make shrub-steppe rangeland highly valuable winter range, especially during severe winters. In eastern Oregon and Washington, large numbers of migratory deer and elk display this seasonally intense use of shrub-steppe winter range, although during the warmer months they use higher elevation forests.

Reptile and Amphibian Communities in Shrub-Steppe

Relative to other classes of terrestrial vertebrates, diversity of amphibians in shrub-steppe habitat of Oregon and Washington is low (10 of the 32 species occurring in these two states). Only 3 of 21 species of salamanders occur in shrub-steppe habitat: long-toed salamander, tiger salamander, and roughskin newt. Seven of 11 native species of anurans occur in shrub-steppe. Great Basin spadefoot toad, western toad, and Woodhouse's toad are the anuran species most likely to be found in shrub-steppe away from standing water. In southeastern Idaho, Great Basin spadefoot toads may be found in shrub-steppe as far as 5 km from standing water (S. Cooper Doering and C. Peterson, Idaho State University unpubl. data). Ranid frogs are most closely associated with wetlands. Columbia spotted frogs in southwestern Idaho, for example, spend most of their time within several meters of water (T. Carrigan, Bureau of Land Management unpubl. data).

The occurrence and distribution of some anuran species has changed within the last 30 years. Northern leopard

frogs have disappeared from many sites in Oregon and Washington where they occurred previously.¹³¹ Bullfrogs have been introduced into Oregon and Washington and pose a threat to native species such as northern leopard frogs, spotted frogs, and western pond turtles.^{72, 131}

In contrast to amphibians, reptile diversity in shrub-steppe habitat is relatively high (21 of 28 native species in Oregon and Washington). Lizards are the group of reptiles most associated with shrub-steppe (9 of 11 species in Oregon and Washington). No lizard species occurs exclusively in shrub-steppe, but 3 species (Mojave black-collared lizard, long-nose leopard lizard, and desert horned lizard) occur only in shrub-steppe, dwarf shrub-steppe, and desert playa/salt scrub shrublands.

Ten of the 15 (67%) snake species in Oregon and Washington occur in shrub-steppe habitat. The ground snake occurs only in shrub-steppe, dwarf shrub-steppe, and desert playa/salt scrub shrublands. Striped whipsnakes occupy these three habitats plus juniper and mountain mahogany woodlands, whereas night snakes are found in the same habitats as striped whipsnakes plus eastside canyon shrublands. Three species (racer, gopher snake, and western rattlesnake) occur in a wide variety of habitats, including shrub-steppe. Three more species (rubber boa, western terrestrial garter snake, and common garter snake) also occur in a wide variety of habitats, including shrub-steppe, especially near water.

Although both species of freshwater turtles (painted turtle and western pond turtle) occur more frequently in other habitats, they use shrub-steppe if near permanent water (marshes, slow rivers and streams, ponds, or lakes with abundant aquatic vegetation). These turtles venture onto land to bask or to disperse, and they may lay their eggs in nests up to 150 and 800 m, respectively, away from water.^{98, 134}

Although species richness of amphibians and reptiles is lower than that of birds and mammals in Oregon and Washington shrub-steppe, amphibians and reptiles can be very important ecologically. Because their long-term conversion efficiencies are many times higher than those of birds and mammals, they can contribute disproportionately to biomass production and make large amounts of energy available to other trophic levels.¹¹⁰ For example, Turner et al.¹⁴⁰ found that the annual biomass produced by side-blotched lizards in the Nevada desert was equal to or greater than that of birds and mammals in desert and grassland habitats.

General Organizing Principles:

Reptiles and Amphibians

The presence of water is an essential habitat feature for the amphibians occurring in Oregon and Washington shrub-steppe. All of these amphibians breed in lentic environments (e.g., marshes, pools, ponds, side-channels, or oxbows). Consequently, the presence of standing or slow-moving water for at least the time required for eggs to hatch and larvae to complete metamorphosis is required for successful reproduction. However, because many of these species can live for considerable lengths of time (>10

years in some species), suitable breeding habitat does not have to be present every year. Temperature variation among shrub-steppe communities does not seem to explain differences in the occurrence of amphibian species within Oregon and Washington.

Because reptiles are ectothermic, thermal conditions play a key role in determining the occurrence, distribution, and numbers of reptiles that will be found in shrub-steppe habitats. In general, reptile species richness decreases with increasing latitude and altitude.⁶⁰ The number of reptile species decreases by over 40% between southern Oregon and northern Washington. For example, Mojave black-collared lizards and ground snakes do not occur in Washington, and side-blotched lizards and striped whipsnakes do not occur north of central Washington. Within a landscape, the distribution and abundance of reptiles will vary with topography. For example, snake dens are usually located on south facing slopes^{43, 61} (S. Cooper Doering and C. R. Peterson, Idaho State University unpubl. data).

For many species of reptiles, it is likely that the time available for embryo development at appropriate temperatures is the condition that limits distribution. For example, biophysical analyses indicate that adult and juvenile desert iguanas could survive in shrub-steppe habitat in Washington, but that soil temperatures are too low to allow successful incubation of eggs.¹⁰⁹ Gravid rubber boas and western rattlesnakes have been observed at den sites in the late fall of cool years in southeastern Idaho, indicating that summer temperatures were not sufficiently high to allow the embryos to develop (M. E. Dorcas, Davidson College, pers. comm., J. Lee, Idaho State University pers. comm.). These field observations, combined with laboratory studies of the thermal dependence of embryo development¹⁴ and observations of the inability of embryos to survive simulated hibernation (M. Dorcas, Davidson College pers. comm.), suggest that the amount of time at suitable temperatures available for embryo development may play an important role in setting the distributional limits of snakes. Indeed, the evolution of viviparity in reptiles is generally viewed as an adaptation to cool conditions.¹¹¹

Vegetation structure and floristics seem to explain less of the variation in occurrence and distribution of reptiles than in birds and mammals. In developing GIS models for predicting reptile distributions for the Idaho Gap Analysis project, Butterfield et al.¹¹ found that factors other than vegetation appear to limit the distribution of many reptiles. These factors may include temperature, moisture, and the special habitat features previously described. Nevertheless, vegetation does influence reptiles in several ways. Vegetation structure may influence reptiles directly; for example, sagebrush lizards in northcentral Oregon use habitats with tall shrubs (thermal cover and protection from avian predators) and sparse ground cover (ease in detecting and pursuing prey) (G. Green, Foster Wheeler Environmental Corporation, unpubl. data). Because most reptiles inhabiting shrub-steppe are carnivorous, differences in vegetation probably influence reptile occurrence indirectly via the habitat affinities of their prey.

Management Issues in Shrub-Steppe

In this section we consider some of the management issues that have had (and likely will continue to have) considerable impact on shrub-steppe communities at a regional scale. There are certainly other threats to shrub-steppe communities, particularly at the local scale (e.g., real estate development and inundation by water projects), but we limit our discussion here to more widespread issues.

Conversion to Agriculture

There is little doubt that the conversion of native plant communities to agricultural uses has had, and continues to have, profound effects on shrub-steppe habitats in the Columbia Basin. Beginning with the westward migration of Euro-Americans in the mid-1800s that brought farmers into the deserts of Oregon and Washington, and accelerated by the damming of the Columbia River that made large-scale irrigation possible, about 14.8 million acres (6 million ha) of shrub-steppe have been converted to wheat fields, row crops, and orchards.¹¹³ Agricultural development has been most pronounced in Washington where >50% of the land originally in shrub-steppe has been converted²⁷ (Figure 1). This large-scale displacement of one habitat type for another has substantially reduced the area available to native shrub-steppe wildlife. Moreover, the addition of new, human-related habitats (agricultural and rural development) has elevated the food base for some predators (e.g., magpies and gulls) and likely their populations as well, with unknown impacts on shrub-steppe wildlife. The addition of cattle feedlots, pastures, and lawns to the landscape has enhanced the suitability of the area for brown-headed cowbirds, a nest parasite that lays its eggs in the nests of other birds and thereby depresses the host bird's reproductive success.

Agricultural conversion has not occurred randomly across the landscape, but instead has focused on the most arable, deep soil communities. This has resulted in a disproportionate loss of these communities and an increase in the proportion of shallow soil shrub-steppe habitats on the landscape (Figure 2). Some species of shrub-steppe wildlife, such as badgers, ground squirrels, and burrowing owls, depend on deep soil communities. The pygmy rabbit, listed as endangered in Washington, is found only in deep, loamy soil sagebrush stands. Furthermore, some shrub-steppe passerines occur in greater abundance in loamy soil communities than in other soil types.¹⁴⁷ Conversion of deep soil shrub-steppe communities to irrigated agriculture will likely continue in the foreseeable future, making this one of our most endangered arid land communities.

Although loss of native plant communities should be avoided, some habitats associated with agricultural development can have values for wildlife. Wetlands associated with agricultural development provide breeding and feeding areas for species not typically associated with shrub-steppe. Wetlands created as part of numerous irrigation projects provide habitat for various

nesting waterfowl and marshland birds, as well as amphibians and aquatic mammals. These areas also serve as migration stop-over sites for waterfowl. Wetlands with a woodland component provide stop-over sites for passerines that historically used naturally occurring wooded riparian habitats, a resource that has been greatly depleted.

Farm fields enrolled in the Conservation Reserve Program (CRP) can have considerable value to shrub-steppe birds. These fields are taken out of production for ≥ 10 years and planted to tame grasses such as crested wheatgrass, providing nesting habitat for greater sage-grouse (*M. Schroeder*, WDFW pers. comm.) and grasshopper sparrows¹⁰⁷ on lands that offered few such values when under cultivation. As sagebrush colonizes CRP fields via seeds from adjacent shrub-steppe, habitat value increases because of added structure and food for sage-dependent species. The value of CRP fields to shrub-steppe wildlife could be increased by planting them with native vegetation and extending the period of enrollment.

Habitat Fragmentation

The pattern of agricultural conversion within the shrub-steppe of eastern Washington and northcentral Oregon has resulted in a highly fragmented landscape (Figure 1). Where once native grasslands and shrublands stretched unbroken for thousands of square miles, there exists now only fragments of native habitats in a matrix of agricultural fields. This breakup of formerly contiguous habitats can have detrimental effects on species occurrence and population dynamics. Much of the research documenting fragmentation effects has examined avian communities in forested ecosystems, although some recent work has focused on grasslands and shrublands.^{6, 63, 147}

Some forest bird species are area sensitive and will not inhabit habitat patches below a minimum size.^{34, 117} Extensive surveys in Washington suggest that sage sparrows are most likely to occur in blocks of shrub-steppe >2,470 acres (1,000 ha) and that male sage sparrows found singing in small fragments are unlikely to maintain a territory or attract a mate (WDFW unpubl. data). Numerous studies have documented greater rates of nest predation^{28, 152, 163} and nest parasitism^{9, 118} in fragmented landscapes. Elevated rates of nest predation and parasitism may result from an increase in the number of predators and brown-headed cowbirds in fragmented landscapes and an increase in habitat edge. In Washington, 3 shrub-steppe birds (Brewer's sparrow, lark sparrow, and sage thrasher) showed evidence of lower nesting success in fragmented shrub-steppe compared to continuous, unbroken tracts (WDFW unpubl. data). Camera monitoring artificial nests baited with quail eggs revealed that black-billed magpies and common ravens likely were responsible, at least partly, for increased predation on nests in fragmented landscapes (WDFW unpubl. data). As remnant habitat becomes smaller and more fragmented, it is under greater influence of the surrounding landscape¹⁵⁷ and more susceptible to external influences, be they predators, nest parasites, potential competitors, or the wind-blown seeds of exotic weeds.



Figure 1. Current landcover of four counties in eastern Washington, illustrating the degree of fragmentation in this formerly shrub-steppe-dominated landscape. Landcover classes were derived from Landsat Thematic Mapper data

using multi-temporal analysis (scene dates: May 1993 and August 1994). Counties illustrated are (clockwise from the bottom right) Adams, Grant, Douglas, and Lincoln.

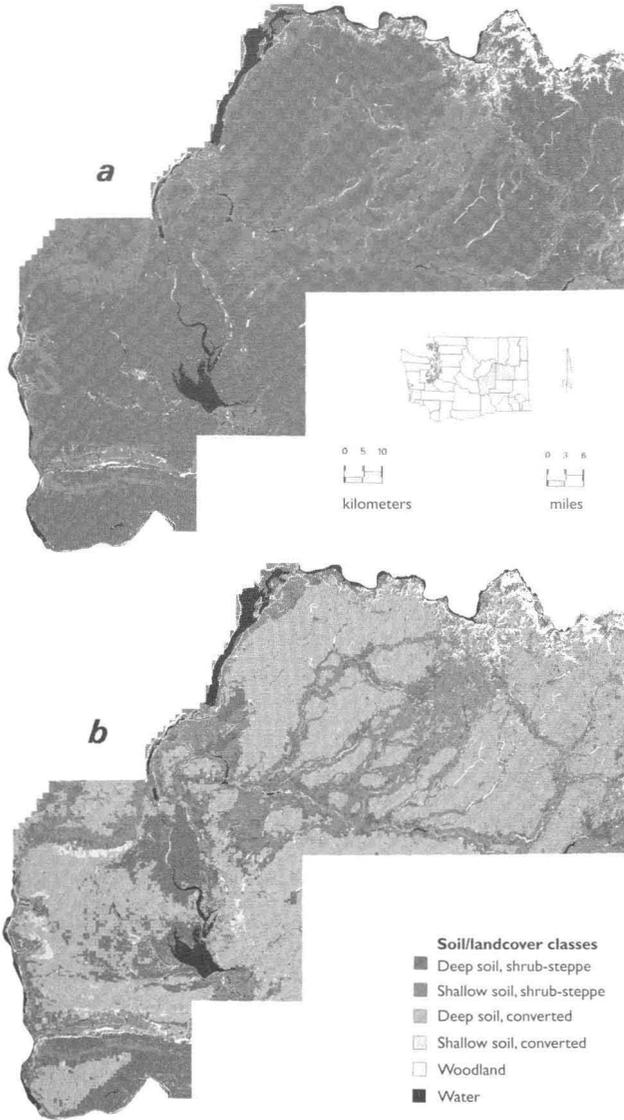


Figure 2. (a) Historical distribution of deep soil and shallow soil shrub-steppe communities in Grant and Lincoln Counties, Washington. (b) Current distribution of deep soil and shallow soil shrub-steppe communities in Grant and Lincoln Counties, illustrating the extensive conversion of deep-soil shrub-steppe (primarily to agricultural fields) and minimal conversion of shallow-soil shrub-steppe.

Photograph 9. Shrub-steppe communities of eastern Washington and northcentral Oregon have been fragmented by agricultural conversion. Douglas County, Washington. (M. Vander Haegen, WDFW).



Fragmentation of the shrub-steppe landscape very likely has disrupted the dynamics of dispersal and immigration that allows populations to persist over large areas. Stochastic events may cause the extirpation of a species from one habitat patch, necessitating recruitment from nearby patches to reestablish a population. Highly fragmented landscapes have lower connectivity, meaning that dispersing individuals must cross unfavorable lands (in this case agricultural fields or developed lands) to move from one habitat patch to another. In theory, the smaller the patch and the more distant other population sources, the lower the probability that recolonization will occur.⁷⁵ ¹⁶⁴ Species with small home ranges and limited dispersal capabilities, such as many small mammals and reptiles, are most likely to be affected (see Box 2). For species that normally occur at relatively low densities, such as the northern grasshopper mouse and pygmy rabbit, small breeding assemblages could become genetically isolated and vulnerable to extirpation.^{65, 66} Likewise, for populations that are prone to dramatic cyclic fluctuations in population size, such as lagomorphs, fragmentation may increase the probabilities of local extinctions associated with decline phases in isolated populations. Although research has addressed the consequences of genetic isolation and the probability of persistence for small populations in fragmented forest communities,^{71, 93} little work has been done in shrub-steppe.

Livestock Grazing

With the rise of the Cascade Range in the early Pliocene, maritime influences east of the range diminished and the Intermountain West became drier, with rainfall patterns for the most part centered in the fall and winter. Grasses capable of estivating during the dry summer months, such as *Agropyron*, *Poa*, and *Festuca*, dominated the landscape.²³ ⁷⁷ In turn, the lack of moisture in the plants during the summer months, coupled with poor distribution of drinking water, may have imposed severe constraints on the establishment of significant numbers of large

herbivores, especially bison.⁷⁷ For whatever reason, herds of native ungulates never reached the numbers in the shrub-steppe regions of Oregon and Washington that they did east of the Rocky Mountains. Consequently, the *Agropyron*, *Poa*, and *Festuca* dominated grasslands of Oregon and Washington may have been poorly adapted to withstand the grazing pressures of European livestock introduced over the last 200-300 years.

The legacy of livestock grazing in the shrub-steppe regions of Oregon and Washington began about 1700 when the Shoshone brought horses into southeastern Oregon from the Spanish missionaries at Santa Fe.⁴⁶ By 1730, horses had reached the Columbia Basin, where the Nez Perce and Cayuse built herds into the thousands by 1800.³⁵ The impact of these horses on the local grassland ecology is unrecorded. Cattle grazing as an industry did not begin east of the Cascades until the 1860s, but quickly expanded, reaching its zenith in the late 1870s. At about the same time cattle began competing with hundreds of thousands of sheep and the thousands of horses needed for cattle raising, plus thousands more unattended Indian ponies called "cayuses." By 1885 the range was showing signs of deterioration. Farming in the latter part of the century not only fueled greater competition on less and less range, but it brought with it exotic seed contaminants such as cheatgrass, Jim Hill mustard (*Sysimbrium altissimum*), and Russian thistle (*Salsola kali*), that facilitated further deterioration of the range. As a result of public outcry about poor range conditions, the Federal government finally gained control of all unclaimed rangelands with the Taylor Grazing Act in 1934.

Today, grazing management is dictated by the science of range management defined by Stoddart et al.¹³³ as optimizing the returns from rangelands in those combinations most desired by and suitable to society through the manipulation of range ecosystems. Manipulation in the Intermountain West mostly has involved reseeding of deteriorated rangelands with non-native grasses (largely because seed sources for many

2: Spatial Scale

The scale at which different species use a landscape varies widely, as does our knowledge of this component of wildlife ecology. Sage and sharp-tailed grouse, both resident species, may cover a considerable area over the course of a year as they fill their various needs for breeding, food, and cover. A female sharp-tailed grouse must visit a male on his lek in the spring, then locate suitable nesting cover to lay and incubate a clutch, rear her young in suitable brood cover, perhaps move to another area as she tracks changing food resources in the fall, and then complete the year in riparian cover where hardwood trees provide buds as a source of winter food. Her annual home range may cover 1,000 acres (405 ha) and include a multitude of vegetation communities.¹⁶ A female greater sage-grouse may include >10 miles² (26 km²) in her breeding season home range alone.¹²⁴ In contrast, a Brewer's sparrow arrives in the shrub-steppe after having spent the winter in South America, establishes a <2.5 acre (1 ha) territory in a big sagebrush stand¹⁶⁰ and may spend the entire breeding season nesting and rearing young on this small territory. Fragmentation and other changes in the landscape likely will affect these two species quite differently. However, our knowledge of the habitat needs of most shrub-steppe passerines is meager and is focused primarily on the breeding territory. There may be other needs, such as critical premigratory habitats or post-fledging habitats, that we are not aware of and that would expand the landscape use of species like Brewer's sparrows.

Large mammals have relatively large home ranges, and in shrub-steppe they may require

access to large tracts of habitat to be successful.^{29, 84, 86, 169} Large mammals such as elk have remarkable dispersal abilities, however, and thus are less prone than smaller mammals to becoming genetically isolated by fragmentation unless the distance between patches becomes very large.

Meso-sized and small mammals have smaller home ranges, and therefore patch scale has different implications relative to large mammals. Small mammals can, in theory, continue to exploit small patches of shrub-steppe.⁶⁴ However, because of small home range sizes and limited dispersal abilities, fragmentation of shrub-steppe habitat may effectively isolate many populations of meso-sized and small mammals, with undetermined consequences.

Although reptiles generally respond to their environments on a finer spatial scale than birds or most mammals, a wide range of variation exists in the size of areas used by different species. Territorial, sit-and-wait predators, such as side-blotched lizards, move on a scale of feet and have home ranges of <5,000 feet² (500 m²).¹³⁹ In contrast, active, widely foraging species, such as the western whiptail lizard, have home ranges several times larger.⁹⁰ Some species of snakes that use communal overwintering sites may seasonally migrate several miles in one direction and have home ranges of hundreds of acres (e.g., western rattlesnakes).¹⁴ Species with smaller spatial requirements may be better able to persist for short periods of time in fragmented habitats; however, it is unclear whether their long-term persistence will be lesser or greater than those species that require large home ranges but are better able to recolonize areas where populations have gone locally extinct.

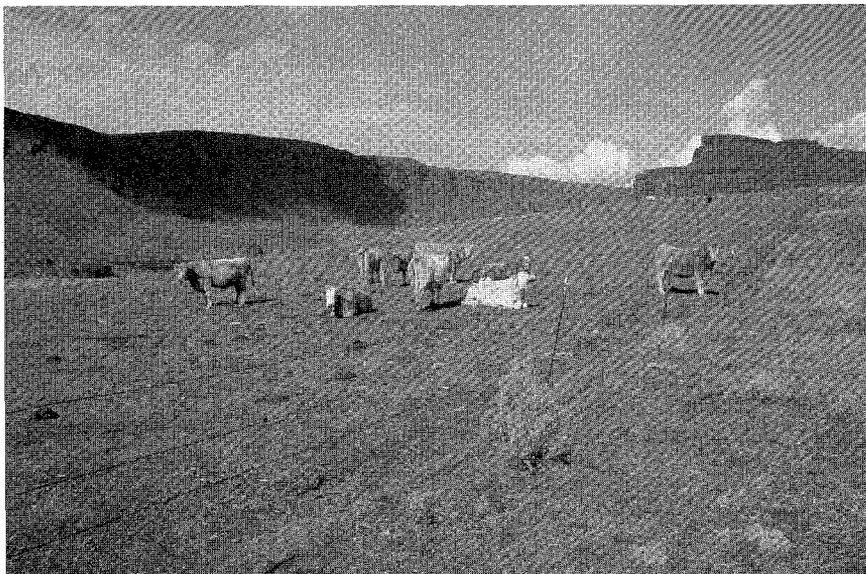
native grasses were simply not available), and establishing seasonal grazing regimes designed to prevent further deterioration of rangeland.^{51, 133} However, these present-day systems are still designed to maximize livestock production, often to the detriment of shrub-steppe wildlife.

Do present day grazing practices benefit or adversely affect shrub-steppe wildlife? The answer is mixed. Some wildlife species, such as long-billed curlews¹⁰⁴ and burrowing owls³⁸ may actually benefit from reduced vegetational structure (grazed perennials or low-statured annuals), and Great Basin pocket mice will attain high population numbers in pure cheatgrass stands.¹²⁷ However, ground-nesting birds and small mammals that require protective cover from vegetation may not benefit, especially if they become more susceptible to predation.

The greatest impact from grazing, however, is probably the perpetuation of the weed legacy from livestock

trampling of the soil. The friable soils of the shrub-steppe zone, especially in the drier areas, are held together by layers of cryptogamic mosses and lichens. This cryptogamic crust can prevent establishment of annual weeds and provide a moisture cap that reduces soil evaporation. However, the trampling action of livestock, especially horses and cattle, can degrade these layers and provide seed beds for cheatgrass and weedy forbs. Dense stands of cheatgrass not only outcompete native bunchgrasses (especially for moisture in the early stages of growth), but are also susceptible to hot wildfires that can virtually eliminate sagebrush.²² Consequently, whereas the proximate effect of livestock grazing on wildlife may be the removal of grass and forb biomass important as forage and cover to many wildlife species, the ultimate effect may be perpetuation of weedy annuals that out-compete native plants that local wildlife have adapted to use.

Photograph 10. Grazing by livestock has profoundly influenced the vegetation in many shrub-steppe communities. Grand Coulee, Douglas County, Washington. (M. Vander Haegen, WDFW).



The Fire/Cheatgrass Cycle

Another human-caused agent of change that threatens to degrade shrub-steppe habitats, related in part to agricultural practices and to livestock grazing in particular, is the conversion of extensive areas to simplified annual grasslands. Cheatgrass is an exotic annual grass that was introduced to the Intermountain West sometime in the late 1800s, probably as an agricultural pest.⁷⁶ Overgrazing of native bunchgrass communities by livestock led to deterioration of the range and opened the door for the widespread invasion of this exotic annual grass.⁷⁶ Each of the arid and semi-arid grassland and shrubland habitat types in eastern Oregon and Washington is susceptible to cheatgrass invasion.¹¹³ Characteristics of cheatgrass's life history and physical structure, coupled with a native flora ill-equipped to compete with this new invader, have allowed it to change the composition of shrub-steppe communities and even alter ecosystem processes.²¹

Cheatgrass is a winter annual that goes to seed early in the year and generally desiccates in spring or early summer. A native of the Mediterranean region, it is adapted to the climate of eastern Oregon and Washington and, unlike the native bunch grasses, can thrive under heavy livestock grazing. Cheatgrass rapidly colonizes bare soil and moves readily into disturbed sites. Intact communities with native bunchgrasses and a healthy cryptogamic crust can keep the invader in check; however, heavy grazing of native grasses and mechanical breakdown of the cryptogamic crust through trampling can provide a window for cheatgrass to spread and exert dominance. Wildfire also can provide a window of opportunity by killing shrubs and making valuable soil moisture available to cheatgrass for germination and growth. Cheatgrass recovers quickly following wildfires and can out-compete native grasses.⁹¹

The most extreme changes that cheatgrass has caused in the West have resulted from repeated wildfires and the response of cheatgrass to post-fire conditions.²¹ Native bunchgrasses generally grow sparsely, with forbs and bare

soil or cryptograms between plants. This discontinuous fuel layer does not carry a fire well, and wildfires in these communities typically burn patches, creating a mosaic of burned and unburned areas.¹⁵⁴ Cheatgrass, in contrast, forms continuous stands that desiccate early in the season and carry fires well.¹⁵⁴ (Photograph 11). As a result, burns in cheatgrass are larger and more frequent. As cheatgrass biomass increases, the ability of the community to carry fire also increases, resulting in a positive-feedback loop where fire promotes cheatgrass dominance, leading to more frequent fires.²¹ On Idaho's Snake River plain, sagebrush communities evolved with a fire-return interval of 35-100 years; following invasion by cheatgrass, fire-return intervals in some shrub-steppe communities are now as low as 3-5 years.¹⁵⁴

Increased fire frequency in steppe and shrub-steppe vegetation leads to a vegetation community with lower species richness.¹⁵⁴ On frequently burned areas of Idaho's Snake River plain, almost all of the vegetation was introduced annuals—primarily cheatgrass.¹⁵⁴ Vegetation life forms react differently and predictably to the fire/cheatgrass cycle; essentially, annuals increase dramatically and all other plants decrease.¹⁵⁴ Wildfire kills big sagebrush, and because most species of sagebrush do not resprout from root crowns after fires, regeneration depends on the existing seed bank. Big sagebrush seeds are short-lived, and if fire returns before the new seedlings reach reproductive age (4-6 years) the species can be eliminated from the community.¹⁵⁴ Even rabbitbrush, a common successional shrub in sage communities that readily sprouts after fire, can be lost from the community with fire-return intervals of 2-4 years.¹⁵⁴ As cheatgrass-fueled fires lead to more extensive burns, seed sources from adjacent, unburned areas become more distant and the patch dynamics that likely promoted revegetation in these communities historically no longer functions. This change in the fire frequency leads to a change in the trajectory of plant succession and represents an alteration of ecosystem processes.²¹



Photograph 11. Cheatgrass can form continuous stands that burn frequently, preventing reestablishment of the former vegetation community. Hanford Site, Benton County, Washington. Photo: M Vander Haegen, WDFW.

Research Needs

A host of wildlife species have received little attention in ecological studies, yet have great potential to be affected by changes in shrub-steppe landscapes. This list would include many of the reptiles, amphibians, and small mammals. We need studies examining demography and habitat affinities of the Great Basin spadefoot toad, long-nosed leopard lizard, night snake, sagebrush vole, and the full complex of ground squirrels, among others. We need a better understanding of the relationship between fossorial mammals and the species that depend on them for burrows and as prey. Fourteen species of bats are known to use shrub-steppe, yet we know little about their population trends, population dynamics, and habitat needs, or how disturbance by humans affects breeding or roosting activities. We need studies examining the effects of habitat fragmentation on the distribution and demography of shrub-steppe wildlife. We need to develop and implement surveys for sage sparrows, grasshopper sparrows, burrowing owls, and other birds that are not covered sufficiently by the Breeding Bird Survey, as well as for reptiles and mammals that are not easily observed.

We know little about how the condition of extant shrub-steppe varies across the landscape. Mapping shrub-steppe communities across a gradient of conditions, from pristine to highly degraded, would provide a more realistic assessment of the current status of the resource and would be invaluable for future modeling of wildlife distribution. Livestock grazing has altered the vegetation in many shrub-steppe communities, yet we lack information on how these changes affect most wildlife species. We need research on the role of microbiotic crusts in maintaining ecosystem function and as an indicator of ecosystem integrity. Are microbiotic crusts an important component for some species?

Expanding habitat linkages in rfragmented landscapes and increasing the amount of deep soil shrub-steppe for species such as pygmy rabbits and ground squirrels will require restoration of converted agricultural lands. How

do we restore native vegetation on former agricultural sites and maximize the chance of regaining the full range of ecological function? How do we restore native vegetation and ecological function to highly degraded rangelands? Agricultural lands enrolled in CRP are a significant part of the landscape in eastern Washington. Research on the value of CRP to wildlife will help us assess its place in the shrub-steppe ecosystem and guide future enrollments to benefit native wildlife.

Applying the Data Matrixes to a Management Example:

Changes in the Wildlife Community Following Wildfire and Conversion to Annual Grasslands

Loss of Shrubs

Little published work has examined the effects of repeated wildfires and conversion to annual grasslands on shrub-steppe wildlife communities. Loss of the shrub layer through repeated fires eliminates habitat for shrub nesting birds, including some key shrub-steppe obligates (sage sparrow, Brewer's sparrow, and sage thrasher). Although fidelity to their breeding site will sometimes bring adults back in the year following a fire¹⁰⁸ or other catastrophic loss of the shrub layer,^{159,161} without suitable nesting shrubs such returns are likely to be a short-term phenomenon. Loss of shrubs would be detrimental to some lizard species, reducing the availability of shaded sites needed for thermoregulation and cover used to avoid predators. When fire removes shrubs from a community, ungulates that browse on sagebrush, bitterbrush, and other shrubs lose valuable winter habitat. Updike et al.¹⁴² documented a decline in big game winter range following fire, cheatgrass invasion, and suppression of shrub regeneration by cheatgrass. Species that depend on sagebrush for forage during all or part of the year, such as

Table 2. Numbers of species associated with shrub-steppe habitat type, modified grassland structural condition, and shrubs as a key habitat element, in Oregon and Washington.

Species group	Shrub-steppe		Modified Grasslands		Shrubs as a key element
	Generally associated	Closely associated	Generally associated	Closely associated	
Birds	44	22	31	2	22
Mammals	26	27	34	0	12
Reptiles	20	0	7	0	6
Amphibians	9	0	10	0	1
Totals	103	49	82	2	41

greater sage-grouse and pygmy rabbits, likely will be excluded as sagebrush communities degrade to annual grasslands.

The Habitat Element Matrix (contained on the CD-ROM) can be used to determine which species depend on shrubs as an important component of shrub-steppe habitat and to predict which species would be lost from the community as fire removes the shrub layer. A query of the matrix revealed 22 birds, 12 mammals, 6 reptiles, and 1 amphibian that are associated with shrub-steppe habitat and require shrubs for some life function (Table 2).

Conversion of the Herb Layer to Cheatgrass

Changes in structure and composition of the herb layer that follow cheatgrass invasion also affect the wildlife community. Conversion of native forbs and bunchgrasses to exotic annuals results in a less stable food base for small herbivores like Townsend's ground squirrel, increasing the amplitude of their population fluctuations and the potential for localized extinctions.¹⁶⁷ Long-billed curlews seem to prefer cheatgrass dominated sites for nesting in southcentral Washington² and northcentral Oregon,¹⁰⁴ whereas some other ground-nesting birds have been found to occur at abnormally low densities in cheatgrass.⁷ Birds that prefer open ground for foraging (e.g., sage sparrow and loggerhead shrike) avoid sites with dense cheatgrass.^{27,73} Conversion to cheatgrass probably would decrease availability of prey for lizards and make it more difficult for lizards to move about. Some snakes also would be negatively affected by such a conversion; night snakes and striped whipsnakes prey largely on lizards and thus would likely be negatively affected by the loss of lizards due to habitat conversion. Preliminary results from a comparative trapping study conducted in the Snake River Birds of Prey Area in 1978-1979²⁶ and 1997-1998 (J. Cossel, Jr. and C. Peterson, Idaho State University unpubl. data) are generally consistent with these predictions. Located in southwestern Idaho, much of this area has been converted from natural shrubland to non-native grassland. Although there is considerable year-to-year variation in the occurrence and trapping rates of reptiles, side-blotched lizards and night snakes seem to have declined whereas more generalist species like racers have increased.

Changes in the wildlife community that might be expected following conversion of shrub-steppe to annual

grasslands can be derived from the matrix. Sites dominated by cheatgrass are classified as *modified grasslands* in the Structural Condition Matrix. A query of this matrix revealed 82 species "generally associated" with annual grasslands and only 2 species classified as "closely associated." A query of the Wildlife-Habitat Matrix for species in shrub-steppe found 103 species "generally associated" and 49 species "closely associated" with this habitat type (Table 2). From the results of these queries we can conclude that the conversion of shrub-steppe communities to annual grasslands through the fire/cheatgrass cycle can cause dramatic changes in the wildlife community. The change may be particularly severe in the breeding bird community, where 20 species closely associated with shrub-steppe (several of them obligates) are predicted to be excluded. There are limitations to such an analysis, and one must give careful thought to other factors that may influence species occurrence at a particular site.

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Literature Cited

1. Abaturon, B. D. 1972. The role of burrowing animals in the transport of mineral substances in the soil. *Pedobiologia* 12:261-266.
2. Allen, J. N. 1980. The ecology and behavior of the long-billed curlew in southeastern Washington. *Wildlife Monographs* 73.
3. Bailey, V. 1936. The mammals and life zones of Oregon. U. S. Department of Agriculture, Bureau of Biological survey, North American Fauna 55:1-416.
4. Betts, B. J. 1990. Geographic distribution and habitat preferences of Washington ground Squirrels (*Spermophilus washingtoni*). *Northwestern Naturalist* 71:27-37.
5. ———. 1999. Current status of Washington ground squirrels in Oregon and Washington. *Northwestern Naturalist* 80:35-38.
6. Bolger, D. T., T. A. Scott, and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. *Conservation Biology* 11:406-421.
7. Brandt, C. A., and W. H. Rickard. 1994. Alien taxa in the North American shrub-steppe four decades after cessation of livestock grazing and cultivation agriculture. *Biological Conservation* 68:95-105.
8. Braun, C. E., et al. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. *Wilson Bulletin* 88:165-171.

9. Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *Bioscience* 33:31-35.
10. Bryant, L. D., and C. Maser. 1982. Classification and distribution. Pages 1-60 in J. W. Thomas and D. E. Towell, editors. *Elk of North America: ecology and management*. Stackpole Books, Harrisburg, PA.
11. Butterfield, B. R., B. Csuti, and J. M. Scott. 1994. Modeling vertebrate distributions for Gap Analysis. Pages 53-68 in R. I. Miller, editor. *Mapping the diversity of nature*. Chapman and Hall, London, England.
12. Byers, J. A. 1997. American pronghorn: social adaptations and the ghosts of predators past. University of Chicago Press, Chicago, IL.
13. Carson, R. G., and J. M. Peek. 1987. Mule deer habitat selection patterns in northcentral Washington. *Journal of Wildlife Management* 51:46-51.
14. Cobb, V. A. 1994. The thermal ecology of pregnancy in free-ranging Great Basin rattlesnakes (*Crotalus viridis lutosus*). Dissertation, Idaho State University, Pocatello, ID.
15. Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer range. *Journal of Wildlife Management* 47:646-663.
16. Connelly, J. W., M. W. Gratson, and K. P. Reese. 1998. Sharp-tailed grouse (*Tympanuchus phasianellus*). In A. Poole and F. Gill, editors, *The Birds of North America*, No. 354. The Birds of North America, Inc., Philadelphia, PA.
17. Costa, G. 1995. Behavioural adaptations of desert animals. Springer-Verlag, New York, NY.
18. Cox, C. B., and P. D. Moore. 1993. Biogeography: an ecological and evolutionary approach. Blackwell Science, Oxford, England.
19. Csuti, B., A. J. Kimerling, T. A. O'Neil, M. M. O'Shaughnessy, E. P. Gaines, and M. M. P. Huso. 1997. Atlas of Oregon wildlife. Oregon State University Press, Corvallis, OR.
20. Currier, M. J. P. 1983. *Felis concolor*. Mammalian Species 200:1-7, American Society of Mammalogists.
21. D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63-87.
22. Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62. Washington State University, Pullman, WA.
23. ———. 1975. Floristic plant geography of eastern Washington and northern Idaho. *Journal of Biogeography* 2:1-18.
24. Davis, W. B. 1939. The recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, ID.
25. Demment, M. W., and P. J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist* 125:641-672.
26. Diller, L. V., and D. R. Johnson. 1982. Ecology of reptiles in the Snake River Birds of Prey Area. U. S. Bureau of Land Management Snake River Birds of Prey Research Project, Boise, ID.
27. Dobler, F. C., J. Eby, C. Perry, S. Richardson, and M. Vander Haegen. 1996. Status of Washington's shrub-steppe ecosystem: extent, ownership, and wildlife/vegetation relationships. Research Report. Washington Department of Fish and Wildlife, Olympia, WA.
28. Donovan, T. M., F. R. Thompson III, J. Faaborg, and J. R. Probst. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380-1395.
29. Eberhardt, L. E., E. E. Hanson, and L. L. Cadwell. 1982. Analysis of radionuclide concentrations and movement patterns of Hanford Site mule deer. Report BNWL-4420, Battelle, Pacific Northwest Laboratory, Richland, WA.
30. ———, S. M. McCorquodale, and G. A. Sargeant. 1989. Elk and deer studies related to the Basalt Waste Isolation Project. Report PNL-6798, Battelle, Pacific Northwest Laboratory, Richland, WA.
31. Fitzner, R. E., D. Berry, L. L. Boyd, and C. A. Rieck. 1977. Nesting of ferruginous hawks (*Buteo regalis*) in Washington, 1974-75. *Condor* 79:245-249.
32. ———, and R. L. Newell. 1989. Ferruginous hawk nesting on the U.S. DOE Hanford Site: case history of a recent invasion caused by transmission lines. Pages 125-132 in *Proceedings IV: issues and technology in the management of impacted wildlife*. Thorne Ecological Institute, Boulder, CO.
33. Freeman, S., D. F. Gori, and S. Rohwer. 1990. Red-winged blackbirds and brown-headed cowbirds—some aspects of a host-parasite relationship. *Condor* 92:336-340.
34. Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biological Conservation* 36:115-141.
35. Galbraith, W. A., and E. W. Anderson. 1971. Grazing history of the Northwest. *Journal of Range Management* 24:6-12.
36. Gano, K. A. 1979. Analysis of small mammal populations inhabiting the environs of a low-level radioactive waste pond. Report PNL-2479, Battelle, Pacific Northwest Laboratory, Richland, WA.
37. Gavin, T. A., P. W. Sherman, E. Yensen, and B. May. 1999. Population genetic structure of the northern Idaho ground squirrel. *Journal of Mammalogy* 80:156-168.
38. Green, G. A., and R. G. Anthony. 1989. Nesting success and habitat relationships of burrowing owls in the Columbia Basin, Oregon. *Condor* 91:347-354.
39. ———, and M. L. Morrison. 1983. Nest-site characteristics of sympatric ferruginous and Swainson's hawks. *Murrelet* 64:20-22.
40. ———, R. E. Fitzner, R. G. Anthony, and L. E. Rogers. 1993. Comparative diets of burrowing owls in Oregon and Washington. *Northwest Science* 67:88-93.
41. Green, J. S., and J. T. Flinders. 1980. *Brachylagus idahoensis*. Mammalian Species 125:1-4, American Society of Mammalogists.
42. Greene, R. A., and C. Reynard. 1932. The influence of two burrowing rodents, *Dipodomys spectabilis spectabilis* (kangaroo rat) and *Neotoma albigula albigula* (pack rat) on desert soils in Arizona. *Ecology* 13:73-80.
43. Gregory, P. T. 1982. Reptilian hibernation. Pages 53-154 in C. Gans and F. H. Pough, editors. *Biology of the Reptilia*, Volume 13, Physiology D, Physiological Ecology. Academic Press Inc., New York, NY.
44. Gross, J. E., L. C. Stoddart, and F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. *Wildlife Monographs* 40.
45. Hafner, D. J., E. Yensen, and G. L. Kirkland, Jr. 1998. North American rodents. Status survey and conservation action plans. IUCN, Gland, Switzerland.
46. Haines, F. 1938. The northward spread of horses among the Plains Indians. *American Anthropology* 40:429-436.
47. Hall, E. R. 1981. Mammals of North America, 2nd edition. John Wiley & Sons, New York, NY.
48. Hanley, T. A. 1980. Nutritional constraints of food and habitat selection by sympatric ungulates. Dissertation, University of Washington, Seattle, WA.
49. Haug, E. A., B. A. Millsap, and M. S. Martell. 1993. Burrowing owl (*Speotyto cunicularia*). In A. Poole and F. Gill, editors, *The Birds of North America*, No. 61. The Birds of North America, Inc., Philadelphia, PA.
50. Hedlund, J. D., and L. E. Rogers. 1976. Characterization of small mammal populations inhabiting the B-C Crib environs. Report BNWL-2181, Battelle Pacific Northwest Laboratory, Richland, WA.
51. Heitschmidt, R. K., and J. W. Stuth. 1991. Grazing management, an ecological approach. Timber Press, Portland, OR.
52. Hoffmann, R. S., C. G. Anderson, R. W. Thorington, Jr., and L. R. Heany. 1993. Family Sciuridae. Pages 419-465 in D. E. Wilson and D. M. Reeder, editors. *Mammal species of the world: a taxonomic and geographic reference*. Smithsonian Institution Press, Washington, D. C.
53. Hole, F. D. 1981. Effects of animals on soil. *Geoderma* 25:75-112.
54. Holmes, A. L., and G. R. Geupel. 1998. Avian population studies at naval weapons systems training facility Boardman, Oregon. Final report. Point Reyes Bird Observatory, Stinson Beach, CA.
55. Howell, A. H. 1938. Revision of North American ground squirrels, with a classification of Sciuridae. *North American Fauna* 56:1-256.
56. Huey, R. B., C. R. Peterson, S. J. Arnold, and W. P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70:931-944.
57. Inouye, R. S., N. J. Huntly, D. Tilman, and J. R. Tester. 1987. Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia* 72:178-184.

58. Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48:215-267.
59. Johnson, K. H., R. A. Olson, and T. D. Whitson. 1996. Composition and diversity of plant and small mammal communities in tebuthiuron-treated big sagebrush (*Artemisia tridentata*). *Weed Technology* 10:404-416.
60. Kiester, A. R. 1971. Species density of North American amphibians and reptiles. *Systematic Zoology* 20:127-137.
61. Klauber, L. M. 1956. *Rattlesnakes*. Volume 1. University of California Press, Berkeley, CA.
62. Knick, S. T. 1990. Ecology of bobcats relative to exploitation and a prey decline in southeastern Idaho. *Wildlife Monographs* 108.
63. ———, and J. T. Rotenberry. 1995. Landscape characteristics of fragmented shrub-steppe habitats and breeding passerine birds. *Conservation Biology* 9:1059-1071.
64. ———, and D. L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61:75-85.
65. Lacy, R. C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78:323-335.
66. Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
67. Laundré, J. W. 1993. Effects of small mammal burrows on water infiltration in a cool desert environment. *Oecologia* 94:43-48.
68. ———. 1998. Effect of ground squirrel burrows on plant productivity in a cool desert environment. *Journal of Range Management* 51:638-643.
69. Le Houerou, H. N., R. L. Bingham, and W. Skerbek. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* 15:1-18.
70. Leckenby, D. A., D. P. Sheehy, C. H. Nellis, R. J. Scherzinger, I. D. Luman, W. Elmore, J. C. Lemos, L. Doughty, and C. E. Trainer. 1982. *Wildlife habitats in managed rangelands of the Great Basin of southeastern Oregon: mule deer*. General Technical Report PNW-139, Pacific Northwest Forest and Range Experiment Station, Portland, OR.
71. Lehmkuhl, J. F., S. D. West, C. L. Chambers, W. C. McComb, D. A. Manuwal, K. B. Aubry, J. L. Erickson, R. A. Gitznen, and M. Leu. 1999. An experiment for assessing vertebrate response to varying levels and patterns of green-tree retention. *Northwest Science* 73:45-63.
72. Leonard, W. P., H. A. Brown, L. L. C. Jones, K. R. McAllister, and R. M. Storm. 1993. *Amphibians of Washington and Oregon*. Seattle Audubon Society, Seattle, WA.
73. Leu, M. 1995. The feeding ecology and the selection of nest shrubs and fledgling roost sites by loggerhead shrikes (*Lanius ludovicianus*) in the shrub-steppe habitat. Thesis, University of Washington, Seattle, WA.
74. Lowther, P. E. 1993. Brown-headed cowbird (*Molothrus ater*). In A. Poole and F. Gill, editors, *The Birds of North America*, No. 47. The Birds of North America, Inc., Philadelphia, PA.
75. MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
76. Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-Ecosystems* 7:145-165.
77. ———, and J. N. Thompson. 1982. Evolution in steppe with few large, hoofed mammals. *American Naturalist* 119:757-773.
78. Maclean, G. L. 1996. *Ecophysiology of desert birds*. Springer-Verlag, New York, NY.
79. Marr, N. V., C. A. Brandt, R. E. Fitzner, and L. D. Poole. 1988. *Habitat associations of vertebrate prey within the Controlled Area study zone*. Report PNL-6495, Battelle Pacific Northwest Laboratory, Richland, WA.
80. Marshall, D. B. 1992. *Sensitive vertebrates of Oregon*. Oregon Department of Fish and Wildlife, Portland, OR.
81. Mason, E. 1952. Food habits and measurements of Hart Mountain antelope. *Journal of Wildlife Management* 16:387-389.
82. McCorquodale, S. M. 1985. *The ecology of a shrub-steppe elk (Cervus elaphus) population*. Thesis, University of Washington, Seattle, WA.
83. ———. 1987. Fall-winter habitat selection by elk in the shrub-steppe of Washington. *Northwest Science* 61:171-173.
84. ———. 1991. Energetic considerations and habitat quality for elk in arid grasslands and coniferous forests. *Journal of Wildlife Management* 55:237-242.
85. ———. 1993. Winter foraging behavior of elk in the shrub-steppe of Washington. *Journal of Wildlife Management* 57:881-890.
86. ———, and L. E. Eberhardt. 1993. The ecology of elk in an arid environment: an overview of the Hanford elk project. Pages 56-63 in R. L. Callas, D. B. Koch, and E. R. Loft, editors. *Proceedings of the 1990 Western States and Provinces Elk Workshop*. California Department of Fish and Game, Sacramento, CA.
87. ———, ———, and G. A. Sargeant. 1989. Antler characteristics in a colonizing elk population. *Journal of Wildlife Management* 53:618-621.
88. ———, L. L. Eberhardt, and L. E. Eberhardt. 1988. Dynamics of a colonizing elk population. *Journal of Wildlife Management* 52:309-312.
89. ———, K. J. Raedeke, and R. D. Taber. 1986. Elk habitat use patterns in the shrub-steppe of Washington. *Journal of Wildlife Management* 50:664-669.
90. McCoy, C. J. 1965. *Life history and ecology of the Cnemidophorus tigris septentrionalis*. Dissertation, University of Colorado, Boulder, CO.
91. Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7-13.
92. Messick, J. P., and M. G. Hornocker. 1981. *Ecology of the badger in southwestern Idaho*. *Wildlife Monographs* 76.
93. Mills, L. S. 1996. Fragmentation of a natural area: dynamics of isolation for small mammals on forest remnants. Pages 199-219 in R. G. Wright, editor. *National parks and protected areas: their role in environmental protection*. Blackwell Science, Cambridge, MA.
94. Moen, A. N. 1973. *Wildlife ecology: an analytical approach*. W. H. Freeman, San Francisco, CA.
95. Murie, O. J. 1951. *The elk of North America*. Stackpole Books, Harrisburg, PA.
96. Nadler, C. H. 1968. The chromosomes of *Spermophilus townsendi* (Rodentia: Sciuridae) and report of a new subspecies. *Cytogenetics* 7:144-157.
97. Nowak, R. M. 1991. *Walker's mammals of the world*. Fifth edition. Johns Hopkins University Press, Baltimore, MD.
98. Nussbaum, R. A., E. D. Brodie, and R. M. Storm. 1983. *Amphibians and reptiles of the Pacific Northwest*. University of Idaho Press, Moscow, ID.
99. Olsen, B. 1976. Status report: Columbian sharp-tailed grouse. *Oregon Wildlife* 34:10.
100. O'Neil, T. A. and D. H. Johnson. 2001. Oregon and Washington wildlife species and their habitats. Pages 1-21 in: D. H. Johnson and T. A. O'Neil, managing directors. *Wildlife-habitat relationships in Oregon and Washington*. Oregon State University Press, Corvallis, OR.
101. Oregon Department of Fish and Wildlife. 1994. *Oregon Species Information System*. Wildlife Research, Corvallis, OR.
102. Orians, G. H., E. Roskaft, and L. D. Beletsky. 1989. Do brown-headed cowbirds lay their eggs at random in the nests of red-winged blackbirds? *Wilson Bulletin* 101:599-605.
103. Osborne, D. 1953. Archaeological occurrence of pronghorn antelope, bison, and horse in the Columbia Plateau. *Scientific Monthly* 77:914-917.
104. Pampush, G. J., and R. G. Anthony. 1993. Nest success, habitat utilization and nest-site selection of long-billed curlews in the Columbia Basin, Oregon. *Condor* 95:957-967.
105. Parker, K. L., and C. T. Robbins. 1984. Thermoregulation in mule deer and elk. *Canadian Journal of Zoology* 62:1409-1422.
106. Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents of a shrub-steppe ecosystem: the role of shrubs. *Oecologia* 59:145-156.
107. Patterson, M. P., and L. B. Best. 1996. Bird abundance and nest success in Iowa CRP fields: the importance of vegetation structure and composition. *American Midland Naturalist* 135:153-167.
108. Petersen, K. L., and L. B. Best. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. *Wildlife Society Bulletin* 15:317-329.

109. Porter, W. P., and C. R. Tracy. 1983. Biophysical analyses of energetics, time-space utilization, and distributional limits. Pages 55-83 in R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. *Lizard ecology*. Harvard University Press, Cambridge, MA.
110. Pough, F. A. 1980. The advantages of ectothermy for tetrapods. *American Naturalist* 115: 92-112.
111. Pough, F. H., J. B. Heiser, and W. N. McFarland. 1996. *Vertebrate life*. Fourth edition. Prentice Hall, Upper Saddle River, NJ.
112. Price, L. W. 1971. Geomorphic effect of the arctic ground squirrel in an alpine environment. *Geografiska Annaler* 53A: 100-106.
113. Quigley, T. M., and S. J. Arbelbide. 1997. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great Basins. General Technical Report PNW-GTR-405. U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.
114. Rickard, W. H., J. D. Hedlund, and R. E. Fitzner. 1977. Elk in the shrub-steppe of Washington: an authentic record. *Science* 196:1009-1010.
115. ———, and B. E. Vaughan. 1988. Characteristics of contrasting shrub-steppe plant communities. Pages 109-179 in W. H. Rickard, L. E. Rogers, B. E. Vaughan, and S. F. Liebetrau, editors. *Shrub-steppe: balance and change in a semi-arid terrestrial ecosystem*. Elsevier, Amsterdam, The Netherlands.
116. Ricklefs, R. E. 1983. *Ecology* (second edition). Chiron Press, New York, NY.
117. Robbins, C. S., D. K. Dawson, and B. A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic states. *Wildlife Monographs* 103.
118. Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987-1990.
119. Rogers, L. E., R. E. Fitzner, L. L. Cadwell, and B. E. Vaughan. 1988. Terrestrial animal habitats and population responses. Pages 182-250 in W. H. Rickard, L. E. Rogers, B. E. Vaughan, and S. F. Liebetrau, editors. *Shrub-steppe: balance and change in a semi-arid terrestrial ecosystem*. Elsevier, Amsterdam, The Netherlands.
120. ———, and W. H. Rickard. 1977. Ecology of the 200 Area plateau waste management environs: a status report. Report PNL-2253, Battelle, Pacific Northwest Laboratory, Richland, WA.
121. Rotenberry, J. T., and J. A. Wiens. 1991. Weather and reproductive variation in shrub-steppe sparrows: a hierarchical analysis. *Ecology* 72:1325-1335.
122. Saab, V. A., and T. D. Rich. 1997. Large-scale conservation assessment for Neotropical migratory land birds in the interior Columbia River Basin. General technical report PNW-GTR-399. U.S. Forest Service, Pacific Northwest Research Station, Portland, OR.
123. Savage, D. E., J. A. Young, and R. A. Evans. 1969. Utilization of medusahead and downy brome caryopses by chukar partridges. *Journal of Wildlife Management*, 33:975-978.
124. Schroeder, M. A., J. R. Young, and C. E. Braun. 1999. Sage Grouse (*Centrocercus urophasianus*). In A. Poole and F. Gill, editors, *The Birds of North America*, No. 425. The Birds of North America, Inc., Philadelphia, PA.
125. Schwartz, C. C., and J. G. Nagy. 1976. Pronghorn diets relative to forage availability in northeastern Colorado. *Journal of Wildlife Management* 40:469-478.
126. Seidensticker, J. C., IV, M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs* 35.
127. Small, R. J., and B. J. Verts. 1983. Responses of a population of *Perognathus parvus* to removal trapping. *Journal of Mammalogy* 64:139-143.
128. Smith, E. L., et al. 1995. New concepts for assessment of rangeland condition. *Journal of Range Management* 48:271-282.
129. Smith, G. W., and D. R. Johnson. 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. *Ecology* 66:171-178.
130. Springer, J. T. 1982. Movement patterns of coyotes in south central Washington. *Journal of Wildlife Management* 46:191-200.
131. Stebbins, R. C., and N. W. Cohen. 1995. *A natural history of amphibians*. Princeton University Press, Princeton, NJ.
132. Stewart, G., and A. C. Hull. 1969. Cheatgrass, *Bromus tectorum* L.—an ecological intruder in southern Idaho. *Ecology* 30:58-74.
133. Stoddart, L. A., A. D. Smith, and T. W. Box. 1975. *Range Management*. McGraw-Hill Book Company, New York, NY.
134. Storm, R. M., W. P. Leonard, H. A. Brown, R. B. Bury, D. M. Darda, L. V. Diller, and C. R. Peterson. 1995. *Reptiles of Washington and Oregon*. Seattle Audubon Society, Seattle, WA.
135. Sundstrom, C., W. G. Hepworth, and K. L. Diem. 1973. Abundance, distribution, and food habits of the pronghorn. Bulletin 10, Wyoming Game and Fish Commission, Cheyenne, WY.
136. Taylor, W. P. 1935. Some animal relations to soil. *Ecology* 16:127-136.
137. Thorp, J. 1949. Effects of certain animals that live in soils. *Scientific Monthly* 68:180-191.
138. Thorson, T., and A. Svihla. 1943. Correlation of the habits of amphibians with their ability to survive the loss of body water. *Ecology* 24:374-381.
139. Turner, F. B., R. I. Jennrich, and J. D. Weintraub. 1969. Home ranges and body size of lizards. *Ecology* 50:1076-1081.
140. ———, P. A. Medica, and B. W. Kowalewsky. 1976. Energy utilization by a lizard (*Uta stansburiana*). U.S. International Biological Programme Monograph No. 1. Utah State University Press, Logan, UT.
141. Turner, G. T., R. M. Hansen, V. H. Reid, H. P. Tietjen, and A. L. Ward. 1973. Pocket gophers and Colorado mountain rangeland. Colorado State University Experiment Station Bulletin, 554S. Fort Collins, CO.
142. Updike, D. R., E. R. Loft, and F. A. Hall. 1990. Wildfires on big sagebrush/antelope bitterbrush range in northeastern California: implications for deer populations. Pages 41-46 in E. S. McArthur, R. M. Romney, S. D. Smith, and P. T. Tueller, editors. *Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management*. General Technical Report INT-GTR-276. U.S. Forest Service, Ogden, UT.
143. Uresk, D. W., J. F. Cline, and W. H. Rickard. 1975. Diets of black-tailed hares on the Hanford Reservation. Report BNWL-1931, Battelle, Pacific Northwest Laboratory, Richland, WA.
144. ———, and V. A. Uresk. 1980. Diets and habitat analyses of mule deer on the 200 Areas of the Hanford Site in southcentral Washington. Report PNL-2461, Battelle, Pacific Northwest Laboratory, Richland, WA.
145. Van Vuren, D., and M. P. Bray. 1985. The recent geographic distribution of *Bison bison* in Oregon. *Murrelet* 66:56-58.
146. Vander Haegen, W. M. 1996. Survey of breeding bird communities on BRMaP sites, Hanford Site, 1996. Project completion report. Washington Department of Fish and Wildlife, Olympia, WA.
147. ———, F. C. Dobler, and D. J. Pierce. 2000. Shrubsteppe bird response to habitat and landscape variables in eastern Washington, USA. *Conservation Biology* 14:1145-1160.
148. ———, and B. Walker. 1999. Parasitism by brown-headed cowbirds in the shrub-steppe of eastern Washington. *Studies in Avian Biology* 18:34-40.
149. Verts, B. J., and L. N. Carraway. 1998. *Land mammals of Oregon*. University of California Press, Berkeley, CA.
150. Wallmo, O. C. 1981. Mule and black-tailed deer distribution and habitats. Pages 1-26 in O. C. Wallmo, editor. *Mule and black-tailed deer of North America*. University of Nebraska Press, Lincoln, Nebraska.
151. Washington Department of Fish and Wildlife. 1995. Washington State management plan for the bighorn sheep. Game Division, Washington Department of Fish and Wildlife, Olympia, WA.
152. Weinberg, H. J., and R. R. Roth. 1998. Forest area and habitat quality for nesting wood thrushes. *Auk* 115:879-889.
153. Weiss, N. T., and B. J. Verts. 1984. Habitat and distribution of pygmy rabbits (*Sylvilagus idahoensis*) in Oregon. *Great Basin Naturalist* 44:563-569.
154. Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. Pages 4-10 in E. S. McArthur, R. M. Romney, S. D. Smith, and P. T. Tueller, editors. *Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management*. U. S. Forest Service, Ogden, UT.

155. Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *Journal of Wildlife Management* 48:1285-1301.
156. Wiens, J. A. 1985. Habitat selection in variable environments: shrub-steppe birds. Pages 227-251 in M. Cody, editor. *Habitat Selection in birds*. Academic Press, New York, NY.
157. ———, C. S. Crawford, and J. R. Gosz. 1985a. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421-427.
158. ———, and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrub-steppe environments. *Ecological Monographs* 51:21-41.
159. ———, and ———. 1985. Response of breeding passerine birds to rangeland alteration in a North American shrubsteppe locality. *Journal of Applied Ecology* 22:655-668.
160. ———, ———, and B. Van Horne. 1985b. Territory size variations in shrub-steppe birds. *Auk* 102:500-505.
161. ———, ———, and ———. 1986. A lesson in the limitations of field experiments: shrub-steppe birds and habitat alteration. *Ecology* 67:365-376.
162. ———, B. Van Horne, and J. T. Rotenberry. 1987. Temporal and spatial variations in the behavior of shrub-steppe birds. *Oecologia* 73:60-70.
163. Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211-1214.
164. ———, C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 in M. E. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, MA.
165. Yensen, D. L. 1980. A grazing history of southwestern Idaho with emphasis on the Snake River Birds of Prey Area. U. S. Bureau of Land Management, Boise District, Boise, ID.
166. Yensen, E. and D. L. Quinney. 1992. Can Townsend's ground squirrels survive on a diet of exotic annuals? *Great Basin Naturalist* 52:269-277.
167. ———, ———, K. Johnson, K. Timmerman, and K. Steenhof. 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. *American Midland Naturalist* 128:299-312.
168. Yoakum, J. 1958. Seasonal food habits of the Oregon pronghorn. *Interstate Antelope Conference Transactions* 10:58-72.
169. ———. 1980. Habitat management guides for the American pronghorn antelope. Technical Note 347, Bureau of Land Management, Denver, CO.

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