ABSTRACT: We identify wetlands, riparian woodlands and shrublands, green ash woodlands, aspen forests, pinyon-juniper woodlands, and pure and mixed forests of ponderosa pine as important wildlife habitats in the U.S. Forest Service’s Rocky Mountain Region. The relationships of vertebrate species to each of these types are discussed relative to habitat requirements and species conservation. The importance of late-successional lodgepole pine, Douglas-fir, and spruce-fir forests is discussed in the context of regional landscapes and the maintenance of biological diversity.

INTRODUCTION

Species conservation is integral to both the maintenance of viable plant and animal populations and the maintenance of biodiversity. Sustaining biological diversity entails much more than simply maximizing species richness, that is, maximizing the numbers of different species that occur in a local area. A broader view is necessary. The conservation challenge is to ensure that all species native to an entire region are maintained as well-distributed, viable populations (Murphy 1989, Knopf 1992). Federal legislation requiring the protection of species, critical habitats, and biological diversity is already in place. The National Forest Management Act (NFMA) of 1976 and related regulatory mandates are designed to (1) provide for the diversity of plant and animal communities and (2) maintain viable populations of native and desirable non-native plants and animals on national forest lands. Also, the Endangered Species Act of 1973 established the conservation of individual threatened and endangered species as national priority. Individual species are one of the fundamental components of biological diversity. Sustaining biological diversity within a region requires a comprehensive knowledge of regional communities, the biology of associated species, the interconnections of species and ecosystems, and the roles and human uses of resources other than wildlife. We hope that the information we present here will contribute to efforts to sustain biological diversity in the Rocky Mountain Region of the U.S. Forest Service (Region 2), which encompasses Colorado, Wyoming, South Dakota, Nebraska, and Kansas. Some of this material was originally prepared as unpublished background information to support the Rocky Mountain Region’s Biological Diversity Assessment (U.S. Forest Service 1990).

The Biological Diversity Assessment was produced as a supplement to the revised Rocky Mountain Regional Guide, which provides land and resource management planning direction to the national forests and grasslands in the region.

The wide variety of plant communities in the Rocky Mountain Region provides for a regionally diverse fauna (Hoover and Wills 1984), and reduction or loss of any particular species or vegetation type would result in loss of biotic diversity. However, declines in wildlife diversity are more likely when critical habitats are degraded. Habitats that add substantially (more than average) to wildlife diversity can be identified as those with (1) high numbers of wildlife species; (2) high abundances or biomasses of animals; (3) unique, obligatory faunas or specialized wildlife species; (4) limited, disjunct, or shrinking distributions; and (5) threatened, endangered, or sensitive species. Finch (1992) evaluated threatened, endangered, and sensitive species in 15 major vegetation types in the Rocky Mountain Region, concluding that wetlands, riparian areas, and various lowlands contained higher numbers of listed vulnerable species than upland coniferous and deciduous forests. Using this information in combination with summaries by Hoover and Wills (1984) of overall wildlife species richness and abundance in the Rocky Mountain region, we identified six general habitats that have unusually high overall value to vertebrate faunas: wetlands, riparian woodlands and shrublands, green ash woodlands, aspen forests, pinyon-juniper woodlands, and pure and mixed forests of ponderosa pine. To ensure compatibility with Hoover and Wills (1984), we excluded short grass and mixed grass prairie from our consideration. However, we emphasize that Great Plains grasslands are essential habitats to many threatened, endangered, and...
sensitive species (for summary, see Finch 1992).

In this paper, we discuss why woodland and wetland communities have high biological diversity value and describe human land uses that can sometimes contribute to their degradation or loss. In addition, we explain why the late-successional stages of other habitats (lodgepole pine, subalpine spruce-fir, and Douglas-fir) are also very important in the maintenance of regional wildlife diversity. Sustaining regional wildlife diversity will involve management practices designed to conserve and restore all of these natural communities.

**IMPORTANT HABITATS**

**Wetlands**

Wetlands are areas that are permanently or intermittently covered by water, such as marshes, swamps, bogs, potholes, muskegs, shallow lakes and ponds, and overflow land of rivers and streams (Veatch and Humphrys 1966, Schwarz et al. 1976). Freshwater wetlands are valuable for their functions in hydrologic, chemical, and biological cycles; as receivers and transformers of natural and human wastes; as protection from floods; as recharge groundwater aquifers; and as unique habitats for a wide variety of plants and animals (Mitsch and Gosselink 1986). Over 200 migratory bird species visit western wetlands (Capen and Low 1980). Wetlands serve as crucial flyways for migratory ducks, geese, and swans. In the U.S. Forest Service Rocky Mountain Region, 35 species of waterfowl use wetlands regularly or occasionally to breed, migrate, or winter. Other birds in the Rocky Mountain Region that almost exclusively use wetlands include terns (5 species), gulls (6), sandpipers and piplovers (35), cranes (2), rails (4), loons (6), herons (8), grebes (5), pelicans (1), ibises (1), and cormorants (1) (Colorado Field Ornithologists 1978, Oakleaf et al. 1982). Fish-eating predators such as bald eagles, ospreys, mink, and river otters (throughout, see Table 1 for scientific names) rely on wetlands for prey, while big game, upland game birds, and numerous nongame species use wetlands for refuge and water during drought or fires. Wetlands typically have higher numbers of species and individuals of small mammals, songbirds, reptiles, and amphibians than surrounding natural communities (Johnson and McCormick 1978, Szuro et al. 1988, Sharitz and Gibbons 1989).

Seven bird species and subspecies federally listed as threatened or endangered are known to use wetlands frequently or peripherally in the Rocky Mountain/Great Plains region: whooping crane, brown pelican, bald eagle, least tern, Eskimo curlew, and piping plover. Wetland/prairie species identified by the U.S. Fish and Wildlife Service Office of Endangered Species as potentially threatened or endangered (Category 2 species) for the Rocky Mountain/Great Plains Region are snowy plover, long-billed curlew, and white-faced ibis. Some resident wetland species are rare and local. For example, Preble’s race of the meadow jumping mouse, a candidate subspecies (Category 2) on the federal threatened and endangered species list, occupies eastern foothill marshes of Wyoming’s Laramie Range. The Rocky Mountain wood frog, a local inhabitant of the Medicine Bow and Bighorn Mountains, breeds predominately in small standing ponds with emergent vegetation along a shallow north bank (Haynes and Aird 1981). Wyoming toad, a subspecies federally listed as endangered and found in Wyoming’s Laramie Basin (Baxter et al. 1982), and western boreal toad, a candidate subspecies (Category 2) for the federal list, inhabit isolated wetlands and riparian areas.

Prior to recent legislation, wetlands were destroyed at an alarming rate of about 1% per year in the United States (Mitsch and Gosselink 1986). Draining, degradation, and loss of wetlands can severely reduce animal abundance and species diversity; population sizes of resident threatened, endangered, and sensitive species; waterfowl and fur-bearing production; harvest quotas; and hunter-trapper success. Livestock grazing, agricultural conversion, tree-cutting, industry, energy development, urban encroachment, water pollution, recreation, and numerous water-control practices can drastically alter wetland environments, reducing their value to wildlife (Johnsgard 1956, Weller et al. 1968, Christiansen and Low 1970, Horwitz 1978, Sharitz and Gibbons 1989). Changes in water levels, livestock trampling, human disturbance, and nest predation have had disastrous consequences for ground-nesting colonial birds such as pelicans, gulls, and terns, because of impacts to whole colonies (Johnson and Sloan 1976, Capen and Low 1980). Trophic concentration of pesticide residues and other environmental contaminants have resulted in population declines in numerous fish-eating birds such as bald eagle, osprey, western grebe, white-faced ibis, and American white pelican (Herman et al. 1969, McCrow 1974, Capen 1977, Henny and Anthony 1989). In summary, wetland ecosystems provide essential habitats for a large number of vertebrate species, many of which use them exclusively. Wetlands are regarded as important, irreplaceable ecosystems for their characteristic plants and animals (Mitsch and Gosselink 1986).

**Riparian Woodlands and Shrublands**

The term riparian refers to the area bordering a river, stream, or lake (Schwarz et al. 1976). Riparian zones are highly valued as areas of wildlife habitat, recreation, timber, livestock forage, and water; travel passageways for animals and humans; buffer zones between managed and natural areas; natural filters of surface runoff and waste; stabilizers of shorelines and stream channels; interceptors for precipitation; and insulation for streams (Melton et al. 1984). Like wetlands, riparian ecosystems provide water, food, and shelter to a large number of game species, including mule deer, whitetailed deer, moose, elk, waterfowl, and upland game birds. In the Rocky Mountain region, several fur-bearing mammals such as river otter, mink, opossum, ringtail, raccoon, beaver, and muskrat depend on riparian areas for survival and reproduction. Hoover and Wills (1984) reported more species of amphibians (13), reptiles (33), and birds (177) in cottonwood riparian woodlands than in eight other forest types of Colorado, and species richness of mammals (59) was second only to that in pinyon-juniper woodlands (Table 2). Riparian areas may contain the majority of a region’s amphibians and reptiles (Brude and Bury 1984).
In the Great Plains alone, 73% of 325 breeding bird species are reported to use riparian woodlands, and 45% (117 species) of 260 regular breeders nest in riparian areas (Johnsgard 1979). Riparian habitats are valuable in spring and fall as migratory corridors for songbirds (Rappole and Warner 1976, Stevens et al. 1977) and as staging areas for whooping cranes and sandhill cranes (Frith 1974, Aronson and Ellis 1979). Many species of small mammals, bats, songbirds, amphibians, and reptiles reside solely in riparian habitats (Armstrong 1972, Seabloom et al. 1978, Johnsgard 1979, Brode and Bury 1984). Short-tailed shrew, eastern mole, red bat, and river otter are rare Colorado mammals using riparian and wetlands exclusively (Bissel 1978). Population declines in Bell's vireo may be the result of loss of riparian areas and increased cowbird parasitism (Office of Migratory Bird Management 1987).

Cross (1985) found that mammal species diversity in riparian sites exceeded that in conifer sites. Riverbank cottonwood sites also have higher densities and species richness of birds than adjacent uplands (Knopf 1985), grasslands and sagebrush (Ports 1979), conifer forests (Hopkins et al. 1986), or agricultural lands (Helnhe and Stone 1978, Ports 1979). In the northern High Plains, cavity nesters were found to be more abundant in cottonwood-dominated vegetation types than in three other vegetation types (Hopkins et al. 1986). By comparing the percentages of shared species among nine forest types in Colorado, Raphael (1987) demonstrated that cottonwood types are least similar in species composition, limited distribution, and drought may contribute to woodland deterioration (Severson and Boldt 1978, Bjugsd and Girard 1984). Woodland restoration strategies have involved fencing to exclude cattle, felling of low-vigor trees, and transplanting of nursery stock (Boldt et al. 1978).

Lack of regeneration is a major problem in green ash woodlands (Boldt et al. 1978). Grass-forb communities are replacing woodlands in many areas of the northern Great Plains (Boldt et al. 1978). Forests with multiple layers of shrubs reproduce naturally, but open woodlands fail to regenerate (Hodorff et al. 1988). Heavy livestock grazing is probably most responsible for the decline of green ash woodlands, though insect and disease damage, fire suppression, and drought may contribute to woodland deterioration (Severson and Boldt 1978, Bjugsd and Girard 1984).

Bird species richness in green ash woodlands increases with woodland size (Hopkins 1980, Fleckenstein 1981). Hopkins et al. (1986) found that, in comparison to coniferous woodlands, ash woodlands supported higher bird abundances; higher densities of ground foragers, ground nesters, and shrub-sapling nesters; more bird species and more foraging guilds; and higher numbers of bark foragers and canopy foragers. Compared to open, nonregenerating groves of green ash, closed ash woodlands were reported to have higher densities of five mammal species and ten bird species, as well as nearly twice as many birds in total (Hodorff et al. 1988). Greater abundance of animals in closed, regenerating woodlands was related to increased vertical layering of shrubs and saplings (Hodorff et al. 1988).

**Green Ash Woodlands**

Although green ash and other deciduous woodlands comprise less than 1% of the northern Great Plains (Bjugsd and Sorg 1984), they offer valuable cover, forage, and habitat diversity to wildlife, particularly because of their floristic and structural composition, limited distribution, and island-like dispersion (Boldt et al. 1978, Faanes 1984). Green ash woodlands are critical breeding habitats for raptors and songbirds in North Dakota (Gaines and Kohn 1982; Faanes 1983, 1984) and are important areas for birds, small mammals, mule deer, and white-tailed deer throughout the Great Plains (Severson and Carter 1978, Uresk 1982, Petersen 1984, Hodorff et al. 1988). In winter, green ash woodlands contain abundant browse and shelter for deer (Swenson et al. 1983). Deer, turkey, furbearers, and firewood contribute to the high economic value of ash-wooded draws in the northern High Plains (Bjugsd and Sorg 1984, 1987).

As much as 100,000 ha of riparian lands are lost annually in the United States (McCormick 1978). Damage to riparian ecosystems and reductions in biotic diversity have resulted from livestock overgrazing (Ames 1977, Crouch 1978, Boldt et al. 1978, Duff 1979), agricultural conversion (Helnhe and Stone 1978, Conine et al. 1978), upland and floodplain timber-harvesting (Beidleman 1978, Borden 1978, Cross 1985), utilization of exotic plants (Knopf and Olson 1984, Olson and Knopf 1986), recreation (Atchison 1977, Thomas et al. 1979), oil and gas development (Girard and Stots 1985), sand and gravel mining (Graul and Bissel 1978), water use management (Tubbs 1980), and other human practices (Johnson et al. 1985). In some riparian ecosystems, natural events like flooding can also affect species composition, abundances, and habitat selection of ground-dwelling vertebrates (Knopf and Sedgwick 1988, Olson and Knopf 1988). Riparian habitats can deteriorate more rapidly and more extensively than surrounding areas, and the damage can have far-reaching effects. As riparian restoration is expensive, complex, and time-consuming, land managers should take considerable care in planning and executing management strategies (Behnke and Raleigh 1978, Tubbs 1980, Knopf et al. 1988).
Aspen Forests

Geographic variation in the aspen ecosystem, and structural and floristic variation among clones, understories, elevations, and seral stages, produces a wide variety of aspen habitats for wildlife. DeByle (1985) listed 135 bird species and 55 mammal species associated with aspen forests of western North America. Aspen groves are often the primary source of ample forage in western coniferous forests and the only source of wildlife cover in grasslands (Gullion 1977). Elk and moose select aspen over several other available habitats, and deer favor aspen as a browse species (DeByle 1985). In many areas, beaver depend solely on aspen for food and dam construction. Aspen is heavily used by ruffed grouse for food, cover, and nesting in areas of the West where aspen and grouse ranges overlap (Phillips 1967, Rusch and Keith 1971).

Aspen forests often have higher densities and diversities of birds than are found in other plant communities (Salt 1957, Winternitz 1980, Finch and Reynolds 1989). In a study in northeastern Wyoming, bird biomass was at least three times higher in aspen forests than in five other vegetation types (Salt 1957). Insect density and diversity are about twice as high in aspen compared to conifer forests (Schimpf and McMahon 1985), which may explain the high biomass and abundance of avian insectivores in aspen. In comparing bird communities among aspen sites, Flack (1976) found that bird species diversity increased with increased plant community layering, larger tree diameters, and reduced tree densities. The presence of aspen in conifer stands increases bird species richness (Scott and Crouch 1988a,b), but loss of aspen due to conifer succession results in population declines and loss of aspen-associated birds (Finch and Reynolds 1989).

About 34 hole-nesting bird species use aspen cavities (DeByle 1985), comprising as much as 60% of the birds in pure aspen stands (Winternitz 1980). One cavity-nesting species, the purple martin, has a limited distribution in U.S. Forest Service Region 2 (Finch 1992); natural nest sites have only been found in local, disjunct aspen forests in south-central Colorado (Finch 1992). Because cavity nesters prefer mature, live aspens infested with decay fungi for feeding and nesting (Crockett and Hadow 1975, Winternitz and Cahn 1983), they may be particularly sensitive to clear-cutting and fragmentation of mature or so-called decadent aspen forests. As the standing lives of aspen snags and sun-scalded trees left in clear-cuts are short (DeByle and Winokur 1985), retention of snags and live trees

<table>
<thead>
<tr>
<th>Common Name</th>
<th>Scientific Name</th>
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<tr>
<td><strong>AMPHIBIANS</strong></td>
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<tr>
<td>Rocky Mountain wood frog</td>
<td>Rana sylvatica</td>
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<td>Wyoming toad</td>
<td>Bufo hemiophrys baxteri</td>
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<tr>
<td>Desert striped whipsnake</td>
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<td>Mesa Verde night snake</td>
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<td>Yellow-headed collared lizard</td>
<td>Crotaphytus collaris auriceps</td>
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<td>Brown-headed cowbird</td>
<td>Molothrus ater</td>
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<td>Brown pelican</td>
<td>Pelecanus occidentalis</td>
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<td>Columbian sharp-tailed grouse</td>
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<td>Eskimo curlew</td>
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<td>Flammulated owl</td>
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<td>Osprey</td>
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<td>Charadrius melodus</td>
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<td>Pygmy nuthatch</td>
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<td>Sandhill crane</td>
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<td>Snowy plover</td>
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<td>Western bluebird</td>
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<td>Western night heron</td>
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<td>White-breasted nuthatch</td>
<td>Sitta carolinensis</td>
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<td>White-faced ibis</td>
<td>Plegadis chihi</td>
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<tr>
<td>Whooping crane</td>
<td>Grus americana</td>
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does not solve the cavity nest shortage in cut-over aspen. Species that use large, intact forests of mature aspen — for example, hawks, owls, and woodpeckers — are likely to be adversely affected by clear-cutting, while birds that prefer early successional stages of aspen should increase in abundance once regeneration is established (Scott and Crouch 1988c). Overgrazing and fire suppression can result in ecosystem deterioration, lack of regeneration, conifer succession, and ultimate loss of aspen forests (DeBye and Winokur 1985).

Pinyon-Juniper Woodlands

Hoover and Wills (1984) listed more mammal species (62) in pinyon-juniper woodlands than in other forest types of Colorado (Table 2). Several rare arid-land mammals of Colorado, including Yuma myotis, cliff chipmunk, white-tailed antelope squirrel, Apache pocket mouse, desert woodrat, kit fox, ringtail, and hog-nosed skunk are virtually absent from forests other than pinyon-juniper (Bissell 1978). Colorado's pinyon-juniper woodlands are second only to cottonwood riparian woodlands in numbers of species of amphibians (10) and reptiles (23, Hoover and Wills 1984). Pinyon-juniper provides habitat for eastern and yellow-headed collared lizards, long-nosed leopard lizard, mountain short-horned lizard, Mesa Verde night snake, desert striped whipsnake, and midget faddled rattlesnake (Smith et al. 1965, Langlois 1978, Hoover and Wills 1984), uncommon species more typically associated with desert and shrublands in other regions. Three candidate species or subspecies (Category 2) for federal listing as endangered or threatened by the Office of Endangered Species — Texas horned lizard, hog-nosed skunk, and Columbian sharp-tailed grouse — occur in pinyon-juniper woodlands. In addition, at least 107 bird species use various seral stages of pinyon-juniper for survival and breeding (Table 2; Hoover and Wills 1984).

Vertebrate assemblages in Colorado pinyon-juniper are more similar in species composition to the specialized faunas associated with cottonwood riparian, ponderosa pine, and Gamble oak community types than to those found in subalpine spruce-fir, Douglas-fir, lodgepole pine, aspen, and high-elevation riparian communities (Raphael 1987). In areas with high densities of pinyon pine, cavity nesters comprise almost half of the breeding bird species (Hering 1957, Masters 1979). In a pinyon-juniper-ponderosa pine ecozone, foliage-feeding birds selected pinyon pine more often than predicted by chance (Laundersley and Balda 1976). Thus, bird communities are likely to be seriously impacted by selective removal of pinyon pine (Balda and Masters 1980). Some foliage-nesting birds apparently prefer junipers over pinyons (Hardy 1945, Short and McCulloch 1977). Wintering birds depend heavily on juniper berry crops, and winter species diversity is strongly correlated with berry production (Balda and Masters 1980).

In the Badlands of South Dakota, juniper woodlands harbor 22 bird species not found in adjacent grasslands (Sieg and Uresk 1986) and provide specialized habitat for two mammal species — white-footed mouse and bushy-tailed woodrat (Sieg 1988). Isolated juniper woodlands may serve as dispersal sites for woodland mammals in the northern Great Plains (Sieg 1988). In the High Plains ecosystems of South Dakota, steep juniper slopes are highly important habitats for mule deer (Severson and Carter 1978, Severson 1981) and long-eared owls (Paulson and Sieg 1984).

Livestock grazing, oil and gas development, fire suppression, firewood gathering, and urban encroachment can reduce the importance of pinyon-juniper woodlands for wildlife (Uresk 1982, Bjugstad and Girard 1984, Wills 1984, Girard and Stotts 1985). Pinyon-juniper woodlands traditionally have been undervalued because they produce less forage for live-
stock than grasslands and because the trees have low commercial value relative to other harvestable trees (Arnold et al. 1964, Terrel and Spillett 1975). Management of pinyon-juniper woodlands has largely consisted of eradication and type-conversion into grazing lands (Arnold et al. 1964, Terrel and Spillett 1975). Because the pinyon-juniper type is valuable to wildlife and has a limited distribution in the Rocky Mountains and northern Great Plains, it should receive special conservation efforts.

Pure and Mixed Forests of Ponderosa Pine

The ponderosa pine type offers a broad range of natural communities for biodiversity. First, it has the widest distribution of any pine forest in North America. Furthermore, plant associations encompass savannas, mixed broadleaf-conifer forest, mixed conifer forests, and pure yellow pine forests; and local size naturally varies from small, disjunct forest islands to extensive, contiguous forests. Finally, timber production is secondary to noncommercial values (Diem and Zeveloff 1980). Vertebrate faunas in ponderosa pine forests differ greatly in species composition from the shared communities associated with spruce-fir, lodgepole pine, and Douglas-fir forests of Colorado (Raphael 1987). At least 57 mammal species use ponderosa pine forests (Table 2; Hoover and Wills 1984), including rare species like Mexican vole and fringed myotis (Bissell 1978). Abert’s squirrel is dependent on late seral stages of ponderosa pine forests (Keith 1965, Patton and Green 1970).

From 113 to 128 bird species reside in ponderosa pine forests (Diem and Zeveloff 1980, Hoover and Wills 1984). Hoover and Wills (1984) identified 7 bird species (6% of 128) that used only mature to old-growth forests of ponderosa pine and 28 bird species (22%) that used mid- to late-successional stages (Table 2). Diem and Zeveloff (1980) estimated that 22% of the bird species in yellow pine forests had declining populations. Barn owl, flammulated owl, spotted owl, Lewis’ woodpecker, white-breasted nuthatch, pygmy nuthatch, and western bluebird may be especially sensitive to timber management practices in ponderosa pine habitats because of their dependencies on late seral stages, specific plant communities, and cavity-nest sites (Diem and Zeveloff 1980, Reynolds et al. 1989, Finch 1992). Northern goshawk, an open-nesting species that requires large areas of mature forest for breeding, may be negatively affected by harvesting of old growth (Reynolds 1989). The Mexican spotted owl, a species whose range barely intrudes into southern Colorado, was federally listed as a threatened species in 1993. Flammulated owl and northern goshawk are included on the Vertebrate Sensitive Species List issued by U.S. Forest Service Intermountain Region (Region 4, Spahr et al. 1991).

Overharvest of old growth, forest fragmentation, structural simplification of clearcut stands, fire suppression, and snag removal can reduce the value of ponderosa pine forests to wildlife (Bull 1978; Szaro and Balda 1979a, 1979b; Diem and Zeveloff 1980). Quality of Abert’s squirrel habitat is likely to be negatively impacted by forest fragmentation and reduction of stand heterogeneity due to commercial logging (States et al. 1988). Fragmentation or loss of old growth may cause further range restrictions in the Mexican spotted owl (Ganey 1988) similar to the pattern detected in the northern race (Forsman and Meslow 1986, Dawson et al. 1987).

LANDSCAPES, SUCCESSION, AND CONSERVATION

All the natural communities discussed above exist in some context, that is, they are surrounded by dissimilar vegetation and occur in variable physiographic conditions. Any specific community type together with its context subsumes a broader geographical and a broader ecological context or scale than the habitat per se. Punctuated by patterns of habitat patches, this broader area can be thought of as a landscape. Landscapes, in turn, can be ordered by their geographic scope, natural resource values, and patterns of land use into various hierarchical schemes that are of potential interest to researchers and managers. Most conservation issues on state and federal lands are ultimately addressed at ecosystem, watershed, or regional levels of landscape organization because it is at these higher levels of spatial resolution that multiple uses, land management approaches, and socioeconomic factors interact to affect biological diversity.

Still, land management activities modify plant communities at all ecological levels. Compositional and structural features of homogeneous communities (e.g., forests or specific rangeland communities) are modified by management, including land-use adapted to industrial land use. Similarly, overall patterns of vegetation abundance within landscapes are modified; kinds, amounts, and arrangements of vegetation communities are altered. And as landscape-level vegetation mosaics change, so too does wildlife species composition within communities and ecosystems. Most importantly, management-induced changes usually simplify structural and compositional complexity at all levels of ecological organization. An exception is the creation of complex edge areas by logging or fire, but the addition of edge often results in population increases of undesirable wildlife species (e.g., predators, brown-headed cowbirds, competitors) that interfere with survival and reproductive success of bird species that depend on large intact blocks of an ecosystem or plant community (Finch and Stangel 1993).

Most commodity-oriented vegetation management practices truncate (i.e., shorten the duration of) vegetative succession. Accordingly, the natural process of vegetation development is disrupted. In general, natural succession results in vegetation communities of increasing complexity as the developmental sere progresses from young to old (Margalef 1968, Komandny 1969, Odum 1969, Krebs 1985, Franklin 1988). It follows that management activities that curtail succession tend to simplify structure and composition, relative to that which would be expected in the late stages of community development, potentially reducing animal species diversity. Hunter (1990) presents an extended discussion and documentation of the importance of such complexity (e.g., vertical habitat structure) in maintaining animal diversity in managed forests. The reduction of ecological complexity occurs at multiple ecological
scales via a reduction of the structural and compositional complexity within plant communities and a reduction in the amount of late-successional vegetation in the landscape. In addition, the context within which remaining late-successional vegetation exists (i.e., the pattern of older and younger vegetation) is considerably different than would be expected under natural conditions. All these factors can be expected to influence the patterns of abundance of animals that are adapted to interior forest conditions or to the conditions of late-successional forest or rangeland vegetation. In general, populations of such species will become less abundant and the species' distributions will become more limited.

Reductions in the populations of late-successional animals lead to concerns about the maintenance of viable populations and, ultimately, to concerns about species conservation. Because forest management often results in an abundance of early successional vegetation, most wildlife conservation issues will revolve around the kinds, amounts, and arrangements of late-successional forests in managed landscapes. Thus, any discussion of important wildlife habitats must consider the late-successional stages of plant communities and their relationships to native wildlife populations.

**LATE-SUCCESSIONAL HABITATS**

Table 2 shows the relationship between bird and mammal species richness and the stages of development for eight important Rocky Mountain vegetation types (based on Hoover and Wills 1984). Total numbers of species associated with these types range from 76 to 177 for birds and from 38 to 62 for mammals (means of 107 and 47, respectively). As a measure of the variability in the numbers of species associated with each type, the coefficient of variation (CV) for birds is 0.30 and for mammals 0.22. In contrast, when considering only the numbers of species associated with the late-successional stage of each type, we find that the totals range from 5 to 7 for birds and from 0 to 4 for mammals. Also for late-successional stages for each type, the mean and CV for birds is 5.8 and 0.12, respectively, and for mammals 2.1 and 0.59, respectively. These statistics, and a visual examination of the distribution of species from Table 2, reveal that the numbers of bird species associated with late-seral vegetation are significantly less variable than are the numbers of bird species associated with all developmental stages.

This same pattern is found when birds and mammals are combined; the CV for the numbers of species associated with late-successional vegetation is 0.14 compared to a CV of 0.26 for the numbers of species associated with all successional stages (Table 2). Thus there is relatively low among-habitat variation in the numbers of species associated with the late-successional stag-

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**Table 2. Numbers of bird and mammal species in vegetation types of the Rocky Mountains and Northern Great Plains (after Hoover and Wills 1984).**

† Habitat association of American marten was changed from all seral stages to late-seral stages for SF, DF, and LP.

<table>
<thead>
<tr>
<th></th>
<th>SF</th>
<th>DF</th>
<th>PP</th>
<th>LP</th>
<th>A</th>
<th>PJ</th>
<th>HER</th>
<th>RC</th>
<th>MEAN</th>
<th>S.D.</th>
<th>CV</th>
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<tr>
<td><strong>BIRDS</strong></td>
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<tr>
<td>All Seral Stages</td>
<td>76</td>
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<td>128</td>
<td>86</td>
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<td>94</td>
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<td>28</td>
<td>24</td>
<td>19</td>
<td>16</td>
<td>17</td>
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<td>4.58</td>
<td>0.21</td>
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<tr>
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<td>5</td>
<td>7</td>
<td>6</td>
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<td>5.8</td>
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<td>6</td>
<td>7</td>
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<td>7.9</td>
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</table>
es of these communities. Although there is considerable difference among communities with regard to their importance in providing for overall species richness, it appears that these communities are of roughly equal importance with regard to meeting the habitat needs of birds and mammals that are associated with late-successional vegetation. The only exception to this may be for mammals in the late-successional cottonwood-riparian type. In general, though, it follows that the late stages of development for the communities under consideration are all especially important in maintaining regional wildlife diversity. Managers should place special conservation emphasis on these areas where biological diversity is one of their objectives.

KEY HABITATS

The spruce-fir, lodgepole pine, and Douglas-fir forest habitat types generally may not support vertebrate assemblages that are as rich as those of some other communities (e.g., wetlands, riparian cottonwood, or ponderosa pine). However, even though riparian cottonwood (RC) areas (the “richest” community type considered here) has four times the number of species associated with it as are associated with spruce-fir (SF), lodgepole pine (LP), and Douglas-fir (DF), each of these latter forest communities supports more late-successional mammals than does RC. And SF and LP support the same number of late-successional bird species that RC does. Considering that SF, LP, and DF are among the most widespread forest types in the western United States (Eyre 1980), their late-successional stages are especially important in maintaining regional biological diversity. Accordingly, care should be taken to not unnecessarily fragment existing areas of late-successional forest in any of these types. When management is necessary, prescriptions should be applied that minimize the loss of ecological complexity at both local and landscape scales. To maintain regional biological diversity across multiple successional stages and still recover sensitive species that use critical natural communities, we recommend that adaptive management approaches, like the U.S. Forest Service’s “ecosystem management” strategy, be adopted.

ECOSYSTEM MANAGEMENT APPROACH

For socioeconomic, recreational, and legislative reasons, management strategies for single species have traditionally taken precedence over management for multiple species. Single species are highlighted in federal and state management plans when populations of a species need to be recovered, in accordance with the Endangered Species Act. Species have high commercial value (e.g., waterfowl, big game), a species has high recreational or aesthetic value (e.g., large species like raptors and cranes), a species is a keystone or critical link species (e.g., woodpeckers that supply homes for secondary cavity-nesting birds), and a species is an indicator of environmental problems (e.g., eggshell thinning in waterbirds and raptors indicates the presence of contaminants in the local environment).

The conservation of biological diversity involves keeping common species common (Finch and Stangel 1993) while simultaneously maintaining or recovering populations of rare or jeopardized species. To move beyond traditional single-species methods for managing ecosystems, researchers and land managers must expand their vision and recognize broader scales of interaction, thus accounting for natural complexity, population changes, community succession, temporal and spatial landscape dynamics, and shifting patterns of land use. A model program that provides guidance for research, monitoring, and management of multiple species is the new conservation program, “Partners in Flight.” “Partners in Flight” is a cooperative, international program to conserve neotropical migratory birds, particularly migratory songbird species whose collective regional populations have experienced long-term declines (Finch 1991, Finch and Stangel 1993).

Biological diversity conservation must factor in the human dimension early in the management planning stages. This will assure that socioeconomic concerns (jobs, markets, political issues, environmental values, and multiple uses of lands are integrated into plans for biological diversity conservation. To synthesize human concerns, single-species needs, and biological diversity goals, large-scale cooperative strategies like the new ecosystem management approach advocated by the U.S. Forest Service (Overbay 1992) need to be adopted. Ecosystem management is the use of an ecological approach to manage multiple uses of national forests and grasslands; it is achieved by blending the needs of people and environmental values in such a way that national forests and grasslands represent diverse, resilient, productive, and sustainable ecosystems. We believe that the ecosystem management strategy, if implemented as proposed by the Forest Service, can straddle the necessary geography, temporal scales, biotic and abiotic interconnections, species dependency patterns, monitoring needs, and scientific disciplines to effectively conserve biological diversity, including the maintenance of viable populations of rare, common, and human-valued species (Finch et al. 1993). Ecosystem management is adaptive management. It requires that researchers and managers, industry and environmentalists, work as teams to develop suitable techniques and plans for sustaining commercial and noncommercial natural resources within constantly changing environments.

To shift from a single-use, single-species approach to an ecosystem-level, multispecies approach, we recommend that species of concern be evaluated within the context of regional and global species richness and abundance, and that regional goals for species composition be managed at the ecosystem level. If needs of threatened or endangered species are ignored, however, these will be the first species to drop out of ecosystems. Their loss will result in the reduction of overall species richness at any particular spatial scale. Therefore, they can be thought of as the weakest link in biological diversity conservation. To ensure maintenance of regional biological diversity, the following steps can be taken by agencies and their cooperators:

1. Using existing research knowledge, prioritize species of concern, i.e., the weak-
est links of biological diversity, using an objective standardized procedure that accounts for global species rarity, population trends over time, demographic patterns, rates of habitat loss, and effects of current management (e.g., Hunter et al. 1993).

2. Weigh species of current concern alongside those that may become of concern in the future if management practices are changed to favor current high priority species (Finch et al. 1993).

3. Adjust final values to ensure that regional and global biological diversity, as indexed by species richness and composition, does not decline.

4. Determine what future environmental conditions are necessary to sustain populations of multiple current and future species of concern, reasoning that these future conditions will favor overall biological diversity.

5. Develop goals and guidelines that integrate management of these desired conditions with other resource values, including recreational and socioeconomic values. This involves the development of an interdisciplinary team that includes both researchers and managers.

6. Establish management direction that is adaptive to shifts in priorities and successional patterns, managing for a dynamic ecosystem and allowing for population changes, critical habitats, old-growth forests, and a full and natural variety of successional habitats.

7. Involve all those who affect, manage, or value ecosystems early in the planning process.

Once the system components, weakest links, and management directions are defined, demonstration projects can be established. We recommend that natural areas be used to establish model demonstration projects, and that managers of natural areas take an active interest in sustaining biological diversity and ecosystem integrity.

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