Rocky Mountains

"A climb up the Rockies will develop a love for nature, strengthen one's appreciation of the beautiful world outdoors, and put one in touch with the Infinite."

Enos A. Mills (1924)

The Rocky Mountains, the great backbone of North America, extend 5,000 kilometers from New Mexico to Canada. The elevations range from about 1,500 meters along the plains to 4,399 meters, and the widths range from 120 to 650 kilometers (Lavender 1975). The Rocky Mountains are composed of many mountain ranges with unique ecological features. For example, 20 ranges make up the Rocky Mountains in and adjacent to Wyoming (Knight 1994). The natural beauty, abundant wildlife, and fresh water have attracted human inhabitants for the last 10,000–12,000 years (Fig. 1).

Geology and Hydrology

The younger ranges of the Rocky Mountains uplifted during the late Cretaceous period (140 million–65 million years ago), although some portions of the southern mountains date from uplifts during the Precambrian (3,980 million–600 million years ago). The mountains' geology is a complex of igneous and metamorphic rock; younger sedimentary rock occurs along the margins of the southern Rocky Mountains, and volcanic rock from the Tertiary (65 million–1.8 million years ago) occurs in the San Juan Mountains and in other areas. Millennia of severe erosion in the Wyoming Basin transformed intermountain basins into a relatively flat terrain. The Tetons and other north-central ranges are magnificent granitic intrusions of folded and faulted rocks of Paleozoic and Mesozoic age (Peterson 1986; Knight 1994).

Periods of glaciation occurred from the Pleistocene Epoch (1.8 million–70,000 years ago) to the Holocene Epoch (fewer than 11,000 years ago). Recent episodes included the Bull Lake Glaciation that began about 150,000 years ago and the Pinedale Glaciation that probably remained at full glaciation until 15,000–20,000 years ago (Pierce 1979). Ninety percent of Yellowstone National Park was covered by ice during the Pinedale Glaciation (Knight 1994). The "little ice age" was a period of glacial advance that lasted a few centuries from about 1550 to 1860. For example, the Agassiz and Jackson glaciers in Glacier National Park reached their most forward positions about 1860 during the little ice age (Grove 1990).

Water in its many forms sculpted the present Rocky Mountain landscape (Athearn 1960). Runoff and snowmelt from the peaks feed Rocky Mountain rivers and lakes with the water supply for one-quarter of the United States. East of the Continental Divide, the Arkansas, Missouri, North and South Platte, and Yellowstone rivers flow to the Gulf of Mexico. The Colorado, Columbia, Green, Salmon, San Juan, and Snake rivers flow westward to the Pacific Ocean. Water, the "transparent gold" of the West, supports agriculture, municipal supplies, recreation, and hydroelectric power generation and is the lifeblood of all plants and animals. As Emperor Yu of China realized in 1600 B.C., "To protect your rivers, protect your mountains."

Courtesy B. R. McClelland, National Park Service (retired)

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Fig. 1. The Rocky Mountains.

Paleoecology

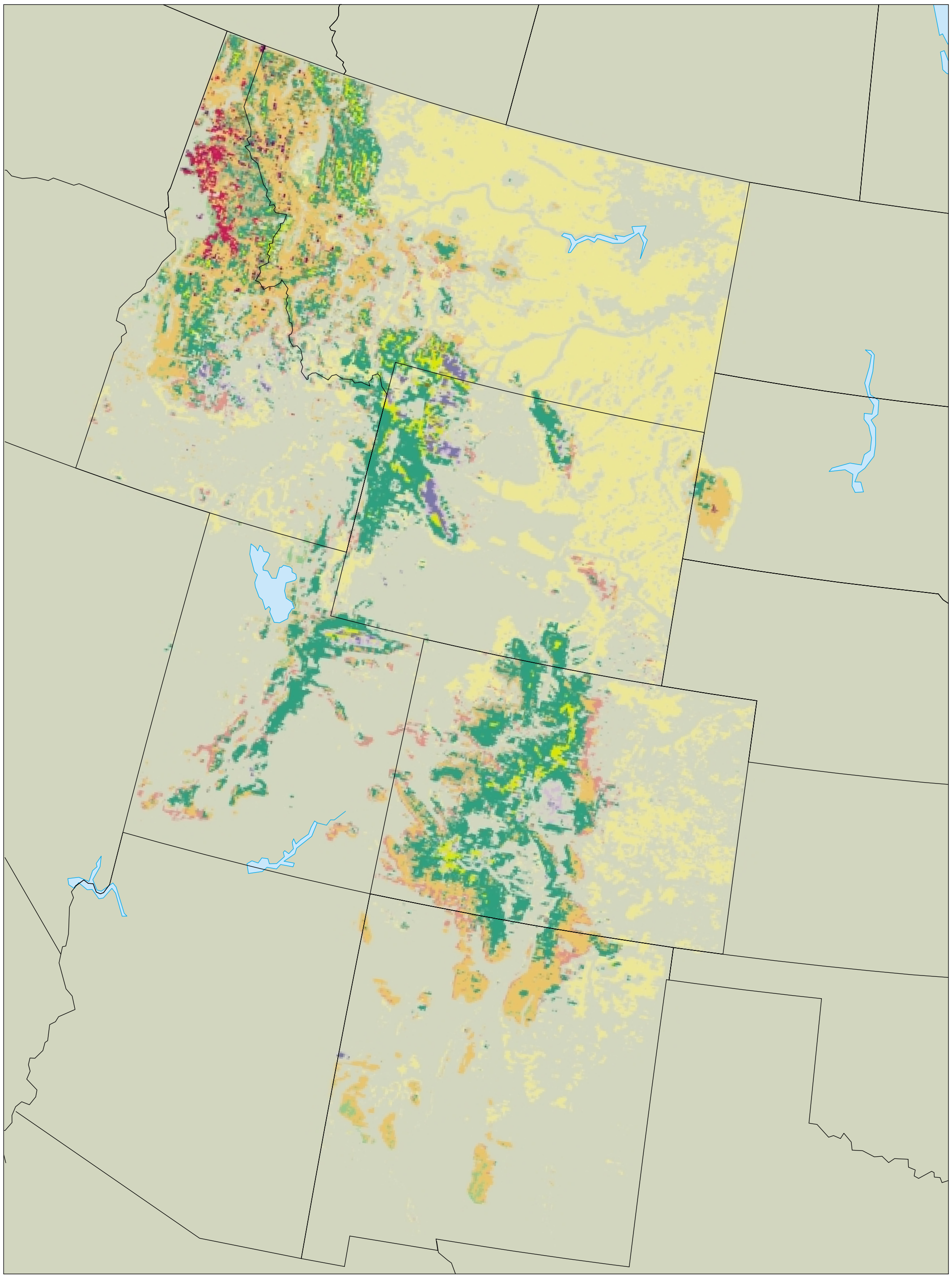
Paleoecological data from the Holocene in the central and northern Rocky Mountains are limited because the interpretation of pollen records is difficult—high winds distribute pollen locally and regionally—and because packrat middens, usually a good source of data, are rare and restricted to lower elevations. Evidence of the climate and vegetation changes since the last ice age is sketchy (Nichols 1982; Whitlock 1993). However, a scenario can be pieced together from paleoecological studies at treeline in Colorado (Benedict 1981; Nichols 1982), from current distributions of forest species in the northern Rocky Mountains (Alexander 1985), and from extensive work in and near Yellowstone National Park (Whitlock et al. 1991; Whitlock 1993), the Great Basin (Wells 1983), the Colorado Plateau (Betancourt et al. 1990), and the Colorado River (Cole 1990).

Paleoclimatic research at treeline in the central Rocky Mountains revealed that the last glacial age waned about 12,000 years ago. The climate changed from cool–moist to warm–moist about 10,000 years ago and then to a warm–dry climate about 4,000 years ago. The climate began to cool again about 2,500 years ago (Nichols 1982). During the Pinedale Glaciation (22,400–12,200 years ago), treeline averaged 500 meters lower than at present. Upper treeline advanced to as high as 300 meters above its present position during the warmest period. Cooling during the past 2,500 years has forced the treeline down to its present location; its decline was perhaps more rapid during the little ice age, between 1550 and 1860 (Nichols 1982).

No one has determined exactly how lower and midelevation tree species migrated, adapted, or changed in response to climate change. Some inferences may be made from recent research in the Grand Teton and Yellowstone national parks (Whitlock 1993) and from studies in the highest mountains in the Southwest, Colorado Plateau, and Great Basin. The vegetation diversity and complex elevation-moisture gradients of these areas are similar to those of the Rocky Mountains (Nichols 1982; Wells 1983; Betancourt et al. 1990; Cole 1990). One probable scenario is that toward the end of the last Ice Age (12,000 years ago), the central Rocky Mountains had relicts of alpine tundra at higher elevations. The lower elevations had subalpine forests dominated by limber pine and Engelmann spruce with an understory of juniper in wet areas and sagebrush outcrops in dry areas. Quaking aspens filled forest openings, and lush meadows lined the streams. During the Holocene transition (12,000–8,000 years ago), subalpine forests migrated upslope, and montane forests of lodgepole pines and Douglas-firs began to expand in the lower elevations. The Ice Age ended gradually; the southern Rocky Mountains and south-facing slopes warmed much earlier than north-facing slopes and the northern Rocky Mountains. As the climate warmed between 9,000 and 4,500 years ago, ponderosa pines, a species absent from the fossil record in the central and northern Rocky Mountains and Great Basin, became abundant in the lower elevations. An accompanying northern expansion of the summer monsoon may have extended the range of ponderosa pines and Douglas-firs. Drier and cooler conditions maintained the ponderosa pines and allowed further expansion of lower-elevation sagebrush-grass communities well up into the Rocky Mountains. Cooler conditions in the past 2,500 years decreased the midelevation fire frequencies that favor spruce-fir and lodgepole pine forests over limber pines; the frequency of fire increased at lower elevations because of the highly flammable structure of ponderosa pine–grassland fuels. The little ice age from 1550 to 1860 forced a descent of the upper treeline and perhaps lengthened intervals between fires. Tree rings from the region record a warming trend in recent decades (Weisberg and Baker 1995). The present rates of ecological change can be gauged against these background levels.

Current Vegetation Patterns

Vegetation patterns in the Rocky Mountains can be explained by elevation, aspect, and precipitation. Merriam (1890) recognized that two-dimensional diagrams of elevation and aspect described plant community distribution in the southern Rocky Mountains. Other ecologists generally embraced this two-dimensional view until the complexities of environmental gradients such as temperature, precipitation, solar radiation, wind, soils, and hydrology could be described and modeled (Peet 1981). Several authors (Alexander 1985; Peet 1988; Allen et al. 1991; Cooper et al. 1991; Knight 1994) described the vegetation patterns in different areas of the Rocky Mountains. Peet (1988) provided the most complete description of 11 major forest community types, which are summarized here. Two nonforested vegetation types, plains and alpine tundra, described by Sims (1988) and Billings (1988), were added to emphasize that nonforested communities play a large role in wildlife conservation in the Rocky Mountains (Knight 1994). The status and trends of many plant and animal populations in montane communities are inseparably linked to the adjacent and interwoven communities of the tundra and the plains (Fig. 2). Because of the variations in latitude and precipitation along this huge mountain range, the elevations presented here are gross generalizations.



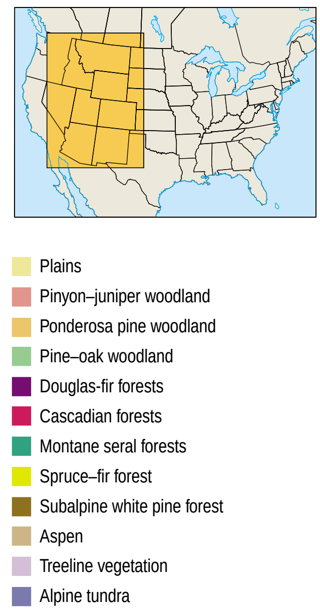


Fig. 2. Common vegetation types of the Rocky Mountains. This map was adapted from 1-kilometer Advanced Very High Resolution Radiometer imagery of March–October 1990, providing digital elevation, ecoregions, and climate data (provided by EROS Data Center, National Mapping Division, U.S. Geological Survey, and the University of Nebraska–Lincoln).

Plains

The eastern side of the Rocky Mountains is bordered by mixed-grass prairie to the north and by short-grass prairie to the south (see Plains; Fig. 2); prairie generally extends to elevations of 1,800 meters. Dominant plants of the mixed grass prairie include little bluestem, needlegrasses, wheatgrasses, sand-reeds, and gramas, with dropseeds and cottonwoods in riparian zones. Short-grass prairie species include little bluestem, buffalo grass, western wheatgrass, sand dropseed, ringgrass, needle-and-thread, Junegrass, and galleta (Sims 1988). Extensions of these vegetation types reach well into the Rocky Mountains along the valleys and on dry slopes. Plant species composition varies locally with changes in soil characteristics and topographic position—that is, from hilltops to valley bottoms (Knight 1994).

Riparian and Canyon Forests

Broad-leaved deciduous cottonwoods, alders, and willows line streamsides and canyons. The herbaceous layer in riparian communities is often more diverse than upslope areas and adjacent forests (Peet 1978; Baker 1990). Riparian and canyon vegetation types are generally too thin or too small to be displayed on regional vegetation maps, but the habitat is extremely important in the arid West.

Pinyon–Juniper Woodland

In the southern Rocky Mountains, a transition occurs between about 1,800 and 2,500 meters, where plains communities are accompanied by pinyon pines (Fig. 2). Mexican pinyons and singleleaf pinyons are found in western Utah, alligator junipers and Rocky Mountain junipers grow to the south, and Utah junipers grow to the north. Many shrubs and grasses of the plains occupy the gaps between tree outcrops. Heavy livestock grazing is associated with the spread of junipers (by reducing competition from grasses), and fire suppression is partly responsible for their continued dominance (West et al. 1975).

Ponderosa Pine Woodland

The appearance of ponderosa pine woodlands varies from scattered individuals in low-elevation or rocky areas to dense forests at higher elevations or on deeper soils (Peet 1981, 1988; Knight 1994). Although ponderosa pines dominate the biomass of this community, other tree species such as Douglas-fir and Rocky Mountain juniper, shrubs (for example, raspberries, big sagebrush, gooseberries, currants, bitterbrush), and herb layers (such as mountain muhly, sedges, and sagebrushes) can develop. Typical intervals between natural fires are less than 40 years in most ponderosa pine forests (Laven et al. 1980; Keane et al. 1990).

Pine–Oak Woodland

In the southern Rocky Mountains, lower slopes of ponderosa pine communities can be accompanied by Gambel oaks, other oak species (for example, Emory oaks, silverleaf oaks, netleaf oaks), and shrubs (such as sumacs, buckbrushes, and mountain-mahoganies). In the absence of fire, the oak stands may be invaded by pines (Peet 1988; Knight 1994).

Douglas-Fir Forest

Douglas-firs grow in a broad range from Mexico to British Columbia, generally from near lower treeline upward in elevation to spruce–fir forests (Fig. 2). In Colorado, the species ranges from about 1,650 to 2,700 meters and is often found in mixed stands with ponderosa pine, blue spruce, or lodgepole pine. Like ponderosa pine, Douglas-fir is tolerant of frequent, low-intensity surface fires. Fire intervals in Douglas-fir forests in Wyoming average 50–100 years (Loope and Gruell 1973).

Cascadian Forest

Several tree species commonly associated with the Cascade Mountains grow on the rain-swept western slopes of the northern Rocky Mountains. These include western hemlock, western redcedar, grand fir, mountain hemlock, and larches. These forests are subject to infrequent, high-intensity fires.

Montane Seral Forest

Lodgepole pine forests interspersed with stands of quaking aspens are fire-resilient forests that dominate the central and north-central Rocky Mountains (Fig. 2). Usually found between 2,500 and 3,200 meters in Colorado, lodgepole pines and aspens grow rapidly after fire in mostly even-aged stands.

Intervals between fires typically range from 100 to 300 years (Romme and Knight 1981). As evidenced by the fires in the Yellowstone National Park in 1988, lodgepole pine forests are rejuvenated by crown fires that replace tree stands. Although aspen stands generally cover less than 1% of the landscape (for example, Rocky Mountain National Park, Grand Teton National Park), they are keystone communities for hundreds of birds and mammals and are especially important forage for deer and elk (Mueggler 1993).

Spruce–Fir Forest

The subalpine forests of the Rocky Mountains are characterized by spruces and firs and are floristically and structurally similar to the boreal conifer forests to the north. Dominant tree species in the Colorado Rocky Mountains subalpine forests include Engelmann spruce and subalpine fir. In the Black Hills of South Dakota, white spruce replaces Engelmann spruce. Stand-replacing fires typically occur at 200- to 400-year intervals. Widespread insect outbreaks in spruce–fir forests occur more frequently (Veblen et al. 1991).

Subalpine White Pine Forest

On exposed, dry slopes at high elevations, subalpine white pine forests replace spruce–fir forests. Common species of the white pine forests include whitebark pine in the northern Rocky Mountains, limber pine in the central and north-central Rocky Mountains, and bristlecone pine in the southern Rocky Mountains. Typical intervals between fires range from 50 to 300 years (Kendall 1995). The white pines are tolerant of extreme environmental conditions and can be important postfire successional species.

Treeline Vegetation

Treeline is the elevation above which trees cannot grow. It is controlled by a complex of environmental conditions, primarily soil temperatures and the length of the growing season—which becomes shorter with higher elevations. The elevation of treeline rises steadily at the rate of 100 meters per degree of latitude from the northern to the southern Rocky Mountains. Dominant treeline species, including spruces, firs, and white pines, often have a shrublike form in response to the extreme conditions at the elevational limits of their physiological tolerance; such dwarfed trees are called *krummholz*. Krummholz islands may actually move about 2 centimeters per year in response to the wind; they reproduce by vegetative layering on their lee sides, while dying back from wind damage on their windward sides. Under favorable climatic conditions, krummholz can assume an upright treelike form or can increase their cone crops and seedling establishment.

Alpine Tundra

Alpine tundra is a complex of high-elevation meadows, fell (barren) fields, and talus (rock) slopes above treeline (above 3,400–4,000 meters). Grasses and sedges dominate the meadow communities, and fens (a type of wet meadow) and willows exist in wet soils. Vegetation in the alpine zone is similar to that in the Arctic: 47% of the plant species in the alpine zone of the Beartooth Mountains in Wyoming and Montana are also found in the Arctic (Billings 1988). This high-diversity area includes alpine sagebrush, tufted hairgrass, clovers, pussytoes, and succulents, and hundreds of grasses and wildflower species (Billings 1988; Popovich et al. 1993).

Extensive investigations have been made of the forests of the Rocky Mountains (Peet 1981; Allen et al. 1991; Veblen et al. 1991). Weber (1976:4–5) cautioned that the vegetation zones "overlap and telescope into each other considerably" in a landscape that is "always full of surprises." The resulting patchwork mosaic of vegetation types and disturbance regimes leads to a complex of side-by-side communities, wildlife habitats, and species distributions.

Wildlife

The charismatic megafauna of the Rocky Mountains includes elk, moose, mule and white-tailed deer, pronghorns, mountain goats, bighorn sheep, black bears, grizzly bears (Fig. 3), coyotes, lynxes, and wolverines. Equally important contributors to the region's biological diversity include small mammals, fishes, reptiles, amphibians, hundreds of bird species, and tens of thousands of species of terrestrial and aquatic invertebrates and soil organisms.

Courtesy R. Stottlemyer, USGS

Fig. 3. Fewer than 420 grizzly bears remain in the United States portion of the Rocky Mountains.

Human History and Cultural Development

Since the last great Ice Age, the Rocky Mountains were a sacred home first to Paleo-Indians and then to the Native American tribes of the Apache, Arapaho, Bannock, Blackfoot, Cheyenne, Crow, Flathead, Shoshoni, Sioux, Ute, and others (Johnson 1994). Paleo-Indians hunted the now-extinct mammoth and ancient bison (an animal 20% larger than modern bison) in the foothills and valleys of the mountains. Like the modern tribes that followed them, Paleo-Indians probably migrated to the plains in fall and winter for bison and to the mountains in spring and summer for fish, deer, elk, roots, and berries. In Colorado, along the crest of the Continental Divide, rock walls that Native Americans built for driving game date back 5,400–5,800 years (Benedict 1981; Buchholtz 1983). A growing body of scientific evidence indicates that Native Americans had significant effects on mammal populations by hunting and on vegetation patterns through deliberate burning (Kay 1994).

Recent human history of the Rocky Mountains is one of more rapid change (Lavender 1975; Knight 1994). The Spanish explorer Francisco Vásquez de Coronado—with a group of soldiers, missionaries, and African slaves—marched into the Rocky Mountain region from the south in 1540. The introduction of the horse, metal tools, rifles, new diseases, and different cultures profoundly changed the Native American cultures. Native American populations were extirpated from most of their historical ranges by disease, warfare, habitat loss (eradication of the bison), and continued assaults on their culture.

The Lewis and Clark expedition (1804–1806) was the first scientific reconnaissance of the Rocky Mountains. Specimens were collected for contemporary botanists, zoologists, and geologists (Jackson 1962). The expedition was said to have paved the way to (and through) the Rocky Mountains for European-Americans from the East, although Lewis and Clark met at least 11 European-American mountain men during their travels. Meriwether Lewis sent this description to Thomas Jefferson on 21 September 1806:

> The passage by land of 340 miles from the Missouri (River) to the Kooskooske (Clearwater River) is the formidable part of the tract proposed across the Continent: of this distance 200 miles is along a good road, and 140 over tremendous mountains which for 60 mls (miles) are covered with eternal snows. (Jackson 1962:320)

Mountain men, primarily French, Spanish, and American fur traders and explorers, roamed the Rocky Mountains from 1800 to 1850. The more famous of these include William Henry Ashley, Jim Bridger, Kit Carson, John Colter, Thomas Fitzpatrick, Andrew Henry, and Jedediah Smith. Beavers had been trapped to near-extinction by the 1840's.

The Mormons began to settle near the Great Salt Lake in 1847. In 1859 gold was discovered near Cripple Creek, Colorado, and the regional economy of the Rocky Mountains was changed forever. The transcontinental railroad was completed in 1869, and Yellowstone National Park was established in 1872. While settlers filled the valleys and mining towns, conservation and preservation ethics began to take hold. President Harrison established several forest reserves in the Rocky Mountains in 1891–1892. In 1905 President Theodore Roosevelt extended the Medicine Bow Forest Reserve to include the area now managed as Rocky Mountain National Park (Buchholtz 1983). Economic development began to center on mining, forestry, agriculture, and recreation, as well as on the service industries that support them (Lavender 1975). Tents and camps became ranches and farms, forts and train stations became towns, and some towns became cities.

Economic resources of the Rocky Mountains are varied and abundant. Minerals found in the Rocky Mountains include significant deposits of copper, gold, lead, molybdenum, silver, tungsten, and zinc. The Wyoming Basin and several smaller areas contain significant reserves of coal, natural gas, oil shale, and petroleum. Forestry is a major industry. Agriculture includes dryland and irrigated farming and livestock grazing. Livestock are frequently moved between high-elevation summer pastures and low-elevation winter pastures. Every year the scenic splendor and recreational opportunities of the Rocky Mountains draw millions of tourists. The National Park System units include Glacier, Grand Teton, Yellowstone, Rocky Mountain, and 16 others.

Abandoned mines with their wakes of mine tailings and toxic wastes dot the Rocky Mountain landscape. Eighty years of zinc mining profoundly polluted the river and bank near Eagle River in north-central Colorado. High concentrations of the metal carried by spring runoff harmed algae, moss, and trout populations. An economic analysis of mining effects at this site revealed declining property values, degraded water quality, and the loss of recreational opportunities. The analysis also revealed that cleanup of the river could yield $2.3 million in additional revenue from recreation. In 1983 the former owner of the zinc mine was sued by the Colorado Attorney General for the $4.8

million cleanup costs; 5 years later, ecological recovery was considerable (Brandt 1993).

Human Population Trends

The human population grew rapidly in the Rocky Mountain states between 1950 and 1990 (Fig. 4). The 40-year statewide increases in population range from 35% in Montana to about 150% in Utah and Colorado. The populations of several mountain towns and communities have doubled in the last 40 years. Jackson Hole, Wyoming, increased 260%, from 1,244 to 4,472 residents, in 40 years.

This rapid population growth increases demands for water, power, and natural resources. Ironically, the montane valley used for the filming of *The Unsinkable Molly Brown* (1964), which features the *Titanic* voyage, is now underwater, flooded by the Blue Mesa Reservoir (Stephanie Two Eagles, Location Specialist, Colorado Film Commission, personal communication).

Status and Trends of Ecosystems

Determining the status and trends of ecosystems requires fairly complete biotic inventories of major biological groups and detailed understanding of the behavior and interactions of plants and animals in complex environments. It also requires the systematic monitoring of key ecological processes (for example, disturbance, predation, competition, nutrient cycling, and energy flow). Although detailed information about some components and processes in certain Rocky Mountain ecological communities is available, information about entire communities is incomplete. Inferences about ecological trends usually are made from data describing selected components or processes in larger landscapes. Some of the most obvious changes that affect Rocky Mountain ecosystems are described in this chapter.

Bordering Prairie and Intermountain Ecosystems

Prairie dogs are keystone species in the plains, piedmont valleys, mesas, and foothills of the Rocky Mountains and throughout the plains of North America (Fig. 5). Prairie dog ecosystems support about 170 vertebrate species, including higher numbers of birds and mammals than the adjacent grasslands without prairie dogs (Miller et al. 1994). Prairie dog towns also have more plant species and more specialized insects and allies than adjacent areas (Knight 1994). Although exact causes of population changes in the Rocky Mountain foothills are unknown, the estimated 98% decline in prairie dog populations throughout North America is in part the result of federal- and state-sponsored prairie dog control (Miller et al. 1990). The U.S. Environmental Protection Agency and the Animal Plant Health Inspection Service estimated that 80,000 hectares of prairie dog habitat are eliminated annually (Captive Breeding Specialist Group 1992). Habitat loss and prairie dog control led to the endangered status (U.S. Endangered Species Act of 1973) of the black-footed ferret and the candidate listings of mountain plovers, ferruginous hawks, and swift foxes.

Because prairie vegetation and associated wildlife extend into the valleys and drier slopes of the Rocky Mountains, the food chain and ecological processes of adjacent ecosystems may be affected in subtle and poorly understood ways. For example, many of the 170 vertebrate species that are supported by prairie dog ecosystems have home ranges that extend into the montane forests of the Rocky Mountains. Reductions in the abundance of prairie dogs probably reduce the numbers of birds, insects (flower pollinators), snakes, and other species with important roles in adjacent ecosystems.

Fig. 4. Human population growth in the Rocky Mountain states and selected towns, 1950–1990, with rate of growth (percentage in 40 years).


Courtesy R. Stottlemyer, USGS

Fig. 5. The black-tailed prairie dog, a species whose habitat in North America has suffered a 98% loss.

Livestock have played (and continue to play) an even more important role in changes to these ecosystems. The most widespread influence throughout most natural ecosystems in the Rocky Mountains (from the plains to alpine meadows) is that of livestock grazing (Wagner 1978; Crumpacker 1984); 70% of the western United States is grazed. Undisturbed herbaceous ecosystems across the western United States are rare. Native vegetative ecosystems have previously been directly converted to agricultural fields and to livestock grazing areas (Grossman and Goodin 1995). A precise determination of the ecological effects of grazing often is difficult to obtain because ungrazed land is extremely rare, exclosures are small, exact figures on grazing intensities are scarce, and approaches to evaluate the effects of grazing are not standardized (Fleischner 1994). Johnson (1987) used paired photographs from 1870 and from the 1980's to show that only minor changes had occurred in landscapes in southern Wyoming during the twentieth century. Still, a recent synthesis of field studies (Fleischner 1994) suggested that in many habitats, grazing may have profound ecological effects that include reduced species richness and reduced density and biomass of native grasses, altered ecosystem processes (nutrient cycling and succession), and altered ecosystem structure caused by changing vegetation patterns, which contribute to soil erosion and decreased availability of water to biotic ecosystems. Livestock grazing aids in the spread of weeds (D'Antonio and Vitousek 1992), prevents native plains cottonwood regeneration in riparian zones (Glinski 1977), and influences the conditions and widths of riparian zones (Knopf and Cannon 1982; Chaney et al. 1990).

Fig. 6. Ponderosa pine.

Personnel of the U.S. Environmental Protection Agency (Chaney et al. 1990) concluded that riparian conditions throughout the West are now the worst in American history (Knight 1994); however, they also correctly caution that generalizations are not possible because of the complexity of the responses to grazing in different habitats over time. Removal of livestock lets riparian communities recover quickly from damage by grazing, except erosion. Trout habitat along Summit Creek in Idaho improved only 2 years after the elimination of grazing (Keller and Burnham 1982); 9 years after cattle exclusion, beavers and waterfowl returned to Camp Creek, Oregon (Winegar 1977). Thus, the potential for rehabilitation and restoration of excessively grazed riparian areas is good.

Ponderosa Pine Ecosystems

In geological time, ponderosa pine ecosystems are relatively new to the foothills of the central Rocky Mountains (Fig. 6). An even newer addition to the ecosystem, European–American settlers, devastated the ponderosa pine forests through logging for houses, fencing, firewood, mine timbers, and railroad ties, and with fire. The ponderosa pine forests were close to the developing population centers at the forest–prairie edge. The scale of the loss of ponderosa pine habitat is demonstrated best in several hundred paired photographs from the early 1900's and 1980's (Gruell 1983; Veblen and Lorenz 1991). However, nearly all the paired photographs also reveal that the most important feature of the ponderosa pine ecosystem is its resilience. Ponderosa pine seedlings establish quickly in disturbed sites. Research in the Front Range of Colorado shows a tenfold increase in ponderosa pine biomass since 1890 in many stands (M. Arbaugh, U.S. Forest Service, unpublished data). This regeneration has restored habitat for many wildlife species. More than 60 years of fire suppression, however, has created hazardous fuels in a forest ecosystem that naturally burned at 20- to 40-year intervals in many areas.

Old-Growth Forest Ecosystems

Old-growth forests were more common in the Rocky Mountains before European–Americans arrived than in recent times. However, presettlement old-growth lodgepole pine or Engelmann spruce–subalpine fir forests were rarer in the south-central Rocky Mountains south of Wyoming (Roovers and Robertus 1993) and more common in the northern Rocky Mountains (Romme and Knight 1981).

Crown fires that lead to the replacement of subalpine forests typically occur at 200- to

400-year intervals (Peet 1988). Extensive fires occurred in the mid-1700's (Robertus et al. 1991), and large-scale logging and the careless use of fire between 1850 and 1950 decimated forest resources (Gruell 1983; Veblen and Lorenz 1991). Insect outbreaks and windthrow can affect thousands of square kilometers of forests every few decades (Veblen et al. 1991; Knight 1994). In the south-central Rocky Mountains, the harm to spruce–fir forests from spruce beetle outbreaks can be as significant as that from fire (Baker and Veblen 1990; Veblen et al. 1991). Five major spruce beetle outbreaks, including a 290,000-hectare outbreak in the White River National Forest in Colorado in 1965, have affected thousands of square kilometers since the mid-1800's (Hinds et al. 1965). An additional natural disturbance, a windstorm, blew trees down in an area of 6 square kilometers in the Teton Wilderness Area in August 1987 (Knight 1994).

Because old-growth forest ecosystems were once more common in Rocky Mountain landscapes, it seems likely that species that depend on these ecosystems probably were also more common in presettlement times. Many threatened, endangered, and vulnerable wildlife species are largely dependent on intact old-growth ecosystems (Finch 1992). Caribou in northern Idaho, for example, feed on lichens that grow only in old-growth hemlock and cedar forests. Wolverines, martens, Abert's squirrels (Fig. 7), and fishers are associated almost exclusively with old-growth forests (Finch 1992). The southern red-backed vole is more abundant and has better body condition in old-growth spruce–fir forests (Nordyke and Buskirk 1991). Several bird species, such as the northern goshawk, flammulated owl, Mexican spotted owl, boreal owl, and olive-sided flycatcher, depend on old-growth conifer resources for either nesting or foraging (Finch 1992; Hayward and Verner 1994). The purple martin resides primarily in mature aspens, and like

Courtesy Rocky Mountain National Park

Fig. 7. Abert's squirrel, a species dependent on old-growth forests.

many other species that depend on old-growth forests, it is showing widespread declines of population sizes (Finch 1992). Given the historical threats faced by old-growth forests from fire, wind, and pathogens, one may ask how well these ecosystems have been protected in the past 40 years.

A recent U.S. Forest Service report on forest resources of the United States contains mixed news on the preservation of old-growth resources in the Rocky Mountains (Powell et al. 1993). Old-growth losses from wildfire (including the fires in the Yellowstone National Park in 1988) have been greatly reduced since the 1950's, but losses from the sawtimber industry have climbed. In the intermountain region (Arizona, New Mexico, Colorado, Wyoming, Utah, Idaho, and Montana), the total volume of available softwood sawtimber increased 3.7% between 1952 and 1992; however, available trees of the largest size class measured (those trees measuring more than 73 centimeters diameter at breast height) decreased 31.1% during the same period (Fig. 8). This represents a change in sawtimber volume from 151.9 million cubic meters to 104.6 million cubic meters. In 1992 only 45,000 cubic meters of these largest trees remained from the original 164,000 cubic meters in the nearby Great Plains (Kansas, Nebraska, North Dakota, and South Dakota), a 72.3% decline in 40 years.

The 35-year annual rate of decline in large tree volume (1952–1987) was 0.7% in the intermountain subregion. From 1987 to 1992, however, the annual rate of decline in large tree volume almost tripled to 2.0%. Old-growth forests are being rapidly replaced by younger, faster-growing forests (Fig. 9). Loss of habitat and increasing fragmentation of habitat may impede the protection of old-growth-dependent species for a long time.

Postdisturbance Ecosystem

Fire suppression has been effective, perhaps too effective for some species (see box on Fire Suppression in Land Use chapter). Nationwide losses of forestlands to wildfires decreased from about 20 million hectares per year in 1930 to fewer than 800,000 hectares per year in the late 1980's (MacCleery 1992). Even the 560,000-hectare fires in the Yellowstone National Park in 1988 that were reminiscent of fires in the 1700's burned less than 12% of the forestlands in Wyoming, Montana, and Idaho (Romme and Despain 1989; Schullery 1989). Thus, fire suppression may be profoundly affecting disturbance-dependent species. For example, the number of three-toed woodpeckers increases greatly for 3–5 years after a fire because the birds feed on larval spruce beetles found in

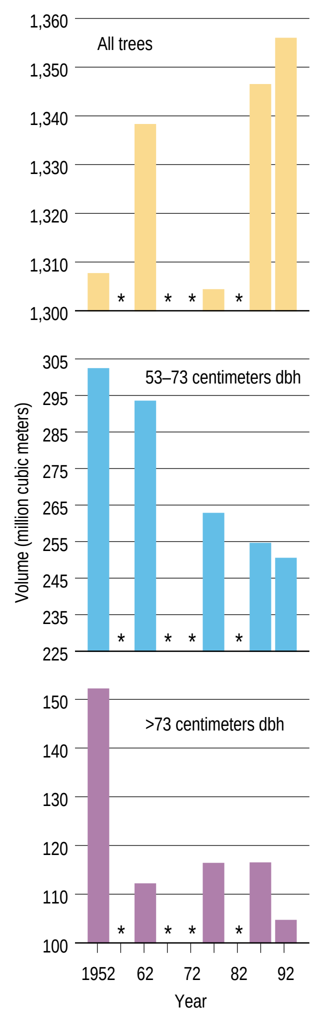


Fig. 8. Sawtimber volume change in the Rocky Mountain states (adapted from Powell et al. 1993); "dbh" = diameter of tree at breast height. "*" = data not available.

Fig. 9. Large trees (such as the one shown here) and old-growth forests may be rapidly disappearing from Rocky Mountain forests.

burned stands. These woodpeckers may significantly affect nearby forest stands by reducing the severity of spruce beetle epidemics. The black-backed woodpecker was absent in the Yellowstone National Park area before the 1988 fire, then it appeared for a few years in the burned forests to feed on insects and larvae.

Herbaceous plant diversity increases abruptly and drastically after a burn. Seventeen years after the 390-hectare burn in the Ouzel Lake area in the Rocky Mountain National Park, twice as many understory species had grown in the burn area than in adjacent stands of unburned forest (Stohlgren et al. 1997; Fig. 10). Species that depend on postdisturbance stands suffer habitat loss with each suppressed fire.

Fig. 10. The Ouzel burn area of the Rocky Mountain National Park, Colorado. The burn area has five times as many species of plants, including twice as many understory species, as nearby forests that were not burned.

Air Pollution Effects on Many Ecosystems

Air pollution, primarily from the combustion of fossil fuels in the Denver–Boulder–Fort Collins metropolitan corridor, may dramatically harm montane forests in Colorado. Chemical analyses of the high-elevation Colorado snowpack are revealing high concentrations (about 15 microequivalents per liter) of sulfate and nitrate in areas northwest of Denver (Turk et al. 1992). Some areas in the Colorado Front Range may have experienced a ninefold increase in wet deposition of nitrogen in the past several decades. Remote areas of the world typically receive less than 0.5 kilograms per hectare per year of inorganic nitrogen, whereas the high-elevation sites in the Colorado Front Range now receive as many as 4.7 kilograms per hectare per year of inorganic nitrogen (M. Williams and colleagues, University of Colorado, Boulder, unpublished data). In February 1995 the Colorado Air Quality Commission increased the Denver metropolitan area's particulate pollution limit from the current 41.2 tons per day to 44 tons per day in the next 20 years. Terrestrial biota of high-elevation areas may not be greatly affected by this increased nitrogen loading (Nams et al. 1993), but we can expect direct and indirect effects on ecosystem functions in forested catchments (Baron et al. 1994).

Aquatic Ecosystems and Wetlands

Information on aquatic ecosystems in the Rocky Mountains is highly fragmented, but available information suggests that the region may be typical of the United States: 80% of the nation's flowing waters are characterized by poor quantity and quality of fish habitat and fish community composition (Flather and Hoekstra 1989). All rivers in the Rocky Mountain region have been altered by reservoirs or other water projects (transbasin canals, irrigation ditches, and small water impoundments; see chapter on Water Use). A major transbasin water import project in Colorado carries about 370 million cubic meters per year from the Colorado River (west of the Continental Divide) through a 7.8-kilometer tunnel to the Big Thompson River (east of the Continental Divide). Ten reservoirs were constructed to support this project. There are approximately 40 major reservoirs in the watersheds of the Arapaho–Roosevelt national

Whitebark Pine

Whitebark pine is a picturesque tree of the subalpine forest and treeline of the Rocky Mountains, Coast and Cascade ranges, and the Sierra Nevada (Fig.1). Slow growing and long-lived, it is typically more than 100 years old before it produces cones. Whitebark pine's growth form ranges from a krummholz mat to a moderately tall, upright tree, but it is often short and heavily branched, with multiple stems.

Whitebark pine typically grows with other high mountain conifers but can form nearly pure stands in relatively dry mountain ranges (Arno and Hoff 1989). Where associated trees are capable of forming closed stands, whitebark pine can be a long-lived dominant seral species if periodic disturbance, such as fire, removes its shade-tolerant competitors. On a broad range of dry, windy sites, however, whitebark pine is a climax tree because it is hardier and more durable than subalpine fir and other tree species (Arno and Hoff 1989). The sites where whitebark pine is seral tend to be moister and more productive than sites where the tree is climax (Arno 1986).

Until recently, little was known of whitebark pine status because it occurs in rugged terrain and has limited use as a commercial timber species. In the last decade, however, its role as a keystone species has been recognized. Whitebark pine seeds are a preferred food of the threatened grizzly bear and many other mammals and birds (Fig. 2).

Because whitebark pine can grow in cold, dry, and windy conditions tolerated by no other tree, and because it pioneers disturbed sites, it plays an important role in tree establishment in high-elevation open sites. Whitebark pine helps stabilize snow, soil, and rocks on steep terrain and has potential for use in high-elevation land reclamation projects (Arno and Hoff 1989). Because of their spreading crowns and penchant for establishing on windswept ridges (Fig. 3), whitebark pines accumulate and retain snow, extending the snowmelt period into the growing season, when water is needed. With the growing appreciation of these values has come more interest and mounting concern over dramatic declines in whitebark pine stands (Arno 1986; Kendall and Arno 1990; Keane and Arno 1993; Lanner 1993).

Causes of Decline

Sixty years of fire suppression have advanced forest succession at the expense of seral whitebark pine communities. The transport and caching of whitebark pine seed by Clark's nutcrackers and the hardiness of seedlings on exposed microsites give a competitive edge to whitebark pine over less hardy wind-dispersed conifers, such as spruce and fir, in reforesting large burns. However, without fire, whitebark pines are shaded out by other trees, and there are few open sites for whitebark pine regeneration. Before fire exclusion, the average whitebark pine stand burned every 50 to 300 years. Even with the prescribed natural fires that have been allowed to burn in wilderness and national parks in the past 25 years, fewer than 1% of seral whitebark pine stands have burned during that period—an average fire return interval of more than 3,000 years (Arno 1986; Keane 1995a). The Selway–Bitterroot Wilderness in Montana has one of the most extensive prescribed fire programs in the United States, yet between 1979 and 1990, burning in the whitebark pine zone was less than half the area burned each year in presettlement times (Brown et al. 1994; Arno 1995).

An exotic fungus, white pine blister rust, has killed many whitebark pine trees in the moister parts of its range. White pine blister rust, which was introduced from Europe to western North America around 1910, has spread to most whitebark pine forests. Although white pine blister rust can damage all North American white pine species, whitebark pine is the most vulnerable (Fig. 4); fewer than 1 in 10,000 trees is resistant to blister rust. Because whitebark pine cones form in the top third of the tree and blister rust tends to kill trees from the top down, a tree's ability to produce seed is eliminated by the rust long before the tree dies (Fig. 5).

Courtesy K. C. Kendall, USGS

Fig. 2. Whitebark pine cones and large, wingless seeds.

Fig. 3. Whitebark pine occupying a windswept ridge in Glacier National Park, Montana.

Courtesy B. R. McClelland, National Park Service (retired)

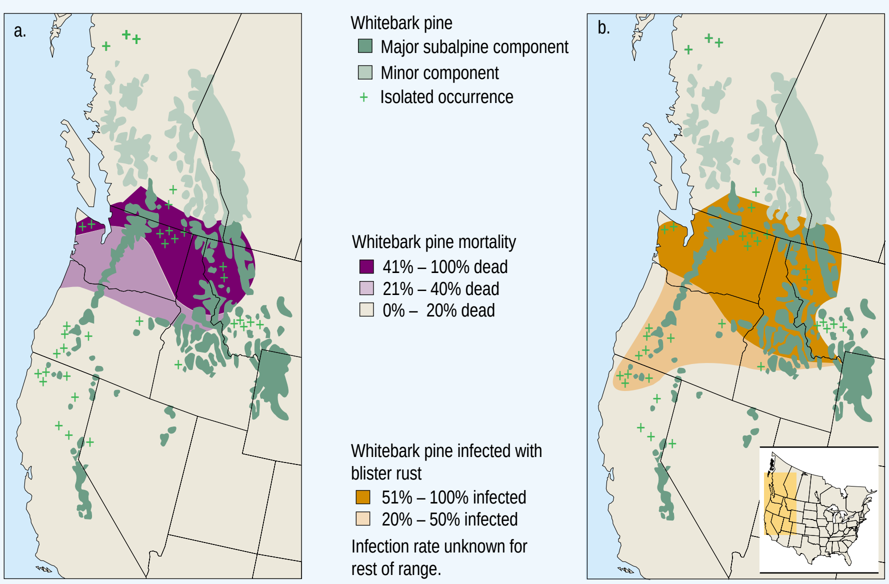


Fig. 1. a) Natural distribution of whitebark pine with amount of mortality from all causes since presettlement; b) white pine blister rust infection rates in whitebark pine. In northern Canada and the southern United States, blister rust is present but infection rates are unknown (revised from original map in Kendall 1995).

Courtesy S. Gniadek, National Park Service

Fig. 4. Heavy mortality from blister rust in a whitebark pine stand in Glacier National Park, Montana.

Courtesy K. C. Kendall, USGS

Fig. 5. An ancient whitebark pine in the Mission Mountain Wilderness, Montana, dying from the top down from the introduced fungus, white pine blister rust.

Declines from Historical Levels

Natural whitebark pine abundance before the recent decline has been summarized by Arno and Hoff (1989). Near the northern end of its range in the British Columbia coastal mountains, whitebark pine is a minor component of treeline communities. In the Olympic Mountains and on the west slope of the Cascades, it grows primarily on exposed sites near treeline. East of the Cascade crest, it is abundant within both the subalpine forest and treeline zone. Whitebark pine is a major component of high-elevation forests in the Cascades of southern Oregon and northern California. Near the northern end of their distribution in the Rockies of Alberta and British Columbia, whitebark pines are generally small, scattered, and confined to dry, exposed sites at treeline. Whitebark pine becomes increasingly abundant southward, especially in Montana and central Idaho. It is a major component of high-elevation forests and the treeline zone in western Montana. In western Wyoming, it is abundant between elevations of 2,440 meters to 3,200 meters. Before the advent of blister rust and fire control, whitebark pine was an important component on about 10%–15% of the forested landscape in the Rocky Mountains of Montana, Idaho, and northwestern Wyoming (Arno 1986). On about 1.2 million hectares of this area, whitebark pine communities are seral.

Although there is not comprehensive information on whitebark pine throughout its range, recent studies have begun to piece together the current status of this species. An assessment of the interior Columbia River basin found that the area of whitebark pine cover types has declined 45% since the turn of the century (Keane 1995b). Most of this loss occurred in the more productive, seral whitebark pine communities; 98% of them have been lost. Practically all the remaining whitebark pine stands are old. In southwestern Montana, a project to reconstruct landscape patterns found that 14% of the sampled stands were dominated by whitebark pine around 1900, but none of them were by the early 1990's (Arno et al. 1993). Moreover, the extent of stands with significant cone-bearing whitebark pine trees had declined by half.

Nearly half of the whitebark pine trees in Glacier National Park and the Bob Marshall Wilderness Complex in northwestern Montana are dead (Fig. 6). Of the remaining live trees, more than 80% are infected with rust and more than a third of their cone-bearing crowns are dead (Keane et al. 1994; Kendall et al. 1996a). Much of this mortality has been recent; few whitebark pines had suffered significant damage from rust in the early 1970's (Keane and Arno 1993). Blister rust is now present throughout the range of whitebark pine in the Canadian Rockies,

Courtesy B. R. McClelland, National Park Service (retired)

Fig. 6. A ghost forest of whitebark pine in Glacier National Park, Montana.

with the highest rust infection rates and mortality within 125 kilometers of the United States border (Smith 1971; R. Hunt, Forestry Canada, unpublished data).

In southern Montana and Wyoming, whitebark pine health improves as the climate becomes drier (Fig. 7). In the Gallatin National Forest and Yellowstone and Grand Teton national parks, an average of 7% of the whitebark pines are dead and 5% of the live trees are infected with rust (Kendall et al. 1996a,b). The highest infection rates (up to 44%) are found in the Teton Range, where conditions are moister than in neighboring areas to the north. Whitebark pine is reported to be functionally extinct on the Mallard Larkins Pioneer area in the Idaho Panhandle National Forest (Zack 1995). Rust infection rates in the Sawtooth National Recreation Area in central Idaho are generally light, but low elevations may harbor some heavily infected sites (Smith 1995).

Courtesy D. Reinhart, USGS

Fig. 7. A healthy whitebark pine in Yellowstone National Park, Wyoming.

There is less information about the status of whitebark pine west of Idaho. As a rule, blister rust is present and whitebark pine infection levels and mortality are high in the Cascade and Coast ranges. For a time, the dry conditions in the Sierra Nevada were believed to protect most white pine stands there, but in 1976 and 1983, unusually favorable weather produced heavy waves of rust infection in California white pines (Kinloch and Dulitz 1990). Although sugar pine has been the most affected and studied of these, rust is also present at low levels in some whitebark pine stands. In Kings Canyon and Sequoia national parks, fewer than 1% of the whitebark pine sampled in 1995 was infected with rust (Duriscoe 1995).

In Washington state, northern Idaho, northwest Montana, and southern Alberta and British Columbia, 40%–100% of the whitebark pine is dead in most stands, and 50%–100% of the live trees are infected with rust (Fig. 1) and have lost most of their capacity to produce cones (Kendall and Arno 1990; Kendall 1994a,b; Kendall 1995). Mortality and rust infection levels decline in the drier areas to the south.

Future Trends

Successional replacement due to fire exclusion is a major cause of whitebark pine decline (Keane et al. 1994). Whitebark pine cannot maintain its functional role in mountain ecosystems unless areas suitable for its regeneration are available across the landscape. Modern fires are restricted in whitebark pine habitats because they normally burn only at the height of very active fire seasons and, under those conditions, managers choose to suppress new fires (Arno 1995). Options for providing sites for whitebark pine regeneration include allowing wildfires to burn near historical levels, having more management-ignited burns with slash cut to help carry the fire in moderate fire weather, and selectively removing whitebark pine's competitors.

It is clear that the blister rust epidemic in whitebark pine has not yet stabilized, even in regions with the longest history and highest infection levels of rust. The most likely prognosis for whitebark pine in sites already heavily infected with rust is that they will continue to die until most trees are gone. In the southern Rockies and Sierra Nevada where there is currently little or no infection of whitebark pine, waves of infection are expected to occur within a few decades (Kinloch and Dulitz 1990; Kendall et al. 1996a). Eventually, whitebark pine in these areas is likely to suffer heavy losses.

Whitebark pine possesses some ability to defend itself from white pine blister rust (Arno and Hoff 1989), and there is evidence that natural selection has already started to enhance that ability. Forty percent more seedlings from stands with high blister rust mortality survived artificial inoculation with rust than seedlings from low mortality stands (Hoff 1994). In the future, whitebark pine trees will be all but absent in most areas, and small, isolated populations will be lost until rust-resistant types evolve. Without intervention, this is expected to require hundreds—if not thousands—of years, because whitebark pine matures slowly and most of the population soon will be lost (Fig. 8). Management strategies such as breeding whitebark pine for rust resistance and establishing natural selection stands will speed this evolution (Hoff et al. 1994).

See end of chapter for references

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Courtesy K. Kendall, USGS

Fig. 8. Winter comes to a whitebark pine stand in Yellowstone National Park, Wyoming.

Limber Pine

Limber pine is a five-needled pine widely distributed in the mountains and foothills of the Rocky Mountains in the western United States and southern Canada (Fig. 1). It is adapted to dry and windy conditions and can grow in some of the driest sites capable of producing trees (Pfister et al. 1977). Limber pine ranges from upper treeline and midelevation sites to lower treeline where the mountain forests give way to shrub steppes or prairie grasslands (Fig. 2). In most old stands, limber pines are widely spaced dominant trees with a short, bushy form; on moister sites, though, limber pines are moderately tall trees. The large wingless seeds of limber pines are a favored food of many animals. Limber pines are not usually commercially harvested because of their low productivity and poor form, thus, information about the species status is scarce. Recent observations of limber pine mortality have sparked increased interest in trends of limber pine communities (Kendall et al. 1996).

Limber pine, like the related whitebark pine, has been damaged extensively in some areas by white pine blister rust (Kendall 1995; Kendall et al. 1996). Blister rust is an exotic fungus for which limber pine has evolved few defenses, so the tree is extremely susceptible to this deadly disease. Limber pine is less affected by fire suppression than whitebark pine; in some areas, limber pine has expanded its range by invading grasslands where it was previously excluded by fire.

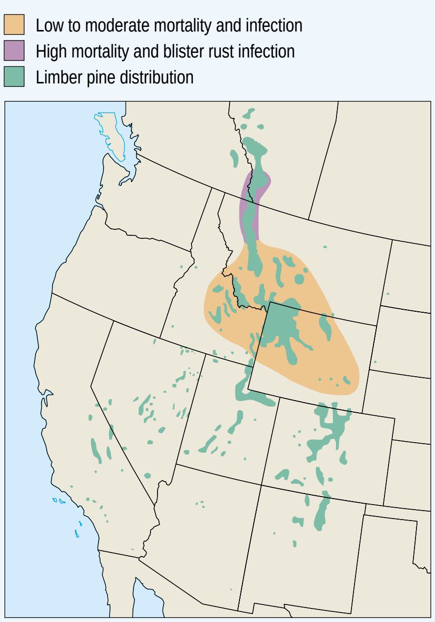

Fig. 1. Distribution of limber pine showing mortality zones and blister rust infection rates (adapted from Little 1971).

Courtesy K. C. Kendall, USGS

Fig. 2. Typical limber pine savannah near the town of Gardiner in southwestern Montana.

Status

Limber pine has suffered extensive mortality and blister rust infection in northwest Montana and southern Alberta (Fig. 1). On average, more than a third of the limber pines are dead and 90% of the remaining live trees are infected with rust (Kendall et al. 1996; Fig. 3). The status of limber pine in the northern Canadian Rockies is not known (Smith 1971). To the south, limber pine rust infection is reduced. In southwestern Montana, northwestern Wyoming, and adjoining areas of Idaho, limber pine mortality and incidence of rust are low to moderate, with a few hot spots of heavy infection. Blister rust incidence on limber pine in the Bighorn Mountains of north-central Wyoming has increased dramatically in the past few years (Lundquist 1993). No rust has been found in Craters of the Moon National Monument in southern Idaho (Smith 1995; Kendall et al. 1996). Blister rust has not been reported in limber pine south of Wyoming (Hawksworth 1990; Duriscoe 1995), and little is known of its status in Utah, Nevada, and California.

Fig. 3. Ghost limber pine forest on the Blackfoot Indian Reservation, with the mountains of Glacier National Park in the background.

Courtesy R. Keane, USDA, Intermountain Research Station

Outlook

Because limber pine grows in very dry areas, biologists hoped that blister rust, with its higher moisture requirements, would not be able to make significant inroads in limber pine stands. Unfortunately, it is now apparent that for most sites it may be just a matter of time before the necessary climatic conditions combine to produce a large wave of infection, even in drier climates in the southern parts of the limber pine range (Kinloch and Dulitz 1990). Once infected, most trees will die.

White pine blister rust was recently discovered in southwestern white pines in southern New Mexico (Hawksworth 1990). The nearest known rust occurrence is 1,000 kilometers to the north on limber pines in southern Wyoming. It is not clear whether this outbreak is a result of infected cultivars brought to the region or a result of long-distance transport of rust spores, but it is likely that few limber pine stands are ultimately safe from rust.

Other North American white pines have a small degree of rust resistance that can be strengthened by natural selection or tree-breeding programs. It is likely that the same is true for limber pine, but this potential remains unexplored. Because it is also likely that some individual trees are naturally resistant to blister rust, limber pine probably is not threatened with extinction. Some isolated populations, however, will be lost, and limber pine will be functionally extinct in areas suffering from heavy mortality for the hundreds of years that will be required for rust-resistant types to emerge. Natural selection could be speeded by a breeding program and establishment of stands where more limber pine seedlings are available for natural rust-resistant type selection because all other competing species are removed (Hoff et al. 1994).

See end of chapter for references

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forests in Colorado alone (C. Chambers, U.S. Forest Service, personal communication). The relationship between reservoir building and human population increases is particularly obvious (Fig. 11). Domestic water use accounts for less than 6% and agriculture for about 90% of the total water use (U.S. Geological Survey 1990). Reservoir building may also correlate with increased irrigation or other uses indirectly related to population growth.

Water quality is a growing concern in the Rocky Mountains. The U.S. Geological Survey (1993) stated that all of Colorado's major drainages are affected to some degree by pollution. Past mining operations still contribute toxic trace elements to more than 2,100 kilometers of rivers and streams in Colorado. More than 900 kilometers of Colorado's 50,300 kilometers of streams do not meet water-quality criteria for fishing. Other Rocky Mountain states report similar problems (U.S. Geological Survey 1993). Although water developments affect riparian zones upstream and downstream from dams (Mills 1991), regional information on the biotic effects of water projects and pollution is either extremely limited, fragmentary, or inaccessible.

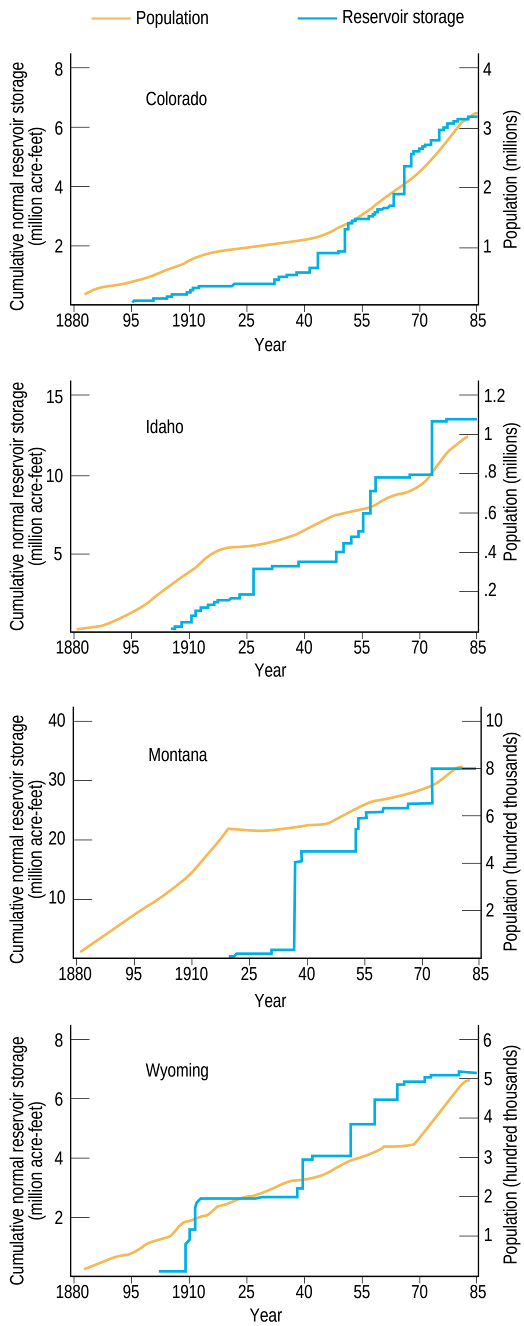


Fig. 11. Relationship between human population growth and cumulative storage of water in reservoirs (adapted from U.S. Geological Survey 1990).

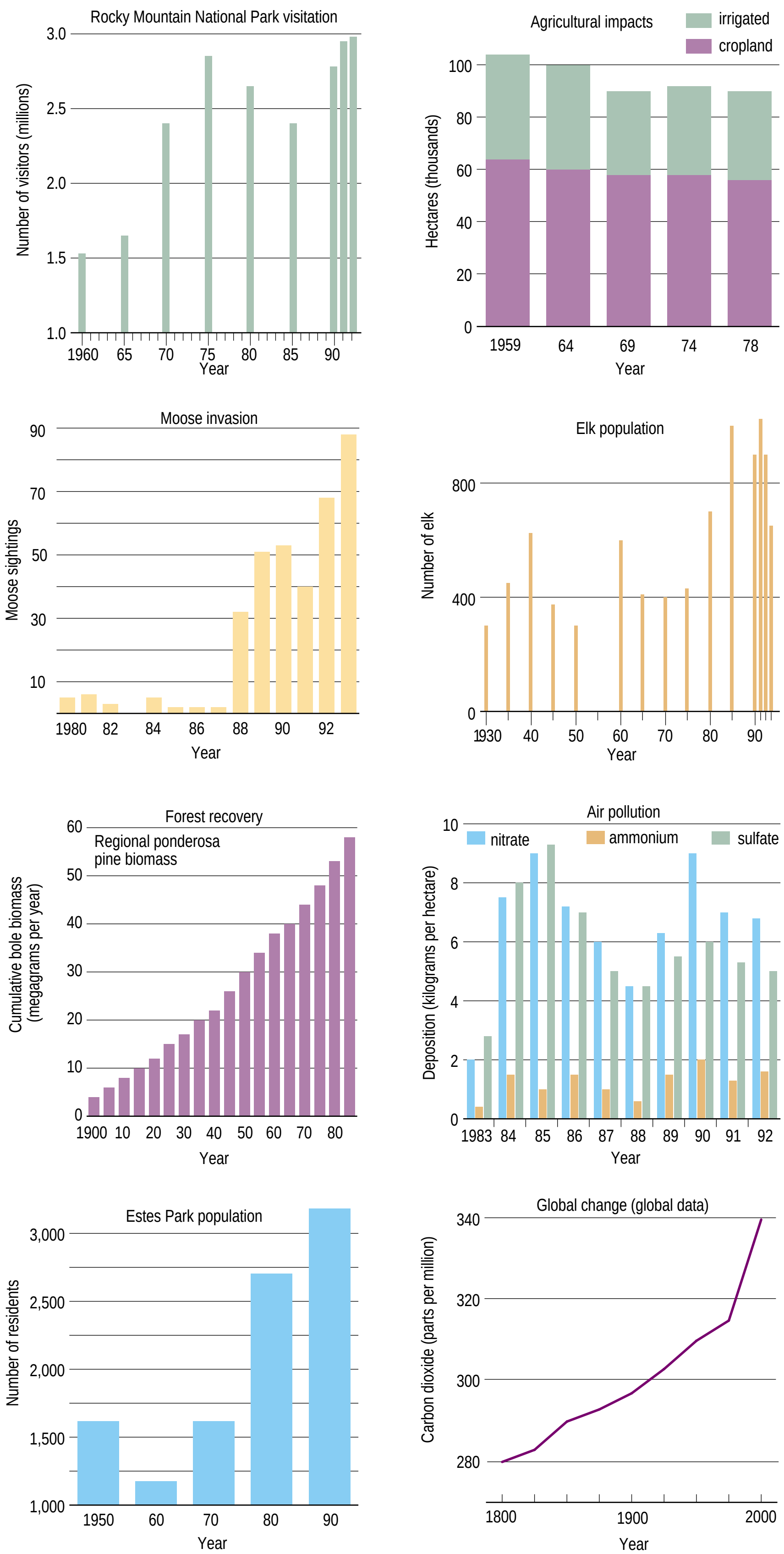
Throughout the conterminous United States, the surface area of wetlands has decreased from 11% to 5% (Brady and Flather 1994). Most of the loss is attributed to agricultural land-use conversions and urban expansion. Although little specific information is available on the status of wetlands in the Rocky Mountains region, urban development and water-control projects on floodplains along the major rivers are clearly modifying critical wildlife habitat.

Beavers helped shape many riparian zones and wetlands in the Rocky Mountains for thousands of years (Knight 1994). Their debris dams influenced vegetation patterns, sedimentation rates, flood severity, and water quality (Knight 1994; Schlosser 1995). Trapping the beaver to near extinction reduced the abundance of willow and moist-grass communities and increased erosion downstream (Knight 1994).

Nearly all native fisheries in the Rocky Mountains have been compromised by introduced fishes (Trotter 1987; Behnke 1992). Of the 13 subspecies of native cutthroat trout once found in the interior West, 2 are extinct and 10 have suffered catastrophic declines (Behnke 1992).

The Greater Rocky Mountain National Park Ecosystem

The Greater Rocky Mountain National Park ecosystem is typical of many park and forest ecosystems in the Rocky Mountains. It serves as an example of how natural ecosystems are confronted by a multitude of simultaneous threats including encroachment from urbanization and development, habitat fragmentation, fire suppression, nonindigenous species invasion, and global climate change (Stohlgren et al. 1995a). The response of the forest to turn-of-the-century logging and wildfires was a fivefold increase in ponderosa pine bole (trunk) biomass (Fig. 12). This is good news for wildlife dependent on ponderosa pine, but fire suppression continues to create a growing wildfire hazard.



Visitor use of the Rocky Mountain National Park has almost doubled since 1960, and the human population in Estes Park has more than doubled (Fig. 12). Urban development throughout the Front Range of Colorado caused habitat loss and fragmentation and increased air pollution. Annual values of wet deposition of nitrate, sulfate, and ammonium in the Loch Vale watershed of the Rocky Mountain National Park are significantly greater than the average value of 0.5 kilograms per hectare found in remote areas of the world (Fig. 12).

Elk and moose populations continue to increase in the park (Fig. 12) because of a complex of causes including reduced hunting and predation (wolves have been extirpated) and diminished habitat and migratory corridors outside the park. Agricultural land use in Larimer County has declined slightly in recent years (Fig. 12), but landscape and ecosystem integrity are challenged by fire suppression, nonindigenous species invasions, weather modification (that is, cloud seeding; Stohlgren et al. 1995b), and global climate change (Stohlgren et al. 1993).

The Greater Yellowstone Ecosystem

Scientists who study the Greater Yellowstone National Park ecosystem have long acknowledged the ecosystem-scale issues surrounding wildlife management (Leopold et al. 1963). Migratory populations of elk, bison, and deer; a wild grizzly bear population; the Yellowstone cutthroat trout fishery; and world-renowned geothermal resources are challenged by increasing visitor use, introduced diseases and competitors, and global climate change

Fig. 12. Trends in Rocky Mountain National Park, Colorado (see inset map): number of visitors to the park, agricultural land use, elk populations, moose invasion, forest recovery, air pollution, human population of nearby Estes Park, and global change in carbon dioxide.

(Schullery 1995). Increasing numbers of elk (31,000 summer in the area) may be having adverse effects on the elks' winter range (Knight 1994). Livestock grazing is permitted on about 40% of grizzly bear habitat in the Greater Yellowstone ecosystem, and many bears have been killed in these areas (Keiter 1991). Evidence now shows that only 15%–20% of the park was subjected to the crown fires of 1988, and the burned areas are recovering rapidly (Knight 1994). The park's geologic features were unscathed by the fires, large mammal populations are thriving, and visitation (and tax revenues) are increasing (Knight 1991).

Pressures from outside the park include commercial development, logging—in some instances up to the border of the park—threatened exploitation of geothermal resources, and hunting of stray animals. Several population-size trends of plant and animal species are issues in the Greater Yellowstone ecosystem requiring consideration (Schullery 1995). Park personnel must manage grizzly bear persistence, wolf reintroduction, elk population increases, introduced diseases (brucellosis in bison, white pine blister rust), and introduced fishes, all while coping with more than 3.2 million visitors per year.

Status and Trends of Plant and Animal Populations

Because information on trends in population sizes of most species in the Rocky Mountains is incomplete, the status and trends of only a few species can be reported. Species such as the black bear and mountain lion, many small mammals, and common bird and plant species are described because, in most instances, the populations are persistent and not rapidly increasing or declining. Even basic regional information is not available on many nocturnal species (for example, bats, raccoons, and so forth); invertebrates; lichens, mosses, and fungi; and soil microorganisms. In essence, information for only the high-profile species is available and accessible. The status of each individual species, however, affects and is affected by the status and trends of other species in its ecosystem.

Invertebrates

Although most of the animals in the Rocky Mountains are invertebrates, little is known about this component of the region's fauna (Mason 1995). As one entomologist stated, "We do not know how many species of moths and butterflies live in any state, county, or locality in North America" (Powell 1995:170). In a few areas in the western United States, information is available on the species richness of moths and butterflies. Most of the Rocky Mountain states and the Front Range of Colorado in particular support high species richness of butterflies and moths (Opler 1995). In Colorado, the diverse habitats—from prairie to tundra—support about 2,000 species of butterflies, moths, and skippers; more than 1,000 species are in the Front Range (Opler 1995). Some species of grasshoppers are unique to individual mountaintops in Colorado, New Mexico, Arizona, Nevada, and Utah (Otte 1995). The Rocky Mountain locust, a common pest to farmers in the 1800's, is now extinct. Heavy grazing along river valleys in Montana and Idaho is thought to have irreparably destroyed locust breeding areas (Otte 1995).

Amphibians

Globally, populations of amphibians are declining in size as a result of habitat loss, predation by nonindigenous sport fishes, timber harvest, increased ultraviolet radiation, and disease (Bury et al. 1995). The widespread declines of amphibian populations throughout the Rocky Mountains mirror these global trends. Western toads, once common between altitudes of 2,300 and 4,200 meters throughout the central and northern Rocky Mountains, now occupy less than 20% of their previous range, from southern Wyoming to northern New Mexico (Bury et al. 1995). Eleven populations of western toads disappeared from the West Elk Mountains of Colorado between 1974 and 1982 because of a bacterial infection and, perhaps, multiple sublethal environmental causes (Carey 1993). In the past two decades, western toads disappeared from 83% of their historical range in Colorado and from 94% of Wyoming sites (Bury et al. 1995). Populations of northern leopard frogs are significantly declining throughout the Rocky Mountains (Corn and Fogelman 1984; Bury et al. 1995).

Fishes

Greenback Cutthroat Trout

Greenback cutthroat trout historically inhabited the cold-water streams in the mountains of Colorado (Fig. 13). The species was near extinction by the early 1900's because of broad-scale stocking of these streams with nonindigenous brown trout from Europe and rainbow trout from the Pacific Coast, and because of land and water exploitation, mining, and logging. Native genetic diversity is now lost in greenback cutthroat trout because this species hybridizes with the introduced fishes. Interagency efforts began in 1959 to save the species. With viable populations now at 48 sites, the greenback cutthroat trout is one of the

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Amphibians of Glacier National Park

Reports of amphibian declines worldwide have raised concerns about the status of the amphibians of Glacier National Park, a 410,360-hectare federal reserve in the northwest corner of Montana. The headwaters of three continental river systems flow from the park: the North Fork and the Middle Fork of the Flathead River drainages of the Columbia River basin; the upper Missouri River drainage; and the South Saskatchewan (Hudson Bay) River drainage. More than 700 lakes and 3,660 kilometers of streams create a mosaic of aquatic habitats ranging in elevation from 925 meters to more than 3,000 meters.

As many as a dozen species of amphibians have been reported to occur in the park (Manville 1957; Davis and Weeks 1963; Metter 1967; Black 1970a,b; Thompson 1982; R. B. Brunson, University of Montana [retired], unpublished manuscript). However, a recent study, which used geographic information system processing of species-sighting data, confirmed only five species as park residents. Field investigations were supplemented by examination of specimens and collection records from the park museum and 13 other museums that had specimens from Glacier National Park.

Columbia Spotted Frog

The Columbia spotted frog is the most common frog in Glacier National Park. It occurs in both green and brown color phases and prefers small shallow ponds, marshes, and bogs with mud bottoms and dense emergent nonwoody vegetation (Fig. 1).

Courtesy L. Marnell, National Park Service

Fig. 1. Natural camouflage of the adult Columbia spotted frog makes it difficult to see in its natural habitat.

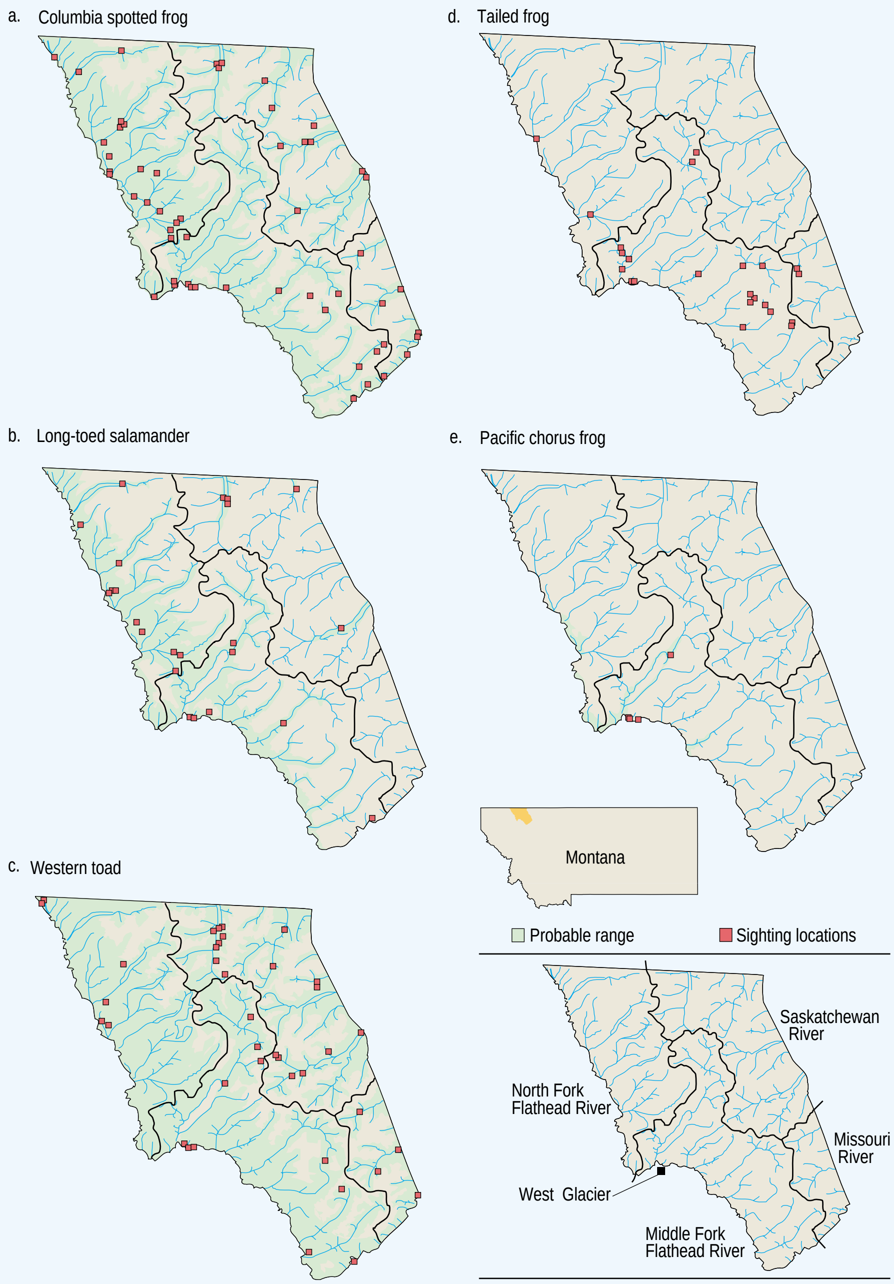

Fig. 2. Sighting locations and probable ranges in Glacier National Park of a) Columbia spotted frogs, b) long-toed salamanders, c) western toads, d) tailed frogs, and e) Pacific chorus frogs.

The species occurs on both sides of the Continental Divide at elevations between 1,050 meters and 1,845 meters (Fig. 2a). Columbia spotted frog egg clusters were observed by early May, with hatching from late May through mid-June. High egg mortality was observed at some locations. Many of the documented breeding locations were beaver ponds.

Long-Toed Salamander

The long-toed salamander is the only resident salamander species in Glacier National Park. Local forms display a prominent dorsal stripe variable from dull green to bright yellow, and the rest of the body is typically dusky black or charcoal with fine white or bluish-white speckles on the lower

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sides. This salamander is common throughout valleys and midelevation forests west of the Continental Divide at elevations from 1,055 meters to 1,515 meters (Fig. 2b). Long-toed salamanders are found at only a few locations in the South Saskatchewan River drainage and are common there only in the Waterton Valley. A large breeding population occurs near Waterton Townsite.

Adults are nocturnal and are active aboveground for only a short period during spring and early summer. After breeding, these salamanders disperse rapidly into woodland habitats. Adults can be found in the rotting bark of downed trees or under rocks and logs. Small clutches containing 5–20 salamander eggs have been seen by late April in most years. Hatching typically occurs by mid-May and is complete by late May at low to midelevations. Metamorphosis to adults is complete by early August followed by rapid dispersal to nearby woodlands. However, breeding periods and incubation times vary considerably. For example, in a spring-fed pool below Upper Kintla Lake at 1,397 meters elevation, salamander larvae were still relatively small by late August 1991. In late October the pool was mostly frozen over, and salamander larvae were still visible on the mud bottom beneath the ice.

Western Toad

Western toads in Glacier National Park vary from medium brown to black with a pale yellow or cream-colored dorsal stripe. Toads occur on both sides of the Continental Divide from low-elevation valleys upward to timberline (Fig. 2c). Western toads are the most wide-ranging amphibians in the park; sightings were recorded from 1,045 meters to 2,255 meters elevation. Among 41 sighting locations, 17 (41%) were above 1,650 meters, and 7 sites (17%) were higher than 1,980 meters. Manville (1957) reported a toad sighting near the Mount Brown fire lookout at 2,320 meters. A breeding site was located at 2,088 meters elevation at a glacial tarn near Logan Pass. Although western toads are distributed parkwide below timberline, they are not abundant at most locales.

Breeding times for western toads are strongly correlated with elevation and water temperatures. Egg strings typically appear at low elevations in early May in shallow ponds with mud or silt bottoms, often attached to the edges of algal mats in water 10 to 20 centimeters deep. About half of the 14 documented breeding sites for western toads were beaver ponds. Hatching occurred at most locations by the second or third week of June.

Tailed Frog

Tailed frogs seldom stray far from their preferred habitat of cold turbulent headwater streams with cobble substrates. Glacier National Park lies near the eastern limit of their range. The body color of adult tailed frogs in Glacier National Park is typically gray-brown to rust, fading to a lighter-colored belly (Fig. 3). Adult tailed frogs are nocturnal and are often difficult to locate. The species occurs throughout much of the Middle Fork of the Flathead River drainage but is intermittent and widely dispersed in the North Fork and upper Missouri River drainages of Glacier National Park (Fig. 2d). Tailed frogs are most often seen at elevations between 1,045 meters and 2,140 meters. The range map (Fig. 2d) probably underrepresents the distribution of tailed frogs in Glacier National Park because only a small proportion of suitable habitats was searched.

Courtesy L. Marnell, National Park Service

Fig. 3. Adult tailed frogs are nocturnal and are rarely seen during daylight.

Little is known about the breeding activities of tailed frogs in the streams of Glacier National Park. Researchers believe that development time from hatching to emergence is highly variable for this species (Metter 1967). Time to metamorphosis is up to 4 years in the Washington Cascades and an additional 5–6 years is required for the froglets to attain sexual maturity (Leonard et al. 1993). From 3 to 5 years may be required for metamorphosis in the higher-elevation streams of Glacier National Park.

Pacific Chorus Frog

Pacific chorus frogs have the most restricted distribution of any frog or toad in the park. Glacier National Park is near the eastern limit of this species. Most sightings have been made near the community of West Glacier at about 1,035 meters elevation (Fig. 2e). Breeding occurs in several small ponds above the floodplain of the Middle Fork of the Flathead River, upstream from West Glacier. Chorus frogs appear to travel on warm summer nights and are capable of dispersing several kilometers from breeding sites.

Pacific chorus frogs begin breeding in Glacier National Park in late April and early May. Vocalizations usually peak during the first week of May. Egg deposition has not been observed during daylight, but egg clutches containing 10 to 30 eggs are present at several of the ponds by mid-May. Hatching occurs from late May through the first week of June, and by the end of June most adult chorus frogs have left the breeding ponds. Development is rapid, with emergence occurring by the first week in August. Juvenile chorus frogs are present in shallow waters among shoreline vegetation at the edges of several of the ponds by mid-August. Dispersal into nearby riparian zones occurs a few days after emergence. Most juvenile frogs have left the breeding ponds by late August.

Effects of Fish Introductions

The introduction of sport fish into a large number of formerly fishless lakes (Marnell et al. 1987; Marnell 1988) may have contributed to the loss or decline of several amphibians in portions of Glacier National Park. The presence of fish has been implicated in the decline of some amphibian species (Bradford 1989; Bradford et al. 1993; Corn et al. 1997). Long-toed salamanders were particularly vulnerable to predation by introduced fishes in portions of the Cascade Mountains in western Washington and Oregon (Leonard et al. 1993). Long-toed salamander larvae were not observed in any Glacier National Park water harboring fish, and this species existed close to fish at only 2 of 25 sites. Concerns about fish predation may be especially warranted in parts of the upper Missouri River drainage and in the Many Glacier Valley (South Saskatchewan River drainage). The extent of damage to native amphibians in Glacier National Park as a consequence of fish introductions may never be fully understood.

See end of chapter for references

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Fig. 13. Restoration of the greenback cutthroat trout in Colorado has been highly successful.

few species that will be removed from the endangered species list (Colorado Division of Wildlife 1986; Henry and Henry 1991). Three of the four other native subspecies of the cutthroat trout are extinct (Greenback Cutthroat Trout Recovery Team 1983).

Westslope Cutthroat Trout

Most aquatic ecosystems in the Rocky Mountains are now influenced by nonindigenous brown trout and rainbow trout. One of the more subtle, yet devastating, trends in the Rocky Mountain fishery is loss of genetic diversity in native fishes resulting from introductions of nonindigenous fishes. For example, only 15 of 32 lakes in Glacier National Park, Montana, contain pure genetic strains of the native cutthroat trout. The others contain totally nonindigenous fishes or hybrids with the introduced Yellowstone cutthroat trout or rainbow trout. Introductions of nonindigenous fishes to improve the sport fishery have compromised about 84% of the historical range of the native cutthroat trout (Marnell 1995).

Yellowstone Cutthroat Trout

Yellowstone Lake in Yellowstone National Park, Wyoming, is the site of the most recent catastrophic species invasion. *The Washington Post* (2 October 1994) reported that the nonindigenous lake trout, a native of the Great Lakes, had been insidiously introduced into one of the nation's premier fisheries. The native Yellowstone cutthroat trout may not compete well with lake trout because lake trout eat cutthroat trout. The potential ecological repercussions are staggering. If populations of cutthroat trout decline, grizzly bears could lose an important posthibernation food because the native cutthroat trout spawn in the streams and are easy prey for the bears, whereas the nonindigenous lake trout spawn in deep water.

White Sturgeon

The largest freshwater fish in the Rocky Mountains (and North America) is also in trouble. The white sturgeon historically ranged from the mouth of the Columbia River to the Kootenai River upstream to Kootenai Falls, Montana. The Kootenai River population of the white sturgeon is unstable and declining in size (Miller et al. 1995); fewer than 1,000 remain, 80% are older than 20 years, and virtually no recruitment has occurred since 1974, soon after Libby Dam in Montana began regulating flows (Apperson and Anders 1990).

Birds

Bald Eagles

The coniferous and deciduous forests of North America have long been the home of bald eagles (Fig. 14). Bald eagle populations are now recovering after years of hunting, habitat destruction, and pesticide-induced deaths (Finch 1992). In the early 1970's, Colorado had just one breeding pair of bald eagles but by 1993 biologists counted 19 breeding pairs (Colorado Division of Wildlife 1993). In Wyoming nesting attempts increased from 20 in 1978 to 42 in 1988 (Finch 1992). The bald eagle is not yet fully recovered, however; pesticide residues continue to inhibit bald eagle reproduction, and habitat loss and lead poisoning remain serious threats (Henry and Anthony 1989).

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Fig. 14. The bald eagle is recovering throughout the United States.

Peregrine Falcons

Peregrine falcons are cliff-dwelling raptors that once ranged through most of North America. Like the bald eagle, this species was driven to near extinction by pesticides. By 1965 fewer than 20 breeding pairs were known west of the Great Plains (Finch 1992). Even in the Greater Yellowstone ecosystem, federal spruce budworm control relied on DDT, which accumulates in the food chain, causing eggshell thinning and reduced reproductive success in raptors (Boyce 1991). Six breeding pairs of American peregrine falcons were found in Colorado in the early 1970's (Colorado Division of Wildlife 1986). By 1994, 53 pairs were breeding in Colorado. In Wyoming, Montana, and Idaho combined, 8 of 59 historical sites were used by falcons in 1987. Low breeding densities, reproductive isolation, habitat loss, and pesticide poisoning on wintering grounds remain threats to peregrine falcon recovery (Finch 1992).

White-Tailed Ptarmigans

White-tailed ptarmigans have been monitored in Rocky Mountain National Park, Colorado, since 1966 (Colorado Division of Wildlife 1994). Short-term population cycles are well documented in populations that are not hunted but not in populations outside the park, which are hunted. Although detailed population size data are available from more than 28 years of monitoring (Fig. 15), scant information is available on habitat change, predator populations, or other potential causes of change in ptarmigan populations. A 2-year study (Melcher 1992) revealed lower ptarmigan densities where elk use was greater, although characteristics of willow, which is ptarmigan habitat, did not significantly differ in the high- and low-use elk sites (Melcher 1992). Furthermore, a 2-year study of ptarmigan habitat cannot explain 28-year trends in population size. Habitat loss and other factors partly responsible for ptarmigan deaths—such as predation and competition—were not studied during the 28-year period.

Trumpeter Swans

Trumpeter swan populations were seriously threatened in the 1930's; fewer than 70 birds were thought to exist (Boyce 1991). Now protected from hunting, more than 1,500 swans winter in the Greater Yellowstone ecosystem, but the size of the breeding population has declined in recent years because of habitat loss (Boyce 1991).

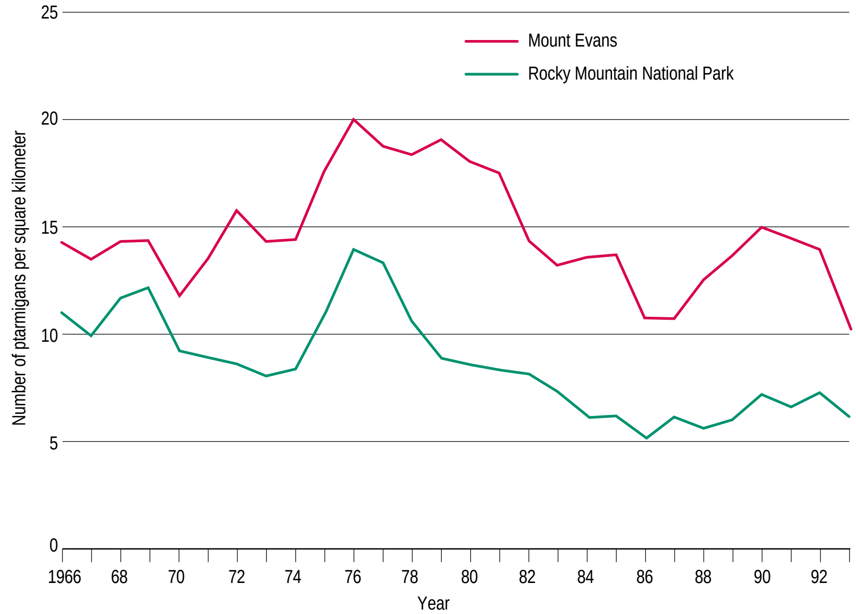

Fig. 15. White-tailed ptarmigan populations show cycles in hunted populations (Mount Evans) and in unhunted populations in the Rocky Mountain National Park, but the causes of these cycles remain unclear (Colorado Division of Wildlife 1994).

Neotropical Migrant Songbirds

Many forest-dwelling songbirds breed in the Rocky Mountains and winter in Central and South America. Wildlife biologists suspect that population size declines in the songbirds may be partly the result of increased predation and brood parasitism. Brood parasitism by brown-headed cowbirds, for example, increases as a result of nearby logging (Evans and Finch 1994). In conifer forests in west-central Idaho, common songbirds benefited from timber harvest, whereas the abundances declined of rare species that inhabit old-growth forests (hermit thrush, Swainson's thrush, and pileated woodpecker; Evans and Finch 1994).

Mammals

Grizzly Bears

Grizzly bears once roamed throughout the Rocky Mountains and the western Great Plains. They were hunted relentlessly by European settlers in the 1800's and early 1900's (Mattson et al. 1995). The last known grizzly bear in Colorado was killed in 1979. The decline of the bears to just 2% of their original range (Fig. 16) tells of the human-caused extirpation of large predators in the Rocky Mountain region. Only 700–900 grizzly bears may be alive today in the conterminous United States (Servheen 1990). During the last 20 years, about 88% of all grizzly bears studied in the northern Rocky Mountains were killed by humans (Mattson et al. 1995).

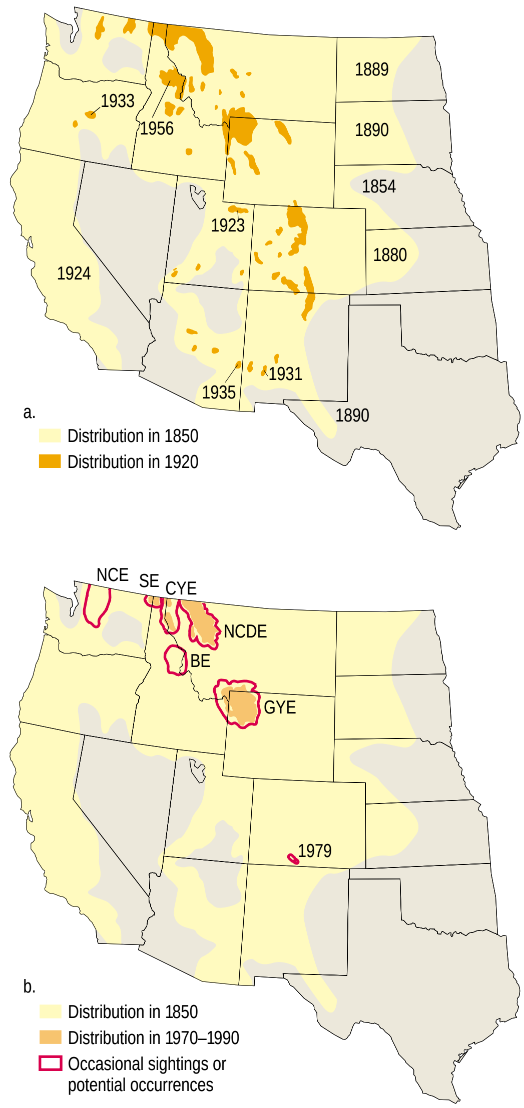

Fig. 16. a) Approximate distribution of grizzly bears in 1850 compared with 1920 and with b) 1970–1990. Local extinction dates appear in a). Populations identified in b) are NCE—North Cascades ecosystem, SE—Selkirk ecosystem, CYE—Cabinet–Yaak ecosystem, BE—Bitterroot ecosystem, NCDE—Northern Continental Divide ecosystem, and GYE—Greater Yellowstone ecosystem. As indicated in b), a grizzly bear was killed in the San Juan Mountains of Colorado in 1979 (Mattson et al. 1995).

Courtesy L. Rogers, International Wolf Center

Fig. 17. The gray wolf is slowly returning to a small portion of its former range.

Gray Wolves

Gray wolves once were common throughout the Rocky Mountains (Cook 1993). They were shot, poisoned, and trapped into local extinction by early settlers and federal agents (Brandt 1993; Cook 1993; Fig. 17). The last gray wolf in Colorado was killed in 1940, and the wolf was first listed as an endangered species in 1967 (Mech et al. 1995). Wolves from southeastern British Columbia recolonized northwestern Montana in 1986; by 1994 the population had grown to 7 packs and about 70–75 wolves (N. Bishop, Yellowstone National Park, personal communication). Wolves from Glacier National Park have dispersed naturally as far away as northeastern Idaho and just south of Yellowstone National Park. A wolf was shot near Yellowstone National Park in 1992. From January to March 1995, 15 adult wolves from 7 different packs in Canada were introduced into central Idaho wilderness areas. Several pairs have bred and produced the first litters of wolf pups born in Idaho in more than 50 years. Fourteen wolves (three family groups) were released in the Yellowstone National Park in late March 1995 (Bishop, personal communication). An adult female from each group may have bred. The status of gray wolves in the northern Rocky Mountains is improving, but the species is still persecuted and probably occupies less than 10% of its historical range in the conterminous United States. More than 70% of Colorado residents support a restoration of wolves in Colorado, but no such effort is under way (Manfredo et al. 1994).

The restoration of the gray wolf to the Yellowstone National Park not only restores an important ecosystem component (the wolf) and process (predation by wolves) to bring the park into better ecological balance, but it also is economically sound. After weighing the costs (including full reimbursement to ranchers for the loss of livestock) and benefits (increased revenues from hunting and tourism), economists estimated (before the actual restoration took place) a net $18 million return during the first year after the wolves were returned, and about $110 million in 20 years (Duffield 1992; Brandt 1993). More tourists are expected to visit the area of the Yellowstone National Park and to stay longer in hope of hearing or seeing wolves in the wild (Duffield 1992). Compensatory payments to ranchers for the loss of cattle and sheep to wolves averaged about $1,800 per year in northwestern Montana (Bishop, personal communication).

Caribou

Caribou were once common in the northern Rocky Mountains. In fact, the head of a caribou killed by Theodore Roosevelt hangs in Jack's Bar in Bonners Ferry, Idaho (Speart 1994). Hunting and habitat loss (logging of old-growth Rocky Mountain juniper and hemlock forests) reduced the herd in Idaho's Selkirk Mountains to 100 animals by the 1950's. By the 1980's the few remaining caribou had crossed the border to the Canadian Rocky Mountains. A lone male reintroduced the species by wandering back into Idaho in 1984 (Speart 1994). The Endangered Species Act of 1973 helped protect some of the last remaining old-growth Rocky Mountain juniper and hemlock stands with the old-growth-dependent lichens that are the primary food of the caribou. A series of three caribou transplants from Canada has helped maintain the newly reestablished herd of about 30 animals.

North American Elk, Deer, Pronghorns, and Moose

Population trends in North American elk and deer (mule deer and white-tailed deer combined) may be heading in opposite directions. The number of elk has increased steadily in Colorado and Wyoming, whereas the abundances of deer are showing signs of decline (Fig. 18). Elk on U.S. Forest Service lands in the Rocky Mountains increased from 268,000 in 1965 to 372,000 in 1984 (Flather and Hoekstra 1989). Similarly, the number of elk on Bureau of Land Management lands rose from 35,000 in 1966 to 114,000 in 1985. Meanwhile, the number of deer on U.S. Forest Service lands declined from 1,742,000 in 1965 to 1,197,000 in 1984. Deer populations also declined on Bureau of Land Management lands. Thus, in some areas in the last 20 years, the abundances of elk have increased by about 40%, whereas deer have decreased by about 30% (Flather and Hoekstra 1989). Possible reasons for the increase in elk populations include mild winters, range extension into lowlands and highlands, increased adaptability to human-modified landscapes, and lack of predation in spite of increased hunting (F. Singer, U.S. Geological Survey, personal communication). The causes of the deer population declines remain unknown (Connolly 1981) but may include excessive harvest in the 1970's and habitat overlap with elk, intensifying competition for similar resources.

Pronghorn populations have fluctuated but generally have increased in the past 20 years in Colorado (Fig. 18) and Wyoming. Moose populations have increased 50% since 1980 in Wyoming and have been rapidly increasing since their introduction into Colorado in 1978 and 1979 (Fig. 18).

Bighorn Sheep

Populations of bighorn sheep are at only about 2% to 8% of their sizes at the time of European settlement (Singer 1995). Causes for the rapid decline from 1870 through 1950 included unregulated harvesting, excessive grazing of livestock on rangelands, and diseases transmitted by domestic sheep. In recent years, 115 translocations were made to restore bighorn sheep into the Rocky Mountains and into many national parks. Only 39% of the 115 bighorn sheep translocations are persisting in 6 Rocky Mountain states. Populations of 100 or more sheep now occur in 10 national park units, populations of 100–200 sheep in 5 units, and populations of more than 500 sheep in 5 units. Populations of fewer than 100 animals exist in 5 other park units (Singer 1995).

Beaver

Beavers once played important roles in shaping vegetation patterns in riparian and meadow communities in the Rocky Mountains (Knight 1994). Studies of beaver populations in one small area in Yellowstone National Park (Tower Junction area) in the early 1920's reported 232 beavers and extensive beaver dams. Repeated surveys in the same area in the early 1950's and in 1986 revealed no beavers or dams (Chadde and Kay 1991). Beavers need aspens or tall willows for food and building materials—resources that are made scarce by lack of both fires and floods and by herbivory by elk, moose, and domestic livestock. Beaver ponds are known to maintain fish and invertebrate populations (Schlosser 1995) and to create and maintain riparian zones that are critical to wildlife (Chadde and Kay 1991; Knight 1994), yet the beaver is virtually absent in many areas (Chadde and Kay 1991).

Introduced Diseases and Plant and Animal Species

Introduced Pathogens

In addition to the pathogen of the white pine blister rust, many other introduced pathogens are having profound effects on native species. When bison were restored to Yellowstone National Park in 1902, they may have transported unwanted guests. The origin and management implications of brucellosis, a disease caused by bacteria in domesticated animals (cattle, horses), bison, elk, and even rodents, are controversial. Although the wild bison may not transmit brucellosis directly to cattle (Meagher and Meyer 1994), some level of human intervention in and adjacent to Yellowstone National

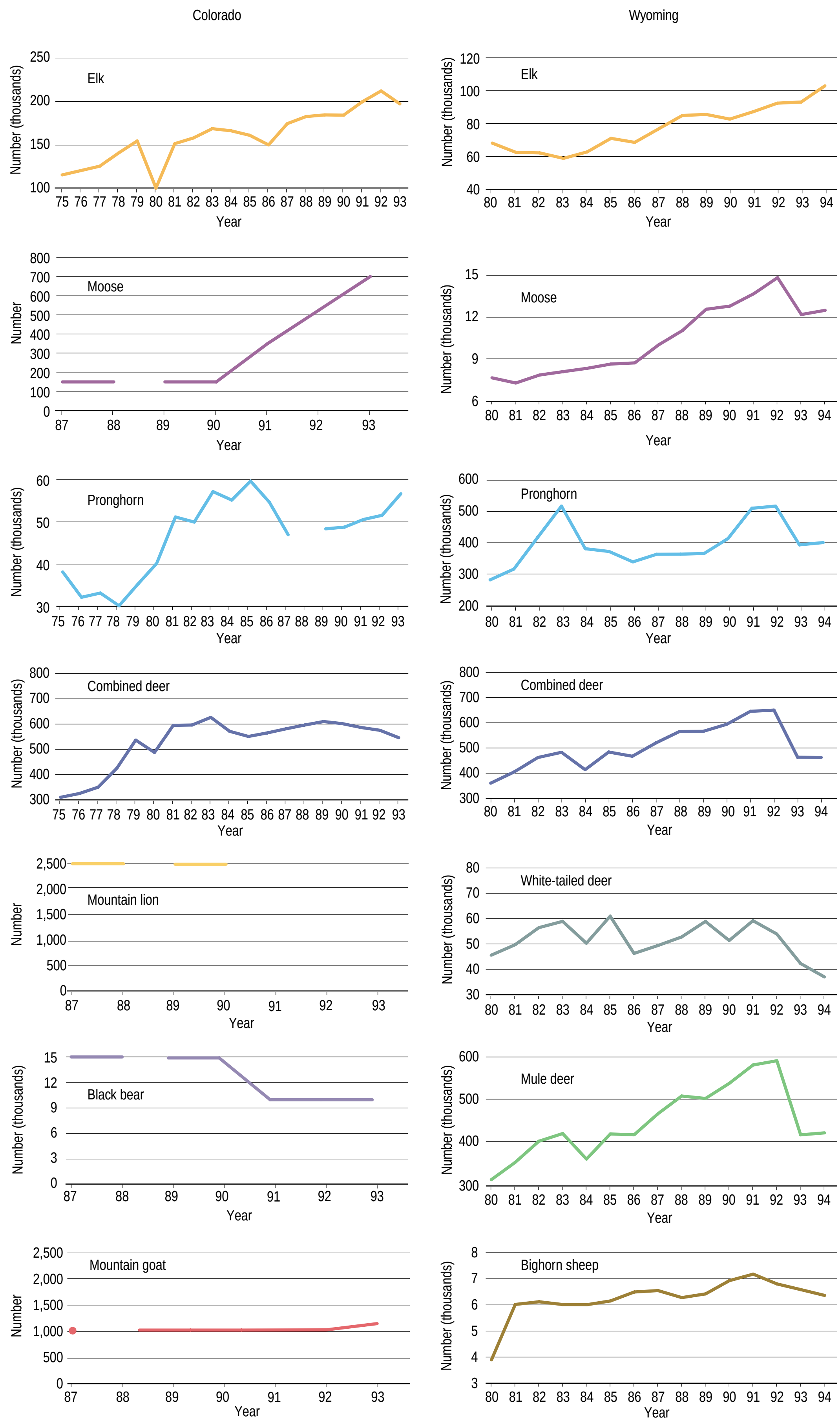

Fig. 18. Big game populations in Colorado from 1975 to 1993 (data from the Colorado Division of Wildlife, Department of Natural Resources Database, Fort Collins) and in Wyoming from 1980 to 1994 (Wyoming Game and Fish Department, Cheyenne, unpublished data). Missing data represent years when populations were not monitored.

Park may be needed to prevent spread of the disease (Aguirre and Starkey 1994).

The lungworm-pneumonia complex is a bacterial disease that causes spontaneous death in the lambs of bighorn sheep in summer. Although some strains of the disease complex are native to bighorn sheep and others are related to domestic sheep, disease exchange can be fatal to both groups (Aguirre and Starkey 1994). Proximity to domestic sheep is highly correlated with deaths in newly reestablished bighorn sheep populations (Singer 1995). In spite of the disease, however, bighorn sheep populations in national forests in the Rocky Mountain region increased from 11,533 individuals in 1965 to 17,658 in 1984 (Flather and Hoekstra 1989).

Whirling disease, introduced from Europe, is a parasitic infection that attacks recently hatched trout. It now affects wild trout populations in Rocky mountain regions. The disease was first thought to affect only hatchery fishes, but the native greenback cutthroat trout also may be susceptible.

Introduced Plants

Cheatgrass has invaded not only the Great Basin but also significant portions of the western pinyon–juniper woodlands and ponderosa pine and Douglas-fir ecosystems in the Rocky Mountains (Peters and Bunting 1994). Many native shrubs and perennial grasses cannot survive the increased competition from cheatgrass (as many as 3,000–10,000 plants per square meter; Barbour et al. 1987). Several rare plant species are being displaced by introduced plants in western rangelands (Rosentreter 1994). A dense cover of cheatgrass has increased the fire frequency in many of these areas. With each fire, the dominance of nonindigenous annual grasses is enhanced at the expense of native perennial grasses. The establishment of cheatgrass is also enhanced by livestock grazing (Fleischner 1994).

More than 1.4 million hectares of Oregon, Washington, Idaho, and Montana are covered with spotted knapweed (Langner and Flather 1994). How much of this coverage is in the Rocky Mountains cannot be estimated.

Purple loosestrife, another European weed, is beginning to invade Rocky Mountain wetlands and streamsides. Purple loosestrife spreads quickly and crowds out native plants that animals use for food and shelter. This invader has no natural enemies in the United States and therefore spreads unchecked (Thompson et al. 1987). The effects of these introduced plants on Rocky Mountain ecosystems are poorly understood.

The battle against introduced weeds has intensified with the use of biological control agents. Biological control usually entails the purposeful introduction of a pathogen or insect that inhibits the establishment, growth, or reproduction of the target species. The biological control agent must be highly specific to the target weed. Extensive laboratory and field tests must be completed before the release of a control agent. A large project is under way in Bozeman, Montana, and in Regina, Saskatchewan, where European insects are being released to control the poisonous European leafy spurge (DeLoach 1991).

Introduced Mammals

Two species of hooved mammals—the mountain goat and the moose—were deliberately introduced into Colorado. Although these species occasionally wandered into Colorado in presettlement times, breeding populations did not occur until after deliberate introduction. Accidentally introduced mammals in Colorado and Wyoming include the house mouse and the Norway rat (Armstrong 1993). The potential effects of these introduced mammals on Rocky Mountain ecosystems are poorly understood.

Challenge of Assessing Status and Trends of Biotic Resources

Assessing the status and trends of most biotic resources in the Rocky Mountains is difficult for many reasons, most importantly because of incomplete inventories, fragmented monitoring, poorly standardized inventory and monitoring, and inaccessible data and information. Future efforts to determine the status and trends of biotic resources in the Rocky Mountains would be helped greatly by improving the accessibility of information and by integrating multiscale research, inventory, and monitoring.

Existing Biotic Inventories Are Incomplete

The best-studied areas in the Rocky Mountains may be within the national park system, but even the biotic inventories in national parks are incomplete (Stohlgren et al. 1995c). Accurate vegetation maps are available for less than half of the national park units and detailed soils and geology maps for less than 25%. Species lists of vascular plants, mammals, reptiles, amphibians, and birds in most park units are generally only 50%–80% complete (Stohlgren et al. 1995c). Even less is known about nonvascular plants and invertebrates (Stohlgren and Quinn 1992; Opler 1995; Powell 1995).

Lists of threatened, endangered, and sensitive species are readily available from the U.S. Forest Service and U.S. Fish and Wildlife Service, but information about population-size trends in most species is not available. In Colorado the status of the river otter, lynx, and wolverine is unknown. The last known occurrence of the river otter was in 1906, of the lynx in 1980, and of the wolverine in 1890 (Colorado Division of Wildlife 1986).

Often, the best information on wildlife populations is available from state departments of fish and game, primarily in the form of brochures and unpublished reports. In general, a great deal of attention is given to the hunted megafauna and little to nongame species. Better information on the plants of the Rocky Mountains is forthcoming; a multiple-volume flora is being developed (R. Hartman and colleagues, University of Wyoming, Laramie). The three best sources of information on biotic resources of the Rocky Mountains have included a recent natural history and ecology text on Wyoming (Knight 1994), a synthesis about rare and threatened species (Finch 1992), and *Our Living Resources*—a relatively new type of publication of the National Biological Service (now the U.S. Geological Survey) that attempts to consolidate biotic status and trends information from diverse sources (LaRoe et al. 1995).

One indication of the incompleteness of biotic inventories is that many species are added to the species list of a park, refuge, or national forest each time an inventory is made (Stohlgren and Quinn 1992). Often, common but previously overlooked species are added, and species thought to be locally rare are found to be less rare. In Rocky Mountain National Park, for example, more than 100 vascular plant species (none of them threatened or endangered) were added to the park checklist in the past 6 years (L. Yeates, Denver Botanical Garden, personal communication). Rocky Mountain National Park has been well studied by botanists, but many more plant species will probably be found there, and even more in the surrounding, less well-studied areas of the Rocky Mountains.

Accurate, landscape-scale surveys are a necessary component of successful resource management. Total recorded amphibian and reptile diversity of the United States increased 12% since 1978 (McDiarmid 1995) as a result of biological surveys. As new subpopulations of declining species are found, hope for species persistence in the larger landscape increases. The hot springs in Yellowstone National Park are home for thousands of species of microbes that are potentially useful to humans for DNA fingerprinting and for the removal of oil spills and low-level radioactive wastes (Robbins 1994). Yet little is known of the taxonomy and diversity of these ecologically important species. Biological surveys may also lead to the removal of species from the endangered species category, as was done with the bald eagle, whose status was downlisted when its soaring numbers were documented.

Most Monitoring Efforts Are Fragmentary

Monitoring of biotic resources has been highly fragmentary. Often, researchers have monitored wildlife populations without also monitoring their habitats. Recording quantitative information about species abundance but not information about habitat quantity, quality, spatial extent, fragmentation, or connectivity is common in bird surveys (for example, the white-tailed ptarmigan; Colorado Division of Wildlife 1994). For studies of birds, a mixture of low- and high-intensity surveys and monitoring is needed to integrate information from local and regional scales. Short- and long-term monitoring are both needed to link changes of habitat with changes in populations (Butcher et al. 1993; Droege 1993).

What researchers have learned from monitoring amphibian populations has yet to be backed up with other needed information. Although amphibian population declines are well documented, amphibian metapopulation dynamics and the highly variable causes of decline are poorly understood (Corn 1994; Bury et al. 1995).

Additional monitoring of grazing effects is also needed (Vavra et al. 1994). Bock et al. (1993a: 304) stated that "virtually nothing is known about effects of grazing on birds of coniferous forests." Areas that are ungrazed are scarce and small, however. New, larger exclosures and sophisticated, statistically sound sampling designs are needed so that whole ecosystems can be monitored. Because the effects of grazing vary spatially (Knight 1994; Vavra et al. 1994), more detailed information is needed on regional range conditions and use. Bock et al. (1993b) proposed that some tracts of public rangelands be protected from livestock grazing in order to study the tracts in detail. Investigations of exclosures may be necessary to provide information for sound management of grasslands and forests.

Inventories of forests continue to focus on timber commodities and net volume increases (Powell et al. 1993) but are not designed to provide information about other resources such as habitat quality, habitat fragmentation or connectivity, nonconsumptive uses, or aesthetic values. Information on the effects of harvesting on old-growth habitat fragmentation and connectivity are perhaps more important to conservation biology and ecosystem management than information on net volume growth.

In short, nearly all of today's monitoring should be improved in four important ways. First, detailed population monitoring should be accompanied by detailed habitat monitoring. Second, observations should be augmented with well-designed experimental research to deduce the causes of population change. Third, intensive population and habitat monitoring at study sites should be coupled with extensive landscape-scale research to assess metapopulation dynamics to determine whether a local population is typical of other populations. Last, spatially explicit, predictive models should be used for a proactive approach to biological conservation. Without these consolidated efforts, the causes of the declines in abundance of many species in the Rocky Mountains—from amphibians to white-tailed deer—may never be determined. Even worse, future declines in abundance of many species may never be predicted or prevented.

Previous Inventories and Monitoring Were Not Standardized

Determining the status and trends of biotic resources in the Rocky Mountains is problematic because inventories and monitoring have been conducted without standardized procedures (Stohlgren and Quinn 1992; Stohlgren 1994; Stohlgren et al. 1995c). Recently, standardized field protocols were recommended for the study of amphibians (Heyer et al. 1994), but such protocols are lacking (and long overdue) for the studies of other biological groups. For example, personnel from no two national parks in the Rocky Mountains have consistently collected bird information with the same categories for habitat, nesting, abundance, or observed behavior. Surveys of vegetation in the same ecosystem by the National Park Service in Rocky Mountain National Park and by the U.S. Forest Service in the adjacent Arapaho–Roosevelt national forests used different remote sensing data, vegetation classification schemes, sampling designs, and field methods for validating the respective vegetation maps. Thus, the consolidation of data on vegetation in the region is a formidable task.

Accessibility of Data is Limited

Existing data are often inaccessible. Different agencies and nongovernment organizations tend to use different hardware, software, geographic information systems (GIS), data management programs, file formats, categories of information, field names, geographic and regional boundaries, classification schemes, and storage media. For example, lists of threatened and endangered plants and animals are accessible, but population-size estimates usually are not (Finch 1992). Information on forest size-class distributions is accessible, but not mapped locations of old-growth forests (Powell et al. 1993). Information on trends in water use and reservoir storage is accessible (U.S. Geological Survey 1990), but information on cumulative regional biotic effects of water projects is not readily available. Information is available on the potential effects of single proposed mining operations in environmental impact statements, but regional effects of mining are lacking.

Conclusion

Based on the previous rates of ecological change and extinctions documented in the paleoecology literature, the current rates of change in species and habitat losses in the Rocky Mountains have increased significantly during the last 200 years (Cole 1995). The human population in the Rocky Mountain region will probably double in the next 20–40 years and will proportionally increase demands for and pressures on natural resources. National parks, forests, and wilderness areas will probably become increasingly insular, and habitat fragmentation will increase in nature reserves and urban areas. Continued declines of species (for example, prairie dogs, amphibians, deer, and species dependent on old-growth forests), habitat loss (wetlands, riparian zones, and old-growth forests), increased air pollution and water developments, and introduced species and diseases will continue to affect many Rocky Mountain ecosystems.

Ecosystem science is not a panacea for declining abundances and degraded ecosystems, but, coupled with standardized biotic resource inventories, predictive models, and long-term monitoring, it is the logical approach to responsible stewardship. Humans have been and will forever be an integral component of Rocky Mountain ecosystems. The greatest challenge is not simply monitoring the status and trends of biotic resources in the Rocky Mountains but preventing future problems by using a proactive approach to conservation biology and ecosystem management. In the words of Chief Seattle, "We do not inherit the land from our ancestors, we borrow it from our children."

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