1

Environments of Colorado

Mammals are a familiar and important component of Earth's biodiversity. Biodiversity is the kinds of organisms and their genetic and ecological relationships—an evolutionary and ecological phenomenon in space and time (E. Wilson 1992). The mammalian fauna of Colorado is a fascinating piece of that whole. To understand the diversity of mammals we need to have a perspective of the ecosphere more generally. Such a perspective is the purpose of this chapter, with a focus on environments of Colorado.

Colorado is known for its scenic beauty—from majestic mountain peaks and rushing white rivers tumbling down dark canyons, to red-rock deserts and ceaselessly shifting sand dunes, to the expansive sweep of the shortgrass prairie. Grandeur is wherever we stop to appreciate it, at every scale, from canyons carved in crystalline rocks 2 billion years old, to bold peaks sculpted by the glaciers of the last Ice Age, to last night's furtive trail of a mouse across the snow. We humans appreciate ecological patterns and processes as beautiful or intriguing; to the rest of the mammalian fauna the evolving landscape represents opportunity, and native mammals respond accordingly. Thus, to understand the distribution and abundance of mammals and the details of their daily lives we must first understand the resource base, the mosaic of Colorado's environments in space and time.

Geography

From the standpoint of political geography, Colorado is simple: it is roughly rectangular (if we neglect some minor old surveyors' errors and the fact that Earth is spherical), measuring approximately 607 km by 444 km (377 by 276 mi.) and encompassing some 270,000 km^2 (104,000 sq. mi.). Colorado lies between approximately 102° and 109° west longitude and 37° and 41° north latitude, and is subdivided into 64 counties (Map 1-1). A few of the counties are nearly natural, ecological units (e.g., Jackson, Grand, and Park counties encompass North, Middle, and South parks, respectively), but most are simply political artifacts with rectilinear boundaries.

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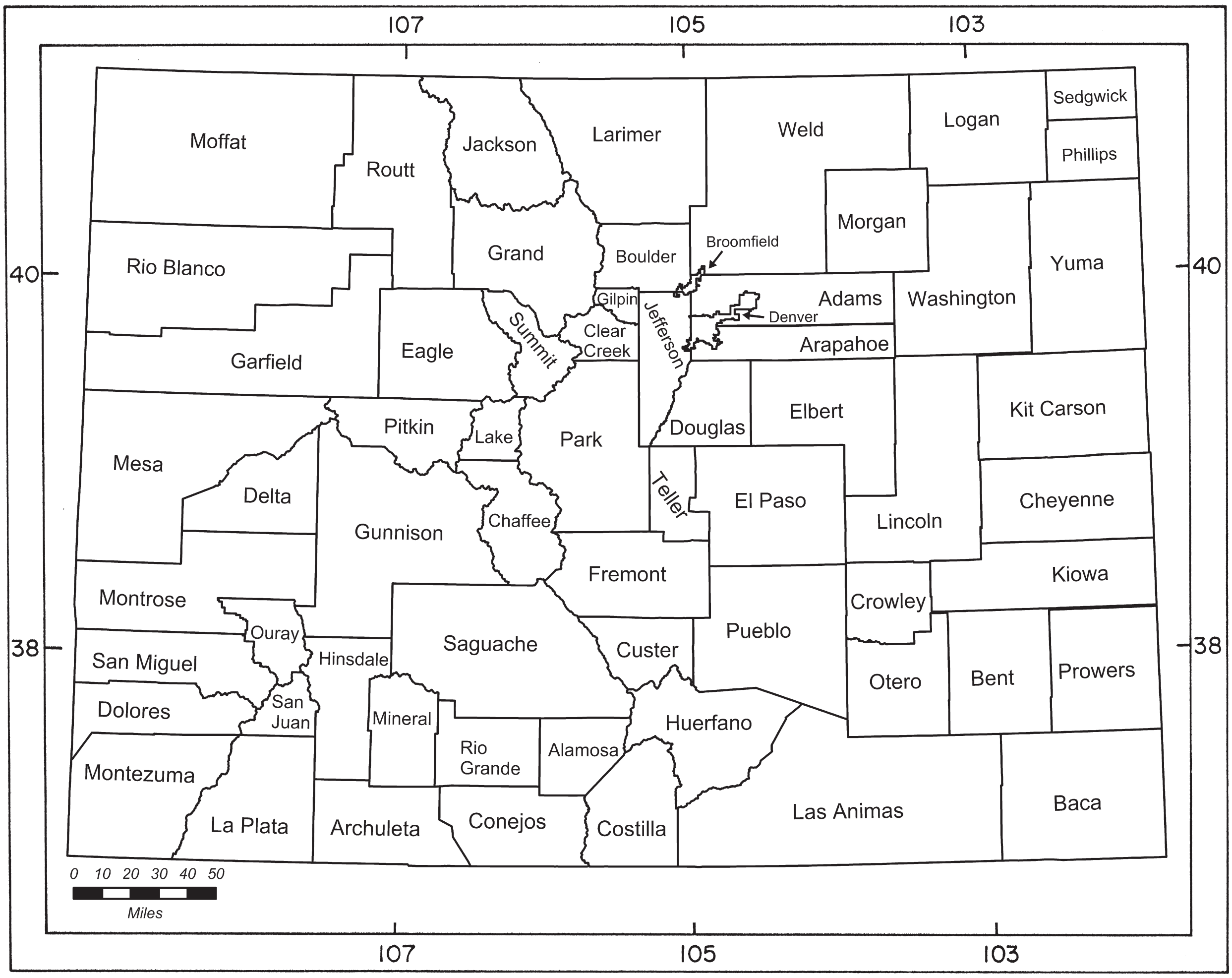


MAP 1-1. Counties of Colorado.

From the standpoints of physical and biological geography, Colorado is anything but simple. The marvelous complexity of the scenery is the subject of this chapter, which describes environments of Colorado from several interrelated points of view. Geologic history and materials underlie environmental patterns. Physiography is the shape of the land, reflecting hundreds of millions of years of landscape evolution. Patterns of drainage reflect and produce the landforms. Vegetation integrates climate and geologic parent material in the development of soils. Plants and animals, fungi and microbes interact as biotic communities, integrated by symbioses, and they interact with the physical environment in ceaseless cycles of materials powered by a flow of solar energy. We observe—and seek to understand—an ecological whole of extraordinary complexity. But let us begin simply, with a little history.

Geology and Landforms

Colorado straddles the "backbone" of North America, the Rocky Mountains. From the mountain front, the Great Plains extend eastward toward the Missouri River. To the west lie canyons and plateaus of the Colorado Plateau and the Wyoming Basin. The juxtaposition of these major physiographic regions affects temperature, precipitation, wind patterns, and drainage.

Colorado is the highest of the United States, with a mean elevation of 2,070 m (6,800 ft.). The lowest point is 1,021 m (3,350 ft.), east of Holly, Prowers County, where the Arkansas River exits the state, and the highest point is 4,399 m (14,433 ft.), the summit of Mount Elbert, Lake County, at the top of the Arkansas watershed. Because of these varied conditions, species richness is high.

Physiographers divide most of Colorado among three "provinces" (see Fenneman 1931): the Southern Rocky Mountains, the Great Plains, and the Colorado Plateau. Northwestern Colorado is on the periphery of two additional provinces: the Middle Rocky Mountains and the Wyoming Basin. For an excellent summary of Colorado's landforms and their development, see A. Benedict (2008).

The present-day Southern Rocky Mountains arose in a long-term event called the Laramide Orogeny, beginning some 72 million years ago, in the Late Cretaceous Period. Prior to that time (during the Mesozoic Era, the "Age of Reptiles") Colorado occupied a low-lying area, alternately covered by shallow seas or exposed as deserts and floodplains. With the rise of the Rockies, Mesozoic and older sediments were broken, bent, and tilted on end, resulting in the familiar hogback ridges and such features as Boulder's Flatirons, the spectacular Garden of the Gods, Loveland's Devil's Backbone, and the Grand Hogback. Streams heading in the newly uplifted mountains eroded the rocks, spreading the bits out in a deep "mantle" eastward across the mid-continent.

In Miocene to Pliocene times, about 5 million years ago, broad, domal regional uplift occurred, "raising the roof of the Rockies" by nearly a mile. Mountain ranges were exhumed from their mantle of Tertiary debris and today's "Fourteeners" reached their greatest elevations, only to face the inexorable processes of weathering we see today—the daily destructive march of rain and snow, wind and calm, freeze and thaw.

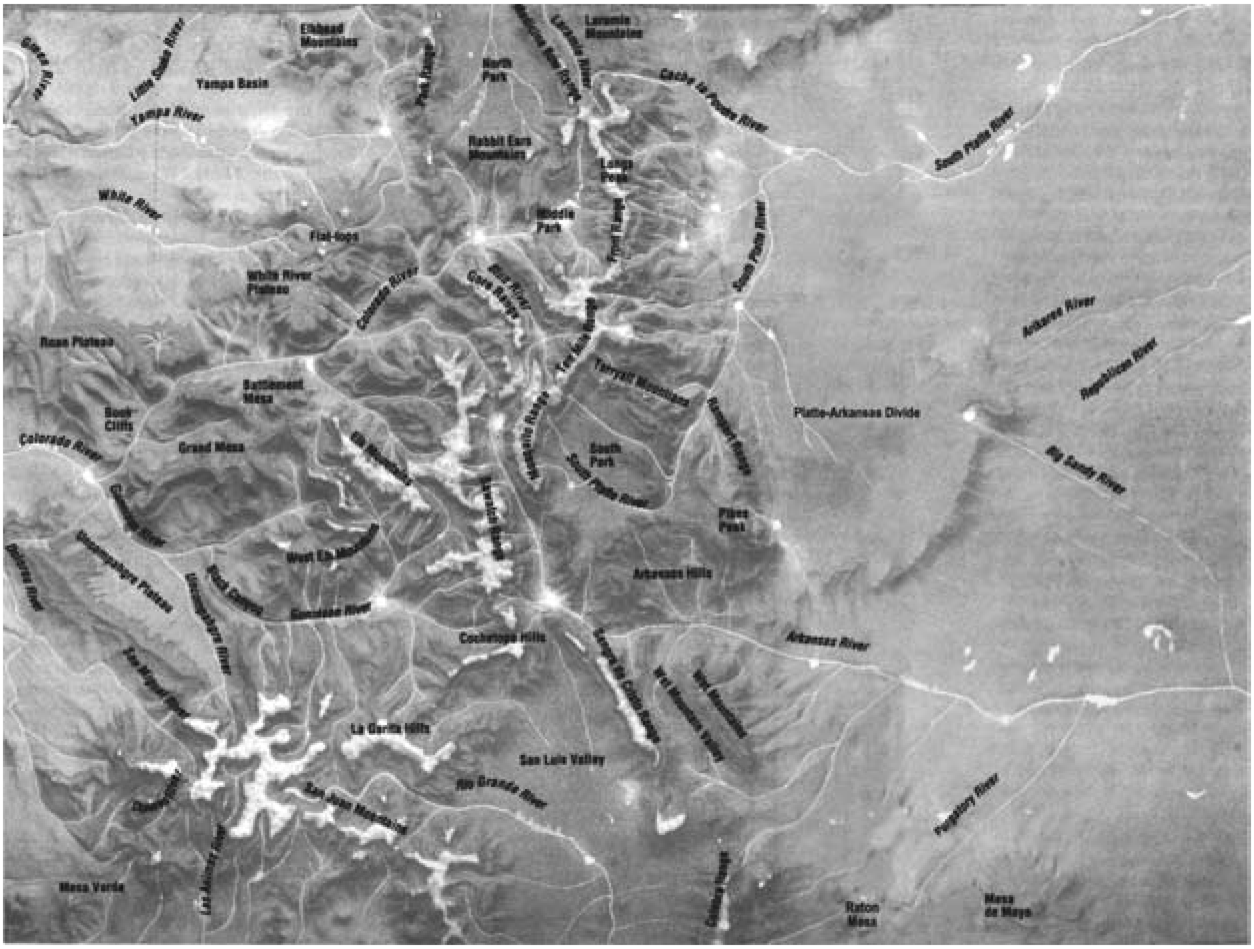
There is nothing simple about the Southern Rockies of Colorado (see Map 1-2), but we may think of the basic structure as two great ridges of granitic rocks arrayed in parallel lines oriented roughly north-south. The eastern series begins north of the Cache la Poudre River as the lower eastern Laramie Range and the higher western Medicine Bow Range. The Front Range extends from the Poudre to the Arkansas, ending in the Rampart Range (which includes Pikes Peak). The Wet Mountains are an independent range south of the Arkansas River.

A western chain of granitic mountains begins in southern Wyoming as the Sierra Madre (called the Park Range in Colorado); continues south as the Gore, Ten Mile, Mosquito, and Sawatch ranges; and then jogs a bit to the east to continue south into New Mexico as the spectacular ridge of the Sangre de Cristos. Between the granitic ridges are structural basins. North and Middle parks occupy a single structural basin, subdivided by the volcanic Rabbit Ears Mountains. South Park occupies a separate basin. West of the Park Range, the Wyoming Basin is continuous with much of southwestern Wyoming.

The San Luis Valley lies west of the main ranges of the Southern Rockies proper, but it looks like one of the parks, because it is surrounded by mountains, the Sangre de Cristos to the east and the younger, volcanic San Juans to the west. A range of volcanic hills marks the southern border of the San Luis Valley, roughly the southern border of Colorado. On the east side of the San Luis Valley is the spectacular Great Sand Dunes National Park and Preserve. *Valley of the Dunes* (Rozinski et al. 2005) provides a moving appreciation of *El Valle* in visual images and compelling prose. Every corner of Colorado deserves such treatment.

The main ranges of the Rockies represent uplifted Precambrian rocks and folded Paleozoic and Mesozoic sediments. Adjacent ranges like the San Juans were produced by Cenozoic volcanic activity. Features like the White River and Uncompahgre plateaus are independent uplifts. Grand and Battlement mesas are built of sedimentary rocks, protected by caps of resistant lava. J. Chronic and Chronic (1972), Matthews et al. (2003), and H. Chronic and Williams (2002) provided accessible introductions to the geology of Colorado; A. Benedict (2008) described the mountains in intimate detail; and Cairns et al. (2002) described the Rockies in the context of the ongoing human transformation of the region.

The eastern two-fifths of Colorado lies in the Great Plains Physiographic Province. When the Rockies rose, erosion and sedimentation clothed the area to the east with the pieces. For millions of years, this alluvium covered nearly all of eastern Colorado. In the Pliocene, and especially during the Pleistocene ice ages (with their high precipitation), the "Tertiary mantle" was largely eroded away and carried out of the state. Today it is preserved mostly on the High Plains, a nearly flat landscape interrupted occasionally by sandhills and eroded along stream courses to form canyons, cliffs, and escarpments. Between the High Plains and the mountain front lies the Colorado Piedmont. There the Tertiary mantle has been largely removed, exposing Mesozoic shales, limestones, and sandstones as hogbacks, low rolling hills, and canyons. Remnants of the Tertiary formations can be seen along the northern border of eastern Colorado. The dramatic Pawnee Buttes and



MAP 1-2. Some physiographic features of Colorado.

the escarpment of the Peetz Table suggest just how much material has been removed from the Colorado Piedmont. The divide between the Platte and Arkansas rivers is a remnant upland, providing an eastward extension of ecosystems of the foothills. The generally forested divide imposes a filter-barrier to north-south movement of many smaller mammals between the valleys of the master streams of the plains (D. Armstrong 1972, 1996).

At the foot of the mountains, sedimentary units generally dip steeply eastward, forming a great debris-filled trough, the Denver Basin. The southern rim of the basin is marked by roughlands south of the Arkansas River, which greatly complicate the ecology of southeastern Colorado, providing habitat for a number of species of Mexican affinities. Indeed, the very name of the physiographic region, the Raton Section, bespeaks its distinctive mammalian fauna, which includes several species of *"ratones,"* woodrats, whose dens are conspicuous features of the landscape.

The Colorado Plateau is a world-renowned showplace for the effects of erosion on flat-lying sedimentary rocks. Add to that the complications of a history of volcanism nearby, and the result is a landscape of remarkable ecological diversity. The country is typified by mesas and plateaus dissected by canyons. These include the Book and Roan plateaus, the Piceance Basin, and lava-capped Grand and Battlement mesas. Farther south, the uplifted Uncompahgre Plateau and isolated peaks like Ute Mountain are conspicuous. Mesa Verde is a major highland near the southern boundary of the state.

The boundaries between physiographic provinces are often visible in ecological patterns. The transition from the Great Plains to the Southern Rockies on the Eastern

Slope is especially dramatic, with the Front and Rampart ranges rising 2,400 m (nearly 8,000 ft.) in less than 30 km (18 mi.). Further, spectacular river canyons often mark gateways from the Rockies to adjacent physiographic provinces: Northgate Canyon on the North Platte, Glenwood Canyon on the Colorado, South Platte Canyon, the Royal Gorge of the Arkansas, the Black Canyon of the Gunnison, and the Big Thompson and Poudre canyons. These and numerous lesser canyons and gulches provide corridors for movements of the biota, their south-facing slopes providing microclimates especially favorable for southwestern species.

Watersheds

Rivers carve landscapes and support moist corridors of opportunity for living things. The influences of rivers are especially striking in the semiarid West. We cannot appreciate natural landscapes of Colorado—or much of human history—without knowing something of the patterns of drainage, the hydrography, of the state.

Colorado lies astride the Continental Divide. Water that falls to the west of the Divide ends up in the Sea of Cortez (Gulf of California). Waters of the Eastern Slope are destined for the Gulf of Mexico, via the Missouri-Mississippi system. The San Luis Valley is partly an internal drainage basin, but the Rio Grande flows through the southern part of the valley on its way to the Gulf of Mexico, having gathered its headwaters in the high San Juans.

The Continental Divide is a fundamental geographic fact in Colorado. The main ridge of the Rockies intercepts moisture coming from the Pacific Ocean. Air is forced up, hence cooled, and its water vapor condenses, falling in the mountains as rain or snow. The Eastern Slope is, therefore, in a "rain shadow." The Western Slope has about one-third of the land area of Colorado but receives more than two-thirds of the precipitation. However, because only about 11 percent of the state's human population lives on the Western Slope, ambitious efforts have been made for more than a century to move water—the lifeblood of agriculture and urban and industrial development—to the Eastern Slope, the center of Colorado's human population. The actual amount of diversion varies from one year to the next and the pattern is complex, but as an example, the amount of Western Slope water diverted annually to northeastern Colorado typically supplements the native flow of the South Platte River by about one-quarter.

Transmountain water diversion has greatly modified environments of Colorado. The South Platte and Arkansas valleys, which nineteenth-century explorer Stephen Long called the "Great American Desert," have been transformed into rich agricultural regions, expanding habitat for a number of species of mammals, including relative newcomers like fox squirrels, raccoons, and opossums. Also, the tunnels through which diverted water flows sometimes provide roosting habitat for bats.

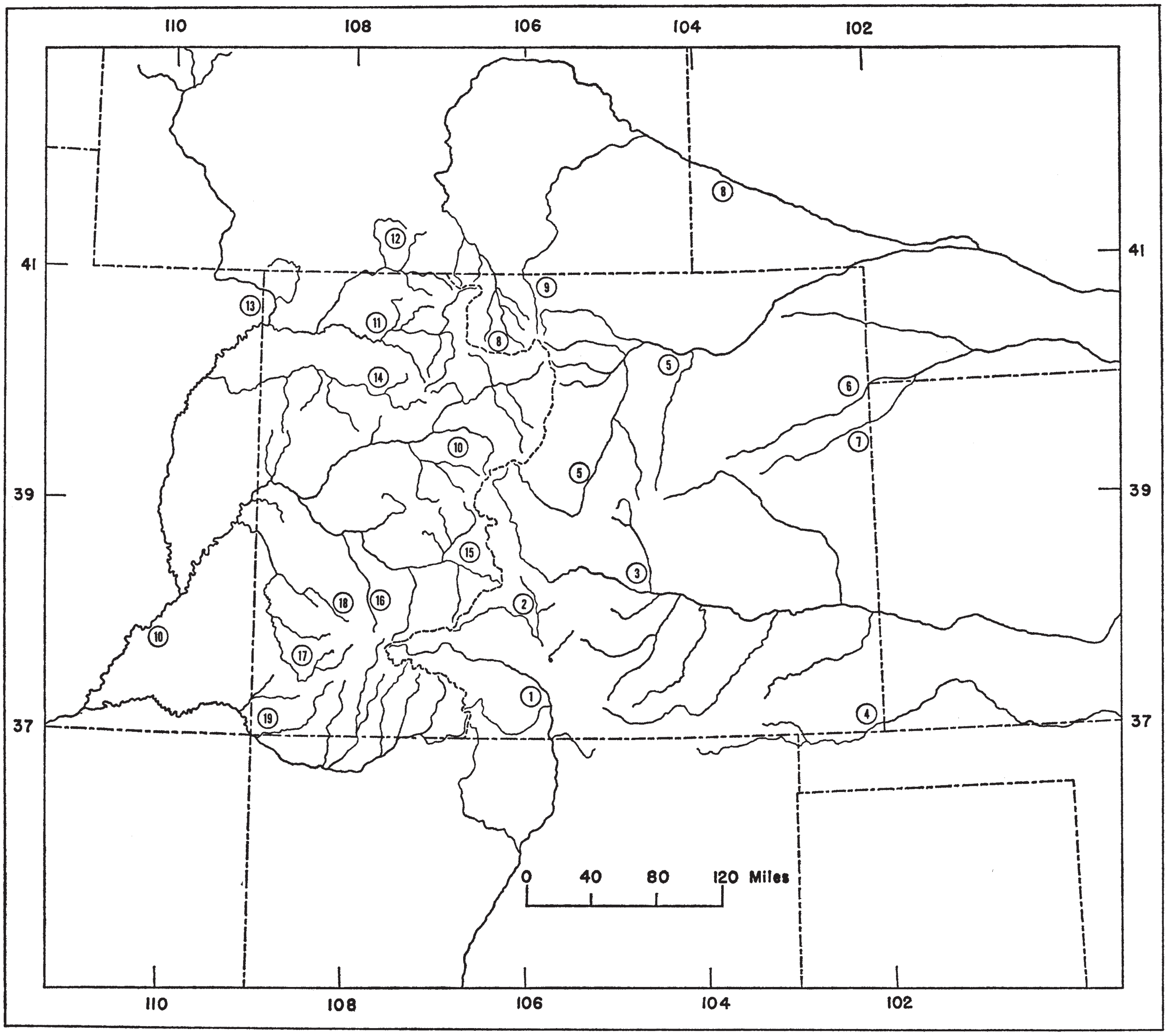
Several of the major rivers of western interior North America originate in the Colorado Rockies. Indeed, the only sizable river that flows into the state is the Green, which heads in the Wind River Mountains of western Wyoming. The master stream of the Western Slope is the Colorado River. The Yampa and White rivers drain northwestern Colorado before they join the Green. The mainstem Colorado—once called the Grand River—drains Middle Park and the western side of Rocky Mountain National Park and then joins the Gunnison at Grand Junction, flowing thence westward into Utah where it is joined by the Green en route to the Grand Canyon in Arizona. Southwestern Colorado is drained by several tributaries of the Colorado, namely the San Miguel, Dolores, and San Juan rivers and their tributaries, all born as mountain snow in the San Juans and destined for a muddy end in Mexico's Sea of Cortez.

The North Platte River heads in North Park and drains much of eastern Wyoming before joining the South Platte in Nebraska. The South Platte and its tributaries drain the Front Range and South Park. The Arkansas River heads in the Rampart, Sawatch, and Mosquito ranges. The High Plains of eastern Colorado give rise to the Republican and Arikaree rivers. The Cimarron heads in New Mexico and drains extreme southeastern Colorado.

Climates and Climate Change

Mammals are endotherms; that is, they maintain a high and constant body temperature by elegantly controlled production and retention of metabolic heat. Endothermy partially liberates mammals from the direct influence of climate, but climate still is an important influence on mammals, affecting individual lives, populations, and broad patterns of the distribution of species.

Weather in Colorado is highly variable from place to place, season to season, and moment to moment, all part of a broader changing climate. We can sketch only the broadest outlines of the pattern of climate. The Southern



MAP 1-3. Watersheds of Colorado and parts of adjacent states; irregular, dashed north-south line is Continental Divide. Key: (1) Rio Grande; (2) northern San Luis Valley ("Closed Basin"); (3) Arkansas; (4) Cimarron; (5) South Platte; (6) Arikaree; (7) Republican; (8) North Platte; (9) Laramie; (10) Colorado; (11) Yampa; (12) Little Snake; (13) Green; (14) White; (15) Gunnison; (16) Uncompahgre; (17) Dolores; (18) San Miguel; (19) Mancos (from Armstrong 1972).

Rockies are the dominant influence. Other important factors are latitude, elevation, exposure, local topography, and location relative to storm tracks and prevailing winds. Far from the moderating effects of oceans (roughly 1,100 km [690 mi.] from the Gulf Coast, 1,600 km [994 mi.] from the West Coast, and 3,200 km [1,988 mi.] from the East Coast), the state has a "continental climate." Colorado's climate is temperate and semiarid overall, with low relative humidity and temperatures that show wide variation at all elevations. For example, annual precipitation ranges from more than 100 cm (39.4 in.) in some parts of the San Juan Mountains to less than 25 cm (9.8 in.) in parts of the San Luis Valley, just 80 km (about 50 mi.) away. The frost-free season in the Grand Valley averages 189 days; at Silverton it averages 14 days. The difference in mean annual temperature between Lamar and the summit of Pikes Peak (only 200 km [124 mi.]

to the west but 3,200 m [10,500 ft.] higher in elevation) is about 20°C (approximately 35°F).

The Great Plains are typified by low precipitation, high winds, and low humidity. Summer daytime temperatures, although frequently hot, only occasionally and locally exceed 38°C (100°F). Winters have relatively warm periods interrupted by Arctic air masses sweeping down from Canada. Precipitation declines along an east-west gradient from an annual mean of about 45 cm (18 in.) along the Kansas and Nebraska borders to about 30–35 cm (12–14 in.) at the foot of the mountains.

Winters near the foothills are milder than on the plains or in the mountains, and the Front Range corridor, from Fort Collins south to Pueblo, supports more than 80 percent of the state's human population. Denver, at an elevation of about 1,610 m (5,280 ft.), has a mean annual precipitation of about 35 cm (13.8 in.) and a mean annual temperature of 10°C (50°F).

In the mountains, temperature decreases with increasing elevation, at roughly 1.7°C (3°F) per 300 m (985 ft.). Above about 2,750 m (about 9,000 ft.), frost is possible any night of the year, particularly in valleys, into which heavier cold air drains. Winter and spring snowfall can be quite heavy in the mountains, but local differences are extreme. In the western mountains more precipitation falls as winter snow than as summer rain. By contrast, winter and summer precipitation are about equivalent on the Eastern Slope. Warm winter winds, or chinooks, melt or evaporate much of the snow on the Eastern Slope. In spring, rapid snowmelt causes peak flows of rivers that head in the mountains. Groundwater from snowmelt contributes to summer streamflow. The enclosed mountain parks and valleys are cooler and drier than the surrounding mountains. They lie in the rain shadow of the mountains and also trap sinking cold air masses for relatively long periods.

Western Colorado has a diversity of climates driven in large part by topography. The high plateaus are similar to the mountains, but the lowlands and river valleys are warmer and drier. Winds generally are less intense than on the Eastern Slope. Stable high-pressure systems often form in winter, resulting in long periods of clear weather with warm days and cool nights. Southwestern Colorado typically has monsoonal, or summer, rains. This increase in moisture during the warm season is in contrast to the pattern for the rest of the Western Slope, where the greatest moisture occurs during winter. Erickson and Smith (1985) summarized a vast amount of information on physical environments of Colorado, including climate. A. Benedict (2008) provided an invaluable account of mountain climates.

There is no question that climatic patterns are changing at present, in part because of the industrial enrichment of Earth's atmosphere with "greenhouse gases," including carbon dioxide released from burning fossil fuels. Colorado, with its high topographic relief and consequent ecological complexity, may expect marked local and regional effects from such changes. Ongoing climate change (which is at least partly anthropogenic) has profound implications for management and conservation of Coloradan mammals; *Season's End* (Wildlife Management Institute 2008) is a sobering assessment of impacts of human-influenced climate change on the wildlife populations upon which recreational hunting depends. S. Saunders and Maxwell (2005) summarized likely change in the climate of the West under the theme "less snow, less water." Summary predictions, all interrelated, were more heat, less snowfall, diminished snowpack, earlier snowmelt, and more wildfires. S. Saunders and Easley (2006) and Saunders et al. (2009) discussed possible impacts of climate change on western national parks, highlighting possible conditions in Colorado's Mesa Verde and Rocky Mountain national parks. S. Saunders et al. (2008) discussed climate change in the American West more generally. Chapin et al. (2000) discussed changes in biodiversity in the context of ecosystem services. K. McDonald and Brown (1992) discussed montane mammals as a model system for predicting extinction as a result of climate change.

Of course, climate change has been a feature of Earth for billions of years. The record of the rocks suggests repeated changes in the climate of Colorado and worldwide over eons. Mammals of Colorado have been influenced by those changes for nearly a quarter of a billion years. There is abundant evidence of strong, natural climatic change in the recent geological past (Kittell et al. 2002; Whitlock et al. 2002). Only 15,000 years ago valley glaciers of the Pleistocene Ice Age retreated to their cirques. Some Coloradan mammals are relicts of glacial times, occurring now on the forested "island" of the Southern Rockies, surrounded by an impassable "sea" of grasslands and shrublands. A geologically "mere" 4,000 to 7,000 years ago, a "Hypsithermal Interval" warmer and drier than the present allowed access to parts of Colorado by a number of species of southwestern affinities—species like Mexican woodrats, rock mice, and a variety of bats that are now restricted to particularly warm, dry locations in the foothills, canyons, and other roughlands of the state (D. Armstrong 1972, 1996).

Clearly, climatic change is nothing new. What is remarkable about ongoing change is its rate (as rapid as any change revealed by fossil evidence except the change at the Cretaceous/Tertiary boundary—which appears to have been almost instantaneous—and maybe the change at the Permian/Triassic boundary) (Hallam 2004; Erwin 2006). Further, what is surely unique about present climate change is its principal cause: our industrial (fossil-fueled) selves.

Climate change is the central environmental issue of our time. In research and management institutions and agencies worldwide, human-influenced climate change has been observed and understood, at least in broad outline, for decades. Depending on the observation point, global mean surface temperatures have increased 0.6°F to 1.2°F since 1890, and the rate of increase is itself increasing. The fact that humans are influencing this change, mostly by augmenting the heat-trapping capacity of the atmosphere through liberation of CO_2 from fossil fuels, also has been known for decades (see, e.g., National Assessment Synthesis Team 2000). Popular interest and understanding of the matter has come much later (perhaps spurred by the 2006 film *An Inconvenient Truth* and the subsequent award of the 2007 Nobel Peace Prize to former vice president Al Gore and the Intergovernmental Panel on Climate Change), and now political discourse and legislative action are beginning to grapple with the challenge. The extent of the challenge and its impacts on many aspects of society can be seen locally in the list of sponsors of the Rocky Mountain Climate Organization, which includes a coalition of municipal water utilities, environmental organizations, industry (especially brewers and the ski industry), and agricultural organizations, among many others.

One of the difficulties of public (hence political) appreciation of climate change is that the climate system of Earth is huge, complex, and variable over the planet and over time. Even the fastest supercomputers are not yet able to model climate in detail sufficient to make local predictions. We speak casually of "global warming," but that is a serious distortion of the likely future. Over the globe—epitomized by a complex place like Colorado—the best guess is that there will be climate change. Some places will be warmer, but some will be cooler; some places will be drier, some wetter. Some places will change a little; others will change dramatically. Earth's rapidly changing polar ice caps have provided some of the most vivid and poignant illustrations of rapid, ongoing change, and a mammal, the polar bear (*Ursus maritimus*)—a recently derived Arctic-endemic Ice Age cousin of the brown or grizzly bear (*U. arctos*)—has become a poster child for climate change.

Coloradans are likely better informed about climate change than are Americans in some other parts of the country. First, much of the basic research on climate change has been conducted at the National Center for Atmospheric Research in Boulder. Second, climate change is already making an obvious difference where we Coloradans live. Some ski seasons have been abbreviated. Agricultural water users have seen their allocations decline. Forest fires have increased in frequency and severity, and the fire season is longer (A. Hansen et al. 2001; Keane et al. 2002). Dramatic outbreaks of some forest insects may be related to milder winters and water-stressed summers.

S. Schneider and Root (2001), T. Root and Schneider (2002), T. Root et al. (2003), T. Root and Hughes (2005), Parmesan (2006), and Janetos et al. (2008) reviewed impacts of climate change on biodiversity in general and focused on several topics of interest in the context of Coloradan mammals: changes in distributions and phenology (seasonal events), changes in pests and pathogens, changes in particularly sensitive ecosystems, and concerns about the adequacy of monitoring systems. Computer models of climate change predict elevated extinction risk by 18–35 percent, with local endemic species (endemism implying narrow ecological tolerance, small geographic range, and small population sizes) being most vulnerable (C. Thomas et al. 2004).

Geographic distributions of species are changing, as detailed in accounts of the Virginia opossum, hispid cotton rat, eastern pipistrelle, and white-backed hog-nosed skunk, for example. See R. Davis and Callahan (1992) for general comments on northward movements of southern mammals. Other changes are expected, as noted in such accounts as that of the nine-banded armadillo. Phenology is the study of seasonal changes, like the flowering of plants, emergence of butterflies, and arrival of migrant birds. At Gothic, above Crested Butte, yellow-bellied marmots have emerged earlier by approximately 1 day per year from 1976 to 1999 (D. Inouye et al. 2000). Barnosky et al. (2003) provided historical perspective, reviewing mammalian response to global warming over the past 4 million years and concluding that present, ongoing climate change may be unprecedented in rate and degree in the history of the class Mammalia.

Comments on impacts of climate change on particular kinds of mammals are included in respective accounts of species, to the extent that they are known. As for changes in pests and pathogens, climatic correlates of some emerging diseases are still poorly understood, but it may not be coincidence that the appearance of hantavirus (see Chapter 4 and the account of the deer mouse in Chapter 8) and chronic wasting disease (see account of the mule deer in Chapter

14) have occurred mostly in the past decade. The explosive expansion of mountain pine beetle appears to be related to climate change, at least indirectly. For a general review of impacts of climate change on forests—and hence on forest-dwelling mammals—see Joyce and Birdsey (2000).

As regional climates change, impacts likely will be most intense at highest elevations, if only because highest elevation bands have the smallest areas. (Imagine climbing a cone; the higher you climb, the less surface area there is per vertical distance.) The impact of mountains on community-level diversity of mammals is complex, involving not only area but also local climate and overall community diversity (C. McCain 2005, 2007). Mountain environments were identified by Janetos et al. (2008) as particularly sensitive to climate change for the obvious reason that many species are tied to particular elevational zones, which tend to be zones with particular climatic conditions. As climates change, those zones are moving. The higher up the mountain they move, the less area there is to occupy, the smaller the populations that can be supported, and the inexorable consequence will likely be local extinction in some cases.

In a sense, mountaintops are "islands" in a "sea" of lower-elevation habitats. Therefore, the principles of island biogeography (R. H. MacArthur and Wilson 1967; Newmark 1986, 1987, 1995) apply. The basic principles are simple enough. The smaller an island, the fewer species it can support. Further, the farther a particular island is from another island or a mainland source of potential colonizing species, the fewer species can reach that island. Principles of area and isolation, of colonization and extinction, underpin much of modern thinking in conservation ecology and the management of Earth's remaining natural landscapes.

Of course, alpine ecosystems and their characteristic mammals, like the American pika and yellow-bellied marmot (species adapted to "life in the cold" [C. Carey et al. 1993]), will be influenced most directly because they already are on mountaintops, so they have nowhere to go. Guralnick (2006a) came to such a conclusion based on statistical modeling of the geographic ranges of 20 mammalian species (most of which occur in Colorado) in the context of regional climate and elevational gradients. However, because the topographic diversity of mountains produces local diversity of habitats, mountain-dwelling species may be able to respond to climate change more effectively than "flatland" species, whose habitats may be extensive but monotonous and so may change over large areas, most of which will not be adjacent to newly suitable habitats (Guralnick 2006b).

For these impacts and others, monitoring—or routine observation of any sort—is woefully inadequate for most mammalian species over most of Colorado. Exceptions are game species, where harvest reports are mandated by regulation, and species under long-term study at particular places, such as work on yellow-bellied marmots at Rocky Mountain Biological Laboratory over several decades by Professor Kenneth B. Armitage of the University of Kansas, studies of bats on Boulder Mountain Parks and adjacent public open space by Professor Rick A. Adams of the University of Northern Colorado, and study of a number of species over more than half a century on Niwot Ridge at the University of Colorado's Mountain Research Station (D. Armstrong et al. 2001). Other long-term, continuous studies of particular species or particular places are strongly encouraged; careful monitoring is essential to understanding change in the short term (years to decades) and planning for the longer term.

The Wildlife Management Institute (2008) edited an excellent volume focused on impacts of ongoing anthropogenic (fossil-fueled) climate change on wildlife and fisheries on a national scale. They visualized decreases in food resources for many species with climate change, accompanied by increasing disease, invasive species, and wildfire. If we remember that sport fish and game mammals and birds provide an "umbrella" that covers terrestrial and aquatic ecosystems generally, this is an important volume. The Colorado Division of Wildlife and Colorado Wildlife Federation (2008) hosted a "Colorado Wildlife Summit" in October 2008 at Keystone. A principal focus of the summit was climate change and its ramifications. Literature in this general field is developing rapidly and much of it is being issued on-line. We recommend periodic searches of the extensive Internet resources of the Environmental Protection Agency, the Colorado Division of Wildlife, and the Rocky Mountain Climate Organization—all excellent points of entry into this emerging literature.

Soils

Soils are the product of interaction over time among geologic parent material, topography, climate, vegetation, and animal activity. As one would expect, the pattern of soils in Colorado is complex. This is reflected in (and influenced by) distributions of biotic communities. The composition, texture, depth, and moisture of soils can influence mammals indirectly through influence on the vegetation of an area. Further, local distribution of burrowing mammals, which usually depend on specific soil characteristics for their activities, is affected directly. Kangaroo rats, for example, occur only in sandy soils. In general, soils of Colorado differ from those of more humid regions by being lower in organic matter and higher in inorganic nutrients. Soils of Colorado were summarized broadly by Erickson and Smith (1985) and have been mapped extensively and in detail in county soil surveys by the Natural Resources Conservation Service (formerly the Soil Conservation Service) of the US Department of Agriculture.

Humans in the Landscape

Human activity has strongly influenced opportunities for native mammals. Prior to permanent settlement, subsistence populations—first of Native Americans and then of Euro-Americans—relied on the native fauna for food and fiber. They influenced local populations of game mammals and furbearers but seldom modified physical environments permanently. The first permanent European settlers came for mineral wealth. The "Colorado Mineral Belt" extends from Jamestown, Ward, and Gold Hill in the Colorado Front Range southwest to Silverton and Rico in the San Juans. Beginning with the discovery of gold in Cherry Creek in 1859, much of mountainous Colorado was transformed. Mountains were turned inside out, changing the topography and hence the environment for many species, many negatively, a few positively. Roosting habitat for bats, for example, was greatly augmented by mining activities, as were the rubbly slopes favored by pikas and bushy-tailed woodrats (and hence their predators, such as long-tailed weasels).

Agricultural settlement of the eastern plains and the western valleys came a little later. Wholesale changes in habitats for mammals resulted from irrigated agriculture, impoundment of rivers in reservoirs and transmountain diversion of water, control of floods and prairie fires, and extirpation of the keystone species of the prairie, the bison. Early ranching activities often involved predator control (and even eradication, as with the gray wolf and grizzly bear) and overgrazing, expanding opportunities for species like the Wyoming ground squirrel and the black-tailed jackrabbit. Urbanization has had profound effects on the fauna of the state, obliterating habitat for some species but increasing it for several others, like white-tailed deer, fox squirrels, and raccoons (and, of course, introduced Norway rats and house mice).

Ecosystems of Colorado

To this point we have described aspects of the physical environments of Colorado that provide opportunities for the native fauna. Geology underlies environmental pattern. Physiography describes the broad shape of the land. Climatic patterns describe the distribution and periodicity of precipitation and temperature. Vegetation clothes the landforms, moderates climate, and uses solar energy to power the integration of air, water, and minerals into the chemical molecules of life. Soils are the dynamic result of the interaction of climate, vegetation, and geologic parent material over time. All of these pieces contribute to the pattern of landscapes that we describe as ecosystems. An ecosystem is an arbitrary volume of Earth's environment, with living organisms (the biotic community) and their physical (abiotic) habitat exchanging materials, the whole system powered by a flow of energy.

For purposes of this book, Coloradan environments are described in terms of eight ecosystem types. This is not the only way to describe the environment, of course. Cary (1911) described environments of Colorado in terms of the classical life-zone concept pioneered by C. Hart Merriam and the US Bureau of Biological Survey. Pattern in the environment was described as a series of elevational bands, ranging from Upper Sonoran Zone grasslands and shrublands, through a Transition Zone typified by ponderosa pine or sagebrush, to a Canadian Zone forest of spruce and fir, through a narrow band of Krummholz or elfin timber (the Hudsonian Zone) at upper tree line, to an Alpine Zone atop the higher mountains. This system describes in broad terms an ecological pattern readily seen in Colorado and elsewhere in the West where environmental change is rapid along steep gradients of elevation. Despite its simplicity, Cary's life-zone map of Colorado still is a valuable tool for the ecologist.

D. Armstrong (1972) tabulated distribution of Coloradan mammals in 14 ecological community types, Gregg (1963) used 31 vegetation types to describe ecological distribution of ants, and Erickson and Smith (1985) mapped 11 vegetation types. Marr (1967) detailed vegetation and climate of a transect from foothills to tundra in Boulder County. (By the way, Marr's original plots were re-sampled and reanalyzed by Korb and Ranker [2001], who noted significant decreases in species richness in aspen woodlands, along with major changes in species composition.) Greenland et al. (1985) quantified zonation of the Colorado Front Range in bioclimatic terms, comparing several pre-

TABLE 1-1. Summary of some physical and biotic characteristics of ecosystems of Colorado

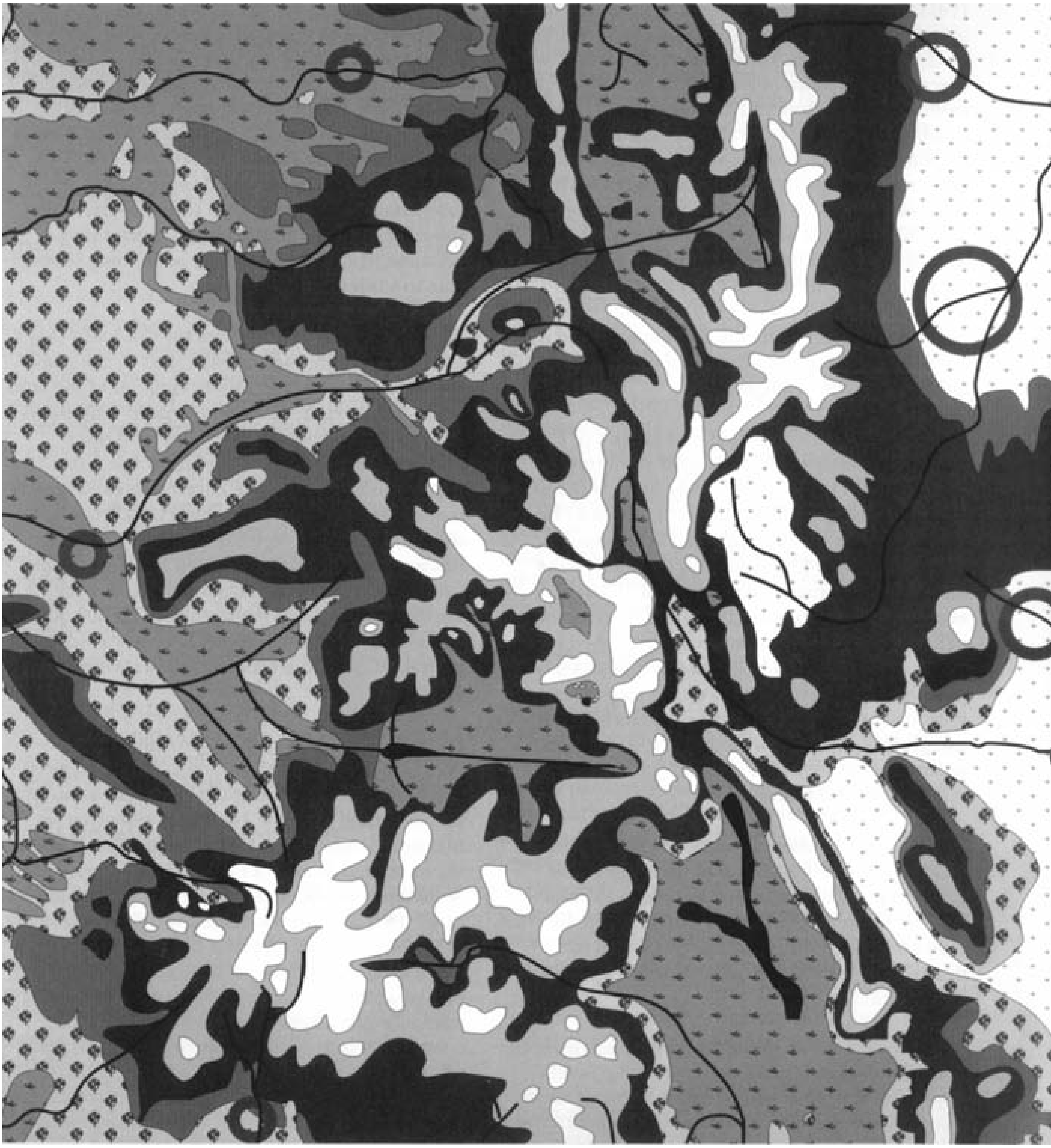
Ecosystem	*Typical Plants*	*Elevation*	*Mean Annual Precipitation*	*Mean Annual Temperature*	*Typical Mammals*
Grassland	grasses, prickly-pear, yucca, fringed sage	1,220–3,050 m (4,000–10,000 ft.)	36 (25–46) cm; 14 (10–18) in.	11°C (52°F)	pronghorn, jackrabbits, pocket gophers, pocket mice
Semidesert shrubland	sagebrush, greasewood, rabbitbrush	1,220–2,440 m (4,000–8,000 ft.)	25 (15–38) cm; 10 (6–15) in.	6°C (43°F)	jackrabbits, ground squirrels, kangaroo rat, mule deer, pronghorn, coyote
Piñon-juniper woodland	piñon pine, juniper, bunchgrasses	1,680–2,440 m (5500–8000 ft.)	36 (25–46) cm; 14 (10–18) in.	10°C (50°F)	cottontails, bats, piñon mice, woodrats, gray fox
Montane shrublands	Gambel oak, mountain mahogany, skunkbush sumac, chokecherry	1,675–2,600 m (5,500–8,500 ft.)	38 (33–43) cm; 15 (13–17) in.	7°C (45°F)	rock squirrel, brush mouse, rock mouse, woodrats, coyote
Montane forest and woodland	ponderosa pine, Douglas-fir	1,700–2,750 m (5,600–9,000 ft.)	51 (38–63) cm; 20 (15–25) in.	7°C (45°F)	mule deer, cottontails, black bear, bobcat
Subalpine forest	spruce, fir, lodgepole pine, aspen, heaths	2,740–3,470 m (9,000–11,400 ft.)	76 (51–102) cm; 30 (20–40) in.	2°C (36°F)	pine squirrel, pine marten, snowshoe hare, elk, lynx
Alpine tundra	cushion plants, willow shrub	above 3,470 m (11,400 ft.)	76 (60–120) cm; 30 (24–49) in.	–3°C (27°F)	American pika, yellow-bellied marmot, elk (summer), northern pocket gopher, coyote
Riparian and wetland systems	cottonwoods, willow trees and shrubs, cattails, rushes, sedges	1,220–3,350 m (4,000–11,000 ft.)	variable; comparable to adjacent uplands	variable, but lower than adjacent uplands	shrews, bats, voles, beaver, cottontails, deer, raccoon, red fox

vious attempts to describe zonation. R. Bailey (1978, following Küchler 1964) mapped 14 types of potential natural vegetation within six ecoregions in Colorado. Ricketts et al. (1999) provided a conservation assessment of North America (including the status of mammals) at the level of ecoregions, four of which were mapped in Colorado: Colorado Rockies Forest, Western Short Grass, Colorado Plateau Shrublands, and Wyoming Basin Shrub Steppe. Mutel and Emerick (1992) described the Coloradan environment in a framework of 15 kinds of ecosystems, and A. Benedict (2008) utilized a hierarchy of 16 ecosystems across 5 zones to describe the landscapes of the Southern Rockies.

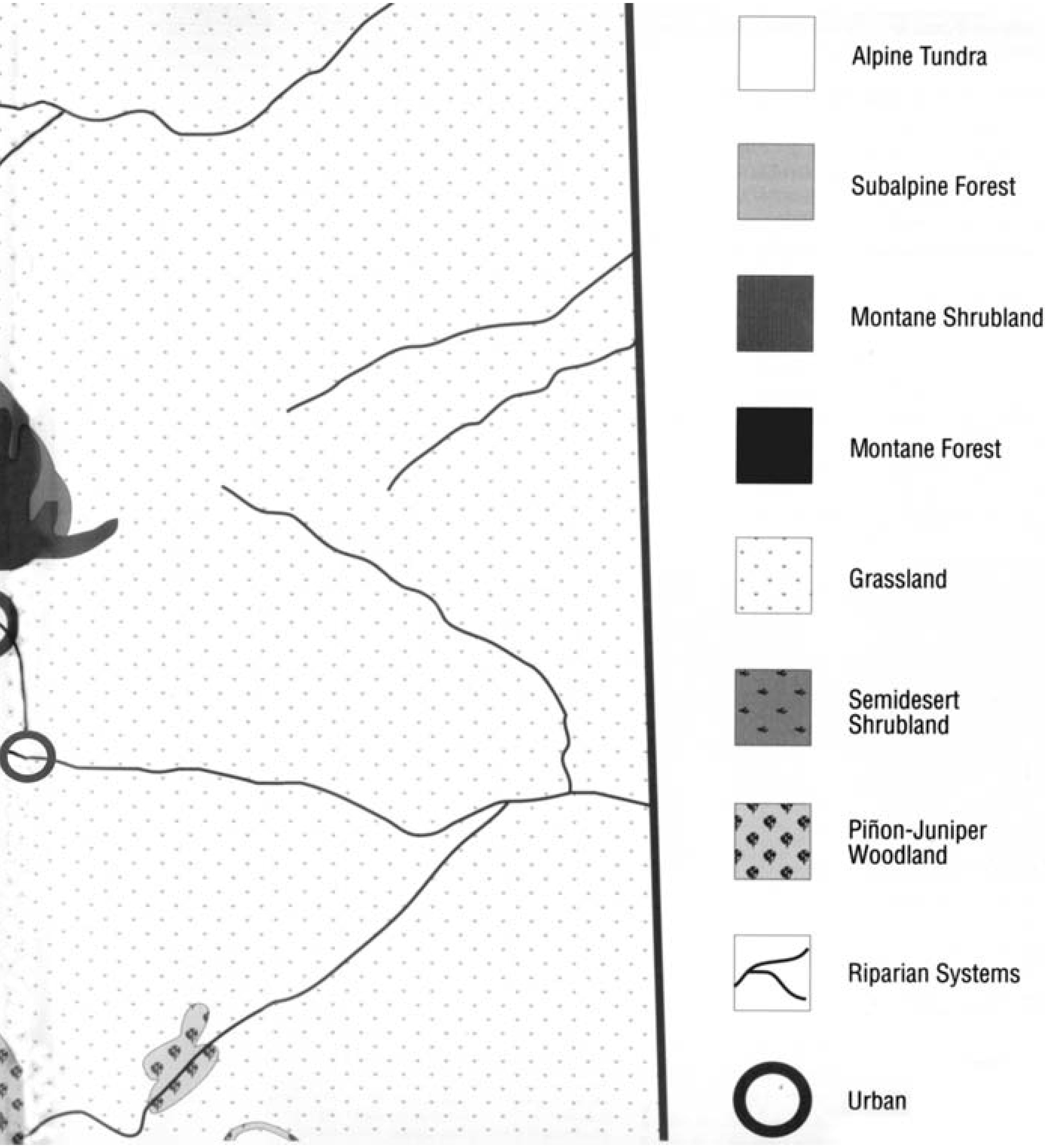
This diversity of alternative classification schemes should not be troublesome to the reader who keeps are mind a simple fact: naming and classifying ecosystems are human activities, done for human purposes. Our particular purpose is to describe the pattern of environmental opportunities for mammals, so we use a simple array of categories consistent with the scheme used in the "Explore Colorado" exhibit at the Denver Museum of Nature and Science (Kruger et al. 1995).

An ecosystem is a functioning volume of environment, involving interaction of living organisms (the biotic community) and non-living (abiotic) factors in continual cycles of materials powered by a ceaseless flow of solar energy. Ecosystems are arbitrary units, delineated for the convenience of people (naturalists, students, or managers, for example). An ecosystem might be as small as a pond, a field, or even an aquarium. It could be as large as the Great Plains. Indeed, one could argue that Earth has just one ecosystem—a single integrated, global ecological whole—the ecosphere. We abstract smaller ecosystems from the whole simply to have something manageable to study and, we hope, to understand.

The geography of the 8 broad ecosystems by which we describe environments of Colorado is sketched in Map 1-4. They are recognizable at a glance by their different biotic communities, the most visible component of the landscape. These 8 ecosystems readily lend themselves to subdivision for further, sometimes necessary, refinement. Estimates of percentage of the state covered by each ecosystem type are rough (determined by tallying townships by ecosystem type from the map, Major Land Resource



MAP 1-4. Ecosystems of Colorado.


Alpine Tundra
Subalpine Forest
Montane Shrubland
Montane Forest
Grassland
Semidesert Shrubland
Piñon-Juniper Woodland
Riparian Systems
Urban

Area and Generalized Land Use Map, Colorado, produced by the Soil Conservation Service, USDA, Portland, 1965, approximate scale: 1:2,000,000). Botanical nomenclature mostly follows Weber (1976).

Some physical and biotic information on the ecosystem types is presented in Table 1-1. For each ecosystem type, we provide a brief sketch of the mammalian fauna. We highlight mammals only because this is a book about mammals and not about wildlife more generally. Sometimes we speak of a "mammalian community." This is perhaps convenient, but at best it is ecologically simplistic, and at worst actually misleading. A biotic community is the living part of an ecosystem: animals, plants, fungi, and microbes. We might reasonably subdivide the community into two functional components: (1) *producers* (the green plants and photosynthetic microbes that have the genetic know-how to use solar energy to assemble parts of water and air into chemical bonds of biological molecules); and (2) *consumers* (which includes mammals and all other animals as well as fungi and many microbial groups).

Table 1-2 is a checklist of Coloradan mammals indicating their general distribution across Colorado's ecosystem types. The species in a community that exploit similar resources in similar ways comprise an ecological *guild*. Visualizing communities of functional guilds often makes more ecological sense than visualizing a community organized taxonomically. For example, we can think of the guilds of primary consumers (grazers, browsers, seedeaters) and secondary consumers (predators, parasites) regardless of taxonomy. This ecological view focuses attention where the action is. In semidesert shrublands, for example, seed-eating kangaroo rats and pocket mice may compete directly with ants for seed resources, and they compete less with other kinds of mammals. On shortgrass prairie, grazing mammals (like bison and prairie dogs) compete with grazing grasshoppers, not with insectivorous grasshopper mice.

GRASSLANDS

Dominant plants. Blue grama (*Bouteloua gracilis*), buffalograss (*Buchloë dactyloides*), western wheatgrass (*Agropyron smithii*), sand sagebrush (*Artemisia filifolia*), yucca (*Yucca glauca*), prickly-pear cactus (*Opuntia* spp.), needle-and-thread (*Stipa comata*), sand bluestem (*Andropogon hallii*), sand dropseed (*Sporobolus cryptandrus*).

TABLE 1-2. Ecological distribution of native, recent mammals in Colorado

	1	2	3	4	5	6	7	8
MARSUPICARNIVORA								
Family Didelphidae: Opossums								
Virginia Opossum—*Didelphis virginiana*								X
CINGULATA								
Family Dasypodidae: Armadillos								
Nine-banded Armadillo—*Dasypus novemcinctus*								X
PRIMATES								
Family Hominidae: Humans and Kin								
Humans—*Homo sapiens*	X	X	X	X	X	X	X	X
RODENTIA								
Family Sciuridae: Squirrels								
Cliff Chipmunk—*Neotamias dorsalis*		X	X					
Least Chipmunk—*Neotamias minimus*		X	X	X	X	X	X	
Colorado Chipmunk—*Neotamias quadrivittatus*			X	X	X			
Hopi Chipmunk—*Neotamias rufus*		X	X	X				

TABLE 1-2. Ecological distribution of native, recent mammals in Colorado—*continued*

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Uinta Chipmunk—*Neotamias umbrinus*		X	X	X	X	X	X	X
Yellow-bellied Marmot—*Marmota flaviventris*				X	X	X	X	X
White-tailed Antelope Squirrel—*Ammospermophilus leucurus*		X						
Rock Squirrel—*Otospermophilus variegatus*			X	X	X			X
Golden-mantled Ground Squirrel—*Callospermophilus lateralis*		X	X	X	X	X	X	X
13-lined Ground Squirrel—*Ictidomys tridecemlineatus*	X	X						
Spotted Ground Squirrel—*Xerospermophilus spilosoma*	X	X						
Wyoming Ground Squirrel—*Urocitellus elegans*	X	X		X	X		X	
Gunnison's Prairie Dog—*Cynomys gunnisoni*	X	X		X				
White-tailed Prairie Dog—*Cynomys leucurus*	X	X		X				
Black-tailed Prairie Dog—*Cynomys ludovicianus*	X	X						
Abert's Squirrel—*Sciurus aberti*					X			
Fox Squirrel—*Sciurus niger*								X
Pine Squirrel, or Chickaree—*Tamiasciurus hudsonicus*					X	X		
Family Castoridae: Beaver								
Beaver—*Castor canadensis*								X
Family Heteromyidae: Pocket Mice and Kin								
Olive-backed Pocket Mouse—*Perognathus fasciatus*	X	X						
Plains Pocket Mouse—*Perognathus flavescens*	X	X	X					
Silky Pocket Mouse—*Perognathus flavus*	X	X	X					
Great Basin Pocket Mouse—*Perognathus parvus*	X	X	X					
Hispid Pocket Mouse—*Chaetodipus hispidus*	X	X						
Ord's Kangaroo Rat—*Dipodomys ordii*	X	X	X					
Family Geomyidae: Pocket Gophers								
Botta's Pocket Gopher—*Thomomys bottae*	X	X	X	X	X			
Northern Pocket Gopher—*Thomomys talpoides*	X	X		X	X	X	X	
Plains Pocket Gopher—*Geomys bursarius*	X							
Yellow-faced Pocket Gopher—*Cratogeomys castanops*	X	X		X				
Family Dipodidae: Jumping Mice and Kin								
Meadow Jumping Mouse—*Zapus hudsonicus*					X			X
Western Jumping Mouse—*Zapus princeps*					X			X
Family Cricetidae: Cricetid Rats and Mice								
Southern Red-backed Vole—*Myodes gapperi*					X	X		
Heather Vole—*Phenacomys intermedius*					X	X	X	
Long-tailed Vole—*Microtus longicaudus*				X	X	X	X	X
Mexican Vole—*Microtus mogollonensis*			X	X	X			X
Montane Vole—*Microtus montanus*				X	X	X	X	X
Prairie Vole—*Microtus ochrogaster*	X							X
Meadow Vole—*Microtus pennsylvanicus*	X							X

continued on next page

TABLE 1-2. Ecological distribution of native, recent mammals in Colorado—*continued*

	1	2	3	4	5	6	7	8
Sagebrush Vole—*Lemmiscus curtatus*		X		X				
Muskrat—*Ondatra zibethicus*								X
Western Harvest Mouse—*Reithrodontomys megalotis*	X	X						X
Plains Harvest Mouse—*Reithrodontomys montanus*	X							
Brush Mouse—*Peromyscus boylii*			X	X				X
Canyon Mouse—*Peromyscus crinitus*		X	X					
White-footed Mouse—*Peromyscus leucopus*								X
Deer Mouse—*Peromyscus maniculatus*	X	X	X	X	X	X	X	X
Northern Rock Mouse—*Peromyscus nasutus*			X	X	X			
Piñon Mouse—*Peromyscus truei*		X	X	X				
Northern Grasshopper Mouse—*Onychomys leucogaster*	X	X						
White-throated Woodrat—*Neotoma albigula*			X	X				
Bushy-tailed Woodrat—*Neotoma cinerea*			X	X	X	X	X	
Eastern Woodrat—*Neotoma floridana*								X
Desert Woodrat—*Neotoma lepida*		X	X					
Mexican Woodrat—*Neotoma mexicana*			X	X	X			X
Southern Plains Woodrat—*Neotoma micropus*	X	X						
Hispid Cotton Rat—*Sigmodon hispidus*	X							X
Family Erethizontidae: New World Porcupines								
Porcupine—*Erethizon dorsatum*			X	X	X	X	X	X
LAGOMORPHA								
Family Ochotonidae: Pikas								
Pika—*Ochotona princeps*						X	X	
Family Leporidae: Rabbits and Hares								
Desert Cottontail—*Sylvilagus audubonii*	X	X	X	X				X
Eastern Cottontail—*Sylvilagus floridanus*								X
Nuttall's Cottontail—*Sylvilagus nuttallii*				X	X	X		X
Snowshoe Hare—*Lepus americanus*						X		X
White-tailed Jackrabbit—*Lepus townsendii*	X	X	X	X	X		X	
Black-tailed Jackrabbit—*Lepus californicus*	X	X						
SORICOMORPHA								
Family Soricidae: Shrews								
Masked Shrew—*Sorex cinereus*					X	X	X	X
Pygmy Shrew—*Sorex hoyi*						X		X
Merriam's Shrew—*Sorex merriami*	X	X	X	X	X			
Montane Shrew—*Sorex monticolus*					X	X	X	X
Dwarf Shrew—*Sorex nanus*				X	X	X	X	X
Water Shrew—*Sorex palustris*								X

TABLE 1-2. Ecological distribution of native, recent mammals in Colorado—*continued*

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Preble's Shrew—*Sorex preblei* (?)				X				
Elliot's Short-tailed Shrew—*Blarina hylophaga*								X
Least Shrew—*Cryptotis parva*	X		X	X				X
Desert Shrew—*Notiosorex crawfordi*		X						
Family Talpidae: Moles								
Eastern Mole—*Scalopus aquaticus*	X							
CHIROPTERA								
Family Molossidae: Free-tailed Bats								
Mexican Free-tailed Bat—*Tadarida brasiliensis*	X	X	X	X				
Big Free-tailed Bat—*Nyctinomops macrotis*	X							
Family Vespertilionidae: Common Bats								
California Myotis—*Myotis californicus*		X	X					
Western Small-footed Myotis—*Myotis ciliolabrum*	X	X	X	X	X			X
Long-eared Myotis—*Myotis evotis*			X	X	X			
Little Brown Bat—*Myotis lucifugus*					X	X		X
Fringed Myotis—*Myotis thysanodes*			X	X	X			
Long-legged Myotis—*Myotis volans*			X	X	X	X		
Yuma Myotis—*Myotis yumanensis*		X	X	X	X			X
Red Bat—*Lasiurus borealis*								X
Hoary Bat—*Lasiurus cinereus*		X	X		X	X		X
Silver-haired Bat—*Lasionycteris noctivagans*		X			X	X		X
Western Pipistrelle—*Parastrellus hesperus*	X	X	X		X			X
Eastern Pipistrellus—*Perimyotis subflavus*								X
Big Brown Bat—*Eptesicus fuscus*		X	X	X	X	X		X
Spotted Bat—*Euderma maculatum*		X	X	X				X
Townsend's Big-eared Bat—*Corynorhinus townsendii*	X	X	X	X	X			
Pallid Bat—*Antrozous pallidus*	X	X	X	X				X
CARNIVORA								
Family Felidae: Cats								
Mountain Lion—*Puma concolor*		X	X	X	X	X	X	X
Lynx—*Lynx lynx*						X	X	
Bobcat—*Lynx rufus*		X	X	X	X	X		X
Family Canidae: Dogs and Kin								
Coyote—*Canis latrans*	X	X	X	X	X	X	X	X
Gray Wolf—*Canis lupus**	X	X	X	X	X	X	X	X
Kit Fox—*Vulpes macrotis*	X	X						
Swift Fox—*Vulpes velox*	X							

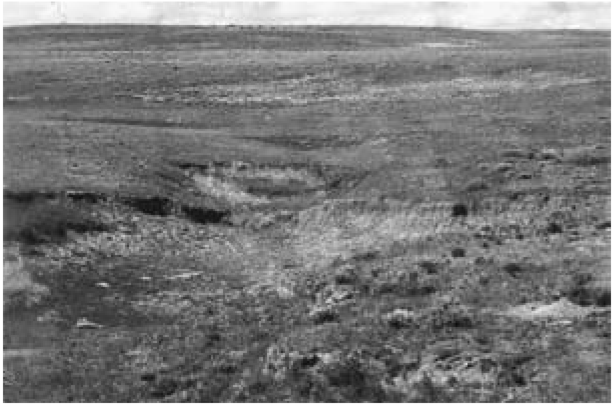
continued on next page

TABLE 1-2. Ecological distribution of native, recent mammals in Colorado—*continued*

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Red Fox—*Vulpes vulpes*				X	X	X	X	X
Gray Fox—*Urocyon cinereoargenteus*		X	X	X	X			X
Family Ursidae: Bears								
Black Bear—*Ursus americanus*				X	X	X		X
Grizzly Bear—*Ursus arctos**	X	X	X	X	X	X	X	X
Family Procyonidae: Raccoons and Kin								
Raccoon—*Procyon lotor*								X
Ringtail—*Bassariscus astutus*		X	X	X	X			X
Family Mustelidae: Weasels and Kin								
American Marten—*Martes americana*					X	X	X	
Ermine—*Mustela erminea*	X				X	X	X	X
Long-tailed Weasel—*Mustela frenata*	X	X	X	X	X	X	X	X
Black-footed Ferret—*Mustela nigripes*	X	X						
Mink—*Neovison vison*								X
Wolverine—*Gulo gulo*						X	X	
American Badger—*Taxidea taxus*	X	X	X	X			X	
Northern River Otter—*Lontra canadensis*†								X
Family Mephitidae: Skunks and Kin								
Western Spotted Skunk—*Spilogale gracilis*		X	X	X	X			
Eastern Spotted Skunk—*Spilogale putorius*								X
Striped Skunk—*Mephitis mephitis*	X	X	X	X	X	X	X	X
White-backed Hog-nosed Skunk—*Conepatus leuconotus*	X	X	X	X	X			
ARTIODACTYLA								
Family Cervidae: Deer								
Elk, or Wapiti—*Cervus elaphus*	X	X	X	X	X	X	X	X
Mule Deer—*Odocoileus hemionus*	X	X	X	X	X	X	X	X
White-tailed Deer—*Odocoileus virginianus*								X
Moose—*Alces alces*‡						X		X
Family Antilocapridae: Pronghorn and Kin								
Pronghorn—*Antilocapra americana*	X	X						
Family Bovidae: Cattle, Goats, Sheep and Kin								
Bison—*Bison bison**	X	X					X	
Mountain Goat—*Oreamnos americanus*‡						X	X	
Bighorn Sheep—*Ovis canadensis*					X	X	X	

Key: 1 = grassland; 2 = semidesert shrubland; 3 = piñon-juniper woodland; 4 = montane shrubland; 5 = montane woodland and forest; 6 = subalpine forest; 7 = alpine tundra; 8 = riparian and wetland systems.

Notes: This checklist does not include adventive species (e.g., Old World rats and mice, feral dogs, cats, pigs, llamas, horses), except deliberate introductions naturalized in the state. Used in conjunction with range maps in accounts of individual species, this list should allow construction of a provisional, hypothetical list of the potential natural mammalian fauna of native ecosystems at any locality in the state. Annotations of ecological distribution generally follow D. Armstrong (1972) and Meaney (1990a); * = extirpated within historic time; † = extirpated but restored; ‡ = deliberate introduction of non-native species; (?) = of questionable occurrence.



PHOTOGRAPH 1-1. Grassland, Pawnee National Grassland, Weld County. © 1993 Wendy Shattil / Bob Rozinski.

Grasslands occur over the Great Plains and in intermountain parks such as South Park and the Wet Mountain Valley. Prior to permanent settlement and cultivation, grasslands were the single most extensive ecosystem type in Colorado, covering 35 to 40 percent of the state. In Colorado, as generally around the globe, grasslands also are the most extensively modified biome (R. White et al. 2000). For review of the conservation challenges, see T. Weaver et al. (1996). Roughly half of Colorado's primeval grassland is now under cultivation, and about a quarter of that cropland is irrigated. Grasslands of the Great Plains and the mountain parks differ in species composition. Generally, grasslands cover a gently rolling topography of fine, deep soils. Winters are dry and most of the precipitation falls during spring and summer. Seastedt (2002) reviewed the history of grasslands of the Rocky Mountain region, emphasizing their deliberate and inadvertent transformation by humans. Over broad areas this ecosystem is a shortgrass prairie of blue grama and buffalograss. Where soil moisture is greater, western wheatgrass (*Agropyron smithii*), needle-and-thread, bluestems (*Andropogon*), reedgrass (*Calamogrostis* spp.), and dropseed interspersed with short grasses form mixed-grass prairies. Areas of low rolling sand hills are typified by sand sagebrush, Indian ricegrass (*Oryzopsis hymenoides*), bluestems, and reedgrass. In southeastern Colorado this ecosystem is characterized by lower precipitation and the presence of the candelabra cactus, or "cholla" (*Opuntia imbricata*).

Grasslands evolved in the presence of fire and with grazing by large and small mammals. Historically, bison, wolves, and black-tailed prairie dogs were a significant component. However, favorable topography and soils have led to such extensive human use that there are no known undisturbed tracts of native grassland in Colorado. About half of the state (some 32 million acres, about 13 million hectares) is devoted to agriculture, including extensive irrigated and dryland crops and grazing. In many areas, even where never plowed, the prolonged effects of livestock grazing have resulted in alteration of the floristic composition (Costello 1954; Adler and Lauenroth 2000) and animal assemblages (Milchunas et al. 1998). Vavra et al. (1994) reviewed ecological impacts of livestock on western grasslands generally, and Rowley (1985) provided historical perspective, particularly for grasslands managed by the US Forest Service. All of Colorado's natural environments are subject to habitat alteration by invasive, exotic plants, but such weed problems probably are most severe on grazing lands and fallow fields, hence grasslands generally. The challenges already are exacerbated by ongoing climate change (B. Bradley et al. 2009), which makes management of native ecosystems a moving target. Asner et al. (2004) reviewed impacts of grazing systems—including grasslands, shrublands, and woodlands—on ecosystem processes on a global scale, emphasizing process of desertification and encroachment of woody plants in response to grazing pressure.

Additional thousands of hectares have been converted to urban, suburban, and exurban landscapes (W. Travis et al. 2002; W. Travis 2007). Efforts to restore grassland and riparian ecosystems have used original land surveys to reconstruct pre-settlement landscapes (Galatowitsch 1990), and historical photographs are also useful for understanding human impacts (McGinnies et al. 1991). The shortgrass steppe of the High Plains of eastern Colorado was the heart of the Dust Bowl of the 1930s. Cooke (1936) provided a classic, contemporary account of the ecology of the area, which deserves wide rereading in the context of changing climates and mammalian habitats.

Mammals. One of two general "adaptive syndromes" characterize mammals of open grasslands: an ability to move rapidly (to escape predators or inclement weather) or an ability to live underground. The pronghorn and the white-tailed jackrabbit epitomize mammals of open grasslands, where their keen peripheral vision and great speed evolved. Most smaller mammals spend some or most of their lives belowground. Soil type determines the distribution of many small mammals of the grasslands. Plains pocket gophers may be abundant in deep sandy soils, Ord's kangaroo rats excavate dunes and sandy banks of ephemeral streams (or roadside borrow pits), and plains pocket mice occur in shrubby areas of sand sagebrush and yucca. In contrast to other pocket mice, the hispid pocket mouse is not limited to sandy soils but prefers open areas with a light cover of bunchgrasses. Prairie voles occur in mixed-grass prairie adjacent to riparian areas in eastern Colorado. Northern grasshopper mice are widespread in both grasslands and semidesert shrublands, and they seem to prefer loamy soils because they are obligate dust-bathers. Thirteen-lined ground squirrels prefer short bunchgrasses on friable sandy loams where they can dig their burrows. Swift foxes prefer sandy loams or loams where they dig dens for shelter year-round. Badgers are wide-ranging in open habitats with abundant burrowing rodents.

Recently, human disturbance has played a key role on the plains. Black-tailed jackrabbits successfully occupy areas disturbed by human activities, taking cover in and feeding on introduced grasses and weedy forbs; white-tailed jackrabbits do not respond as well to disturbed vegetation and are increasingly restricted to more open areas and the mountain parks. Desert cottontails may prefer brushlands and woodland-edge situations, but they occur throughout the open grasslands, where they use burrows excavated by other mammals. Black-tailed prairie dogs are scattered across the eastern plains in both short- and mid-length grasslands, often reaching high densities in unused open lands within urbanized areas, especially areas abandoned by agriculture but not yet permanently modified by residential, commercial, or industrial development.

Coloradan grasslands received intensive study beginning in the 1960s when the Grassland Biome component of the International Biological Program (IBP) was headquartered at Colorado State University, and the Central Plains Experimental Range and Pawnee National Grassland served as principal research sites (e.g., N. French 1971; Flake 1973; N. French et al. 1976; Abramsky 1978; Abramsky and Van Dyne 1980). Ecological work in the area continues as a Long-Term Ecological Research (LTER) site, funded by the National Science Foundation, as documented by numerous studies cited elsewhere in this book. Stapp et al. (2008) provided a thorough review of that literature. In North American grasslands, latitude and moisture gradients underlie broad patterns of community structure, and temporal variability in community composition occurs in all grassland types (Grant and Birney 1979).

Lovell et al. (1985) described successional patterns caused by development of a dam and canal, agriculture, and irrigation around Barr Lake. Changes in species composition occurred as opportunists (raccoons, least shrews, porcupines) moved in and sensitive species disappeared, while other more resilient species persisted. A number of studies have focused on the impact of grazing. Moulton et al. (1981a) found small mammals to be adaptable to habitat perturbation, more responsive to vegetational structure than to plant species composition. Other large Coloradan grassland sites where studies of mammals have occurred include the US Army's Piñon Canyon Maneuver Site southeast of Pueblo, Rocky Mountain Arsenal National Wildlife Refuge northeast of Denver, and a number of Nature Conservancy preserves. R. Benedict et al. (1996) reviewed grassland mammals from a conservation perspective. Recent reviews of the general ecology (natural and human) of the Great Plains include Licht (1997), Seastedt (2002), and Johnsgard (2005).

PHOTOGRAPH 1-2. **Semidesert shrubland, along Rio Grande, San Luis Valley, Costilla County. © 1993 Wendy Shattil / Bob Rozinski.**

SEMIDESERT SHRUBLANDS

Dominant plants. Big sagebrush (*Artemisia tridentata*), mountain sagebrush (*A. vaseyanum*), greasewood (*Sarcobatus vermiculatus*), shadscale (*Atriplex confertifolia*), four-winged saltbush (*A. canescens*), rabbitbrush (*Chrysothamnus nauseosus*), balsamroot (*Balsamorhiza sagittata*).

Often grayish green in general color, semidesert shrublands cover arid regions at lower elevations in western Colorado and the San Luis Valley, occupying about 15 percent of the state. This is a cold desert ecosystem, occurring at the eastern edge of the Colorado Plateau and the Wyoming Basin. Semidesert shrublands follow the canyon bottomlands of western Colorado, extend up onto mesas and plateaus, and penetrate deep into the mountains along the Yampa, Colorado, and Gunnison rivers. Semidesert shrublands are dominated by shrubs over a sparse understory of grasses and forbs or even bare ground where nutrient-poor, alkaline soils and drought prevail. Most of the moisture falls during winter. Early summer drought is common, and June is the driest month in western Colorado (whereas it is one of the wetter months in eastern Colorado).

Greasewood is often well developed on alkaline soils and extends over considerable areas in the San Luis Valley, the Grand Valley, and other arid areas of western Colorado. Herbaceous understory is sparse. Rabbitbrush or sagebrush may border greasewood stands, and where soils are less alkaline these species form mixed stands with the greasewood. White-tailed antelope squirrels burrow under rocks and shrubs in such ecosystems in southwestern Colorado.

Saltbush is widespread at lower elevations on soils that are well drained and less alkaline than those dominated by greasewood. Extensive stands are present in western Moffat, Mesa, Garfield, and Rio Blanco counties and in Delta County between Hotchkiss and the eastern slopes of the West Elk Mountains. Typically, saltbush plants are widely scattered and often are cushion- or mat-like in appearance. There is little herbaceous understory.

Sagebrush covers many thousands of hectares in western Colorado. In North Park and the upper Colorado River drainage (Middle Park, Gunnison Basin, and Blue River Valley), mountain sagebrush predominates, whereas in the northwestern corner of the state big sagebrush prevails. Grass and forb cover is often well developed. At their lower limits sagebrush stands often merge with either saltbush or greasewood. At the upper limits the transition may be with montane shrubland, montane forest, or subalpine forest. The most significant human use of semidesert shrublands has been for grazing, although large portions of the San Luis Valley and the Grand Valley have been converted to irrigated croplands. Shrublands and piñon-juniper woodlands are particularly subject to degradation by ongoing oil and gas development (Morton et al. 2004). A detailed conservation assessment of sagebrush habitats in Colorado was prepared for the Colorado Division of Wildlife by Boyle and Reeder (2005).

Mammals. Herbivores of this ecosystem must contend with foliage of low palatability and low summer moisture. Desert cottontails feed on sagebrush and rabbitbrush in winter. Black-tailed jackrabbits feed on the forb understory and turn to shrubs such as winterfat (*Ceratoides lanata*), shadscale, and sagebrush in late fall and winter. Wyoming ground squirrels feed on pasture sagebrush (*Artemisia frigida*), milk vetches (*Astragalus* spp.), and locoweeds (*Oxytropis* spp.). The Wyoming Basin is home to the white-tailed prairie dog, which favors xeric sites with a mix of shrubs and grasses. Ord's kangaroo rats exploit the rich seed resources of the shrublands. Canyon mice and ringtails favor warm, dry, rocky canyons in semidesert shrublands. Moderately friable sandy loams are favored by northern grasshopper mice. Sagebrush voles feed on the leaves of sagebrush, rabbitbrush, and other aridland shrubs in areas where they are mixed with grasses. Merriam's shrew and the desert shrew occur locally. The Yuma myotis and pallid bat occur in the canyon country of western and southeastern Colorado. Published studies of mammalian communities of Colorado's semidesert shrublands are few, but studies from adjacent Utah (D. Armstrong 1979, 1982) are pertinent.

PHOTOGRAPH 1-3. Piñon-juniper woodland, Colorado National Monument, Mesa County. Photograph by C. A. Meaney.

PIÑON-JUNIPER WOODLAND

Dominant plants. Piñon pine (*Pinus edulis*), one-seed juniper (*Juniperus monosperma*), Utah juniper (*J. osteosperma*) in western Colorado, red cedar (*J. scopulorum*), blue grama (*Bouteloua gracilis*), junegrass (*Koeleria macrantha*), Indian ricegrass (*Oryzopsis hymenoides*), prickly-pear (*Opuntia* spp.), fescues (*Festuca* spp.), muhley (*Muhlenbergia* spp.), bluegrass (*Poa* spp.).

Piñon-juniper woodlands form open stands on warm, well-drained sites, mostly in western and southern Colorado, covering 10 to 15 percent of the state. In southeastern Colorado, they are situated above grasslands and below montane shrublands. Western Colorado presents a more complex pattern. There, piñon-juniper woodlands are bounded below and sometimes also above by semidesert shrublands where the woodlands also interweave with montane shrublands. Piñon-juniper woodlands are found extensively on slopes in western and central Colorado and in the roughlands of the southeastern part of the state. An isolated grove of about 4,500 ha (11,120 acres) is located at Owl Canyon, north of Fort Collins. Soils are variable in composition, although generally coarse and shallow. Junipers are more drought-tolerant and thus dominate on the lower periphery, whereas piñons are more cold-tolerant and dominate the upper extreme. Grasses, cacti, and a variety of annual and perennial composites form much of the sparse ground cover. Many large mammals and birds use this ecosystem seasonally to avoid the rigors of higher elevations. Others are year-round residents. Species diversity in piñon-juniper woodlands is high, in Colorado second only to riparian systems. Native Americans harvested piñon nuts, which are produced by an individual tree only every 3 to 7 years, and they made extensive use of piñon wood and pitch. Early European settlers also used these resources and initiated cattle and sheep grazing, which continues today. The woodlands of Mesa Verde are exemplary and well studied (Floyd et al. 2003). Like semidesert shrublands, piñon-juniper woodlands are being degraded over wide areas by oil and gas development, particularly in western Colorado (Morton et al. 2004).

Mammals. During years of major cone production (sometimes called "mast years"), mammals feed on the rich resource of piñon "nuts." Many use the understory of grasses and forbs also. Townsend's big-eared bats and fringed myotis pick insects off the trees. The long-eared myotis roosts in tree cavities and under loose bark. Desert cottontails feed on the understory of grasses and forbs. Nuttall's cottontail turns to junipers in winter. Rock squirrels occupy areas of broken rock. Piñon-juniper woodlands in Colorado are home to as many as four species of *Peromyscus*. The piñon mouse occurs in areas with large rocks where the woodland is well developed. The canyon mouse inhabits the warm, dry canyons of western Colorado. The brush mouse occurs in piñon-juniper woodlands of both the Eastern and Western slopes, especially in the ecotone with oakbrush. The well-named rock mouse occurs only on the Eastern Slope, extending well northward in rocky foothills beyond the general range of piñon. Piñon-juniper woodland is a favored habitat of the Mexican woodrat, which reaches its northern limit in Colorado. Ringtails frequent rocky canyon country, often in association with channels of ephemeral streams. Gray foxes, mountain lions, and mule deer are common in this ecosystem. The few records of white-backed hog-nosed skunks in Colorado are from piñon-juniper woodlands and adjacent grasslands in the southeastern portion of the state.

PHOTOGRAPH 1-4. Montane shrubland, Black Canyon of the Gunnison, Montrose County. Photograph by David J. Cooper.

Peyton (2008) described small mammals of piñon-juniper woodlands (and adjacent shrub and grassland habitats) on chalk barrens on Fort Carson Military Reservation, Pueblo County. Somers et al. (2003) reviewed some aspects of the ecology of terrestrial mammals of Mesa Verde, focused on interactions with old-growth piñon-juniper woodland. Small mammals of piñon-juniper woodlands often segregate by extent of canopy cover, herbaceous cover, and tree dispersion (Ribble and Samson 1987). Haufler and Nagy (1984) concluded that competition was avoided by selection of different foods. For comparative studies from woodlands in adjacent Utah, see D. Armstrong (1979, 1982) and Sureda and Morrison (1999).

MONTANE SHRUBLANDS

Dominant plants. Gambel oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus montanus*), serviceberry (*Amelanchier alnifolia*), skunkbush (*Rhus trilobata*), smooth sumac (*R. glabra*), wax currant (*Ribes cereum*), wild rose (*Rosa woodsier*), needle-and-thread (*Stipa comata*), blue grama (*Bouteloua gracilis*), western wheatgrass (*Agropyron smithii*), side-oats grama (*Bouteloua curtipendula*), mountain muhley (*Muhlenbergia montana*), rabbitbrush (*Chrysothamnus nauseosus*), chokecherry (*Prunus virginiana*).

Montane shrublands generally occur at higher elevations than either grasslands or piñon-juniper woodlands in eastern Colorado, and in western Colorado they occur upslope from semidesert shrublands or piñon-juniper woodlands and below montane forests. On the Eastern Slope of the Front Range, these shrublands form a distinctive and often quite narrow belt at the mountain front, often in association with sedimentary hogback ridges and other "foothills." West of the mountains, extensive Gambel oak communities often intermingle with piñon-juniper, and mixed stands of serviceberry, snowberry, and rabbitbrush cover extensive areas of northwestern Colorado. All told, such shrublands cover 5 to 10 percent of the state. The topographic setting is rocky, broken country; soils are coarse and well drained. Temperatures are less extreme than in adjacent ecosystems: warmer in winter than ecosystems above and cooler in summer than those lower in elevation. Gambel oak and serviceberry dominate throughout, except for the foothills west of Denver, where Gambel oak reaches its northern limit and is replaced by mountain mahogany. Montane shrublands form a rich and diverse ecosystem that supports plants and animals more typical of adjacent ecosystems, and they serve as winter refuge for some species. Montane shrublands are often areas of intensive human residential use, and they are quite colorful in fall.

Mammals. Many mammals favor the rocky outcrops and hogbacks common to montane shrublands. Abundant fruits, twigs, and foliage of shrubs provide forage, as does the understory of grasses. Rock squirrels prefer areas that have large rocks and can often be found basking on them or feeding on berries and grass seeds. Brush mice, piñon mice, and rock mice frequent montane shrublands, as does the ubiquitous deer mouse. Although four of Colorado's six species of woodrats can be found in montane shrublands, the Mexican woodrat is the most characteristic. Ringtails, western spotted skunks, and gray foxes feed on a broad variety of small mammals, reptiles, arthropods, and fruits. The western small-footed myotis frequents rocky areas where they forage and roost in rock crevices and among, or under, rocks on the ground. They winter in tunnels here and in montane forests. D. Armstrong et al. (1973) described species turnover in assemblages at different elevations, focused strongly on small mammals of montane shrublands.

PHOTOGRAPH 1-5. Montane woodland, City of Boulder Open Space, Boulder County. Photograph by David J. Cooper.

MONTANE WOODLANDS AND FORESTS

Dominant plants. Ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), white fir (*Abies concolor*), limber pine (*Pinus flexilis*), Colorado blue spruce (*Picea pungens*), lodgepole pine (*Pinus contorta*), wax currant (*Ribes cereum*), Arizona fescue (*Festuca arizonica*), sulphur flower (*Eriogonum umbellatum*), kinnikinnik (*Arctostaphylos uva-ursi*), mountain maple (*Acer glabrum*).

Montane forests range from open ponderosa pine parklands to dense Douglas-fir forests and clothe about 10 percent of Colorado. Bounded below by foothills shrublands, piñon-juniper woodlands, or grasslands, they grade into subalpine forests above. Most precipitation falls as snow in winter and spring, although summer showers are also important. Open ponderosa pine woodlands occur on well-drained sites in the Front Range and eastward on the Platte-Arkansas Divide, in the southern and southwestern mountains to Mesa Verde, and on parts of the Uncompahgre Plateau. Douglas-fir predominates in other mountainous regions and generally on moister, steeper slopes at higher elevation, whereas ponderosa pine occupies drier south-facing slopes. In some areas they intergrade along with quaking aspen or lodgepole pine, which will colonize sites after a disturbance, especially fire. This ecosystem has been exploited extensively for timber and also used for mining, grazing, historic and current human settlement, and recreation. Due to fire suppression over most of the past century, many ponderosa pine stands in Colorado are much denser than they would have been pre-settlement and as a consequence are prone to wildfire and insect damage (Cisla 2010).

Mammals. Many mammals in both montane and subalpine forests use the dominant conifers for food and shelter. A number of kinds feed on inner bark (cambium) and

PHOTOGRAPH 1-6. Subalpine forest, Rio Grande County. © 1993 Wendy Shattil / Bob Rozinski.

stems and make their nests or roost in the trees. Both the long-eared and long-legged myotis roost in tree cavities and under loose bark on standing dead snags. Nuttall's cottontails avoid dense forests but can be found at the edge of clearings. Least and Colorado chipmunks feed on fruits, nuts, berries, seeds, leaves, and stems; the Uinta chipmunk also occurs in montane forests but is restricted to higher areas, where it often is sympatric with the least chipmunk. Abert's squirrels make nests in ponderosa pine trees and feed on the twigs and seeds, whereas pine squirrels prefer more dense Douglas-fir or lodgepole pine stands. Porcupines feed on cambium, buds, and twigs of conifers, especially pines. American martens feed on small rodents and are excellent climbers. Numerous studies of Colorado's montane mammals are cited in respective accounts of species. Synecological studies have been remarkably few. Stinson (1978) contrasted communities on north- and south-facing slopes, and many of the observations of D. Armstrong (1993, 2008) pertain to this ecosystem type. Ecology of wildlife diseases in the montane forests of Rocky Mountain National Park was reported by A. Carey et al. (1980), G. Bowen et al. (1981), and McLean et al. (1981). Finch and Ruggiero (1993) emphasized the importance of montane and subalpine forests to wildlife conservation.

SUBALPINE FOREST

Dominant plants. Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), quaking aspen (*Populus tremuloides*), bristlecone pine (*Pinus aristata*), limber pine (*P. flexilis*), lodgepole pine (*P. contorta*), myrtle blueberry (*Vaccinium myrtillus*), broom huckleberry (*V. scoparium*), heart-leaved arnica (*Arnica cordifolia*), Jacob's ladder (*Polemonium delicatum*).

This is a relatively homogeneous, dense coniferous forest ecosystem, often occurring on steep slopes. It is the highest-elevation forested ecosystem in Colorado and occupies about 15 percent of the land area of the state. Soils are shallow. High winter precipitation, in the form of snow, is augmented by windblown snow from the alpine tundra above. The trees are effective snow fences and cold temperatures prevent significant melting until late spring. "Freak" storms may have significant, local impacts on small mammals (Ehrlich et al. 1972). These factors create high snow accumulations. At their upper reaches, subalpine forests become low-growing stands of elfin woodland, or Krummholz (Mutel and Emerick 1992; A. Benedict 2008). Limber pine and bristlecone pine dominate on windy, exposed sites with rocky soils. Fire or other disturbance may lead to colonization by lodgepole pine or aspen. Spruce and fir seedlings are shade-tolerant, allowing them to invade stands of shade-intolerant lodgepole pine and aspen. Regeneration of a spruce-fir forest after disturbance is relatively slow because of the short growing season. In contrast to lodgepole pine and mature spruce fir, aspen stands typically have a luxuriant and diverse understory of forbs and grasses, so they provide important opportunities for mammals (V. Scott and Crouch 1988). Huckaby and Moir (1998) detailed forest communities on the Fraser Experimental Forest in the St. Louis Creek watershed of Grand County. Subalpine forests are used extensively for recreation year-round and provide cover for the watersheds so important to metropolitan areas. Human influences and general ecology of Colorado's forests were reviewed by Elias (2002), Stohlgren et al. (2002), and Tomback and Kendall (2002) and summarized by J. Baron (2002). Elias et al. (1986) studied subfossil pollen and insect remains from Rocky Mountain National Park and concluded that the subalpine forests of today had assembled by about 3,500 years ago; in the interval 6,800 to 3,500 ybp (years before present), pines were more prevalent in high-elevation forests. Schoennagel et al. (2007) discussed occurrence of wildfire in the context of multi-decadal climatic variability; fires should be expected to increase with ongoing warming and drying. W. Baker (2009) emphasized fire as an important and natural influence on forests in the Rocky Mountains, urging the importance of management rather than mere prevention or suppression.

Forests of Colorado are under obvious stress. Sudden Aspen Decline (SAD) is a poorly understood die-off of aspen groves that more than doubled in extent from 217 sq. mi. (approximately 560 km^2) in 2006 to 522 sq. mi. (about 1,350 km^2) in 2007 (Colorado State Forest Service 2007). Ungulates (especially elk) are often implicated in decline of aspen stands. On long-term exclosures in national forests of south-central Utah (Kay and Bartos 2000), aspen subjected to browsing (by mule deer and/or livestock, especially cattle) failed to regenerate or regenerated significantly less than on total exclusion plots. Ungulate herbivory also influenced understory plants. Utilization by deer alone tended to reduce shrubs and tall, palatable forbs while promoting growth of native grasses. Adding livestock to the mix, however, reduced native grasses and promoted introduced species and bare soil.

Aspen decline is not homogeneous across the broad landscape, and—judging from studies in the northern Colorado Front Range—a diversity of factors is involved, including damage by mammalian herbivores (especially elk; see W. Baker et al. 1997), depending on the local site (C. White et al. 1998; Kashian et al. 2007). Dr. Erin Lehmer and students from Fort Lewis College, Durango, are studying possible interaction among SAD, the abundance of deer mice, and the incidence of hantavirus (E. Lehmer, personal communication). For a general review of the ecology of aspen, see DeByle and Winokur (1985).

Mountain pine beetle is killing the older trees in mature lodgepole pine forests at a remarkable rate, with nearly a million acres (over 1,500 sq. mi.) in the high country affected (Colorado State Forest Service 2007). These changes doubtless will impact local mammalian populations. The changes compound deliberate and direct impacts of humans on subalpine ecosystems: mining, road and railroad building, and logging in earlier times, and development of winter resorts and high-speed highways more recently. Colorado's montane and subalpine forests appear to be under increasing stress from a complex combination of insect pests, changing climate, and human-influenced fire regimes and age structure (Romme et al. 2006; van Mantgem et al. 2009; Pennisi 2009). The Colorado State Forest Service reports annually on the status of Colorado's forested ecosystems (see Ciesla 2010).

In forests and other native ecosystems, exurban residential development is a major driver of habitat fragmentation in Colorado, and this has cumulative, negative impacts on native mammals (Theobald et al. 1997; R. Knight et al. 2000). Clustered development may prevent some of these impacts, as spatial pattern of houses was a more important factor in disturbance than was density of homes. Local initiatives like the Southern Rockies Ecosystem Project have been leading the effort to understand and then slow and even reverse the long-term trend toward anthropogenic fragmentation of Colorado's mountain landscapes (Shinneman et al. 2000; B. Miller et al. 2003).

Mammals. A number of mammalian species inhabit subalpine forests. Adaptations to winter include hibernation (yellow-bellied marmots, ground squirrels), seasonal color change (long- and short-tailed weasels, snowshoe hares), and use of runways beneath the snow (mice and shrews). Some species, such as least chipmunks and golden-mantled ground squirrels, prefer forest-edge situations to dense timber. Snowshoe hares select subalpine forests with a well-developed undergrowth of shrubs and forbs where they rest, hidden, during the day. They feed on the leaves and needles, twigs, and bark of the trees and shrubs. Yellow-bellied marmots inhabit rock piles in subalpine clearings, where they bask in the sun and make their hibernacula. Pine squirrels, or chickarees, prefer dense stands of lodgepole pines, spruce and fir, and Douglas-fir, where their chattering calls can often be heard before the squirrels themselves are seen. Southern red-backed voles prefer relatively dense coniferous forests, where they nest under logs, roots, and rocks. They are preyed upon by American martens, as are montane and long-tailed voles. Canada lynx (and wolverines, which may or may not persist in Colorado) are boreal forest predators, largely restricted in Colorado to this ecosystem. Lynx feed almost exclusively on snowshoe hares, whereas wolverines are omnivorous. Elk bed down in these forests during the warmer months.

Mammalian communities of the subalpine forest probably have received more attention than those of any other ecosystem type. D. Armstrong (1977a) reviewed some of the extensive older literature. Raphael (1987) reviewed non-game wildlife of subalpine forests, focused on Colorado and Wyoming. Vaughan (1974) studied differences in feeding strategies of four species of subalpine rodents. The northern pocket gopher (*Thomomys talpoides*) and the montane vole (*Microtus montanus*) were entirely herbivorous but preferred different plants of different sizes and foraged in different microenvironments. Least chipmunks (*Tamias minimus*) and deer mice (*Peromyscus maniculatus*) both ate seeds and arthropods but fed at different times. Roppe and Hein (1978) found species diversity in a subalpine burn to be higher than in adjacent forest. Stinson (1977a) described three periods of high mortality among subalpine small mammals: during spring thaw because of flooding, during summer because of higher physiological demands and predation, and during fall because of freezes. Merritt and Merritt (1978b) emphasized the importance of winter snow to population dynamics of small mammals. In the Upper Williams Fork Basin of Grand County, small mammals generally selected habitat according to structural features of the habitat (D. Armstrong 1977a). Work by D. C. Andersen, MacMahon, and Wolfe (1980) on small mammals in aspen, fir, and spruce forests and adjacent meadows in the Wasatch Mountains of northern Utah is generally relevant to the situation in Colorado, as is that by Nordyke and Buskirk (1988) and Raphael (1988) in the Medicine Bow Range of southeastern Wyoming. Lawlor (2003) provided a general review of ecology and biogeography of mammals in coniferous forests of western North America, and Halfpenny et al. (1986) published a thorough bibliography on the subalpine zone of the Colorado Front Range to that date. Troendle et al. (1987) provided a variety of review papers on important aspects of management, with special attention to the Fraser Experimental Forest in Grand County. Forest dynamics were reviewed by D. Knight (1994).

ALPINE TUNDRA

Dominant plants. Elk sedge (*Kobresia myosuroides*), alpine avens (*Acomastylis rossii*), Arctic willow (*Salix arctica*), tufted hairgrass (*Deschampsia caespitosa*), sedges (*Carex* spp.), American bistort (*Bistorta bistortoides*), alpine sandwort (*Arenaria obtusiloba*), marsh-marigold (*Caltha leptosepala*), old-man-of-the-mountain (*Rydbergia grandiflora*).

Alpine tundra occurs above subalpine forest. The ecotone between them is recognized as timberline (G. Stevens and Fox 1991). Tundra is distributed in Colorado as discontinuous "islands" of habitat and occupies less than 5 percent of the state. High winter winds lead to a dry environment characterized by sedges, grasses, low-growing willows, and low-growing perennials, which develop as cushion plants. Talus, rock outcrops, and areas of exposed, coarse, poorly weathered rock are common. The density of plant cover varies widely with microclimatic conditions, soil development, and moisture regime. Less precipitation falls on the tundra than on the adjacent forest because storm systems tend to move through mountain passes. Furthermore, the snow that does fall on the high peaks tends to be redistributed by wind, forming snowbeds interspersed with snow-free areas; some of the snow blows down into subalpine forests. Soils are subject to freeze-thaw action in spring and fall. This may lead to polygons of sorted ground as rocks are moved differentially according to their size. Much of this patterned ground effect was formed during glacial episodes of the Pleistocene. Because of its severe climate and inaccessibility, alpine tundra generally has less human activity than most other ecosystems, aside from mining and summer recreationists, including backpackers and off-road vehicle traffic. This ecosystem is fragile and highly susceptible to disturbance. Once disturbed, vegetation may take centuries to recover because of the dry, cold climate; short growing season; and slow formation of new soil (Zwinger and Willard 1972). For a review of alpine ecology focused on the National Science Foundation–sponsored Long-Term Ecological Research site on Niwot Ridge above Boulder, see Bowman and Seastedt (2001); the bibliography compiled by Halfpenny et al. (1986) provides access to the rich background literature. Bowman et al. (2002) provided a general appraisal of the ecology of tundra, including human disturbance. For an accessible introduction to Pleistocene environments of the Rockies, see Elias (1996).

PHOTOGRAPH 1-7. Alpine tundra, Rocky Mountain National Park, Larimer County. © 1993 Wendy Shattil / Bob Rozinski.

Mammals. Alpine tundra is a relatively inhospitable environment year-round but especially during winter. Adaptations include deep hibernation (yellow-bellied marmots), use of runways under the snow (mice, voles, and shrews), migration to lower elevations (elk, mountain sheep), and use of windswept, snow-free ridges (introduced mountain goats). In lieu of hibernation, pikas "make hay," accumulating large quantities of alpine grasses and forbs, which become critical in the event of a late snowmelt. Talus slopes provide cover and protection from predators. Northern pocket gophers feed on roots of perennial tundra plants, and their tunnels aerate the soil, contributing to the slow downward slumping of mountainsides. Montane and long-tailed voles range into the alpine tundra, where they are prey for coyotes and long-tailed weasels. Elk feed on tundra grasses and forbs on summer nights and move down to the forest edge during the day. Mountain sheep are well-known for their preference for remote, rugged areas and are found on the tundra during summer. I. Blake and Blake (1969) reported on alpine mammals of Mount Lincoln. Numerous autecological studies have been conducted on the tundra above Rocky Mountain Biological Laboratory at Gothic, Gunnison County. The tundra on Niwot Ridge west of Boulder has been the site of numerous autecological and community studies of mammals (summarized by D. Armstrong et al. 2001). Halfpenny and Southwick (1982) reviewed research on herbivorous small mammals of Niwot Ridge.

RIPARIAN AND WETLAND SYSTEMS

Dominant plants. Plains cottonwood (*Populus sargentii*), narrowleaf cottonwood (*P. angustifolia*), mountain willow (*Salix monticola*), Geyer willow (*S. geyeriana*), peach-leaved willow (*S. amygdaloides*), sandbar willow (*S. exigua*), broad-leaved cattail (*Typha latifolia*), bulrush (*Scirpus lacustris*), field horsetail (*Equisetum arvense*), saltgrass (*Distichlis spicata*), sand dropseed (*Sporobolus cryptandrus*), alder (*Alnus tenuifolia*), river birch (*Betula fontinalis*), rushes (*Juncus* spp.), water sedge (*Carex aquatilis*), beaked sedge (*C. utriculata*).

Riparian ecosystems occur locally throughout Colorado as corridors along rivers and streams (well-watered ribbons threading through other ecosystems at all elevations) and as islands of habitat adjacent to standing water, including ponds, lakes, and marshes. At lower elevations, riparian cottonwoods and willows contrast dramatically with adjacent treeless grasslands and shrublands. Riparian soils are variable. Prior to intensive hydrologic management, many riparian areas, especially at middle to low elevations, were subject to seasonal flooding (during times of intense rainfall or rapid snowmelt), with frequent overbank deposition of alluvial material.

PHOTOGRAPH 1-8. Riparian communities, Conejos County. © 1993 Wendy Shattil / Bob Rozinski.

At higher elevations, willows, alders, and sedges predominate adjacent to streams or other wetlands. This ecosystem is extremely rich in fauna because of the resources it offers: abundant food and water, cover, and travel routes. Riparian systems have the highest species richness of all major ecosystem types in Colorado, but they have the smallest areal extent, covering only 1 to 2 percent of the state. As favored sites for human residential, commercial, and industrial development, riparian lands have been extensively altered by introductions and invasions of non-native species (e.g., tamarisk or salt-cedar [*Tamarix gallica*] and Russian-olive [*Eleagnus angustifolia*]) and by livestock grazing, which significantly alters the structure of streambanks and can lead to substantial problems with erosion. Even greater changes result from dams and water-diversion projects. Knopf (1986) described "cosmopolitanism" of the avifauna along the South Platte near Crook, Logan County, since Euro-American settlement. No such dramatic change has occurred with the mammalian fauna, although there certainly must have been changes in species populations and local distributions. Knopf and Scott (1990) described historical changes in vegetation along the North and South Platte rivers. A thorough environmental history of Colorado's riparian ecosystems would be of great interest; rephotography holds great promise for such an effort (G. Williams 1978). D. Koehler and Thomas (2000) provided an extensive bibliography on riparian communities in the West.

Mammals. Riparian ecosystems of eastern Colorado are home to midwestern and eastern species (such as eastern cottontails, fox squirrels, and white-tailed deer) that have moved westward along these moist corridors with their abundant food and cover. Statewide, beaver, muskrats, and mink are dependent on waterways for shelter and food. Meadow voles are excellent swimmers and prefer moist, boggy areas, and jumping mice occupy riparian thickets. In western Colorado, riparian corridors carry some mountain species (montane and long-tailed voles, montane shrews, western jumping mice) to quite low elevations. Falck et al. (2003) studied small mammals of the regulated Green and unregulated Yampa rivers in Brown's Park, Moffat County, in the periods surrounding spring flooding.

Grazing can have substantial impact on habitat for native mammals, both game species and non-game species. Shultz and Leininger (1991) found differences in the mammalian assemblage between riparian areas grazed by livestock and those excluded from grazing along Sheep Creek, northwest of Fort Collins, at an elevation of 2,500 m (8,125 ft.). Deer mice were more abundant on grazed plots, but western jumping mice were more abundant in exclosures. Moulton et al. (1981b) found that grazing affected mammalian assemblages in riparian woodland more than in shortgrass prairie, and small mammals of grazed sand sagebrush were more similar to those in shortgrass prairie than to those of ungrazed sand sagebrush. Moulton (1978) found higher overall species richness in grazed (8 species) than in ungrazed (4 species) cottonwood riparian woodlands, although the prairie vole (*Microtus ochrogaster*) was negatively impacted by grazing. By contrast, F. Samson et al. (1988) found no difference in small mammal communities from grazing on a floodplain at the South Platte State Wildlife Area near Crook, Logan County. Contrary to the situation found in birds, mammalian species richness on upland shortgrass prairie is higher than that in nearby riparian communities (Olson and Knopf 1988).

Needless to say, dividing a place as complex and dynamic as Colorado into discrete ecosystems is a gross simplification of an almost incomprehensibly complex reality. Minimally, we should note that on their margins, Colorado's various ecosystems overlap or grade into each other. Ecologists term these zones of contact or overlap "ecotones" (from *tonus*, Latin for "tension"). Because of the complexity of the Coloradan fauna, ecotones clearly are high priorities for conservation. With ongoing climate change, such conservation areas need to be large enough to accommodate changes in the distribution of species. The Nature Conservancy of Colorado pioneered concrete action at significant scale with its Laramie Foothills Project, a complex of nature preserves and conservation easements in northeastern Colorado that eventually will provide a nearly continuous protected corridor from the Pawnee Buttes on the east to the Laramie Mountains on the west. A similarly large and dynamic landscape is being protected in a "Peaks to Prairie" project in the area east of Colorado Springs (for updates, see http://www.nature.org wherewework/northamerica/states/Colorado). Military lands (such as Fort Carson and the US Air Force Academy) protect substantial tracts of land in that same general area. Increasingly they are being managed with biodiversity as an important component of success. In a Ranching for Wildlife program, the Colorado Division of Wildlife partners with private landowners to ensure appropriate habitat management and to control access (Colorado Division of Wildlife 2009b). Each of these efforts eventually will contribute to the National Conservation System, now in a preliminary conceptual stage (Dunkel 2008), emerging from a growing consensus that wildlife require protected wildlands for persistence in changing times. *Colorado's Comprehensive Wildlife Conservation Strategy* (Colorado Division of Wildlife 2006a) was a first step toward wildlife habitat conservation on this visionary scale.

Biogeography: Patterns of Mammalian Distribution

Biogeography is the study of the patterns of distribution of organisms: Which species occur where? Why do they occur there? A mammal's presence in a particular place is a consequence of history, geology, physiography, climate, ecological relationships with plants and other animals, and the species' population dynamics. Geologic events have shaped the landscape. Physiography influences the occurrence of plant communities, which create past and present barriers and corridors to movement. Climate can restrict a species at its limit of tolerance. Chance may play a role, as in the documented movement of small rodents as stowaways aboard ships, trains, or hay trucks. Ecological relationships influence how species assemble into communities, a result of symbiotic interactions (competition, predation, and so forth).

Species diversity is a phenomenon of great interest to biogeographers. Two aspects of diversity are often recognized: *species richness*, the number of species in an area, and *species evenness*, which considers not only numbers of species but their relative abundance and is expressed by a variety of different indices (Magurran 1988). Species evenness varies widely over time and space and is too complex to generalize here, except that within a particular community type, species evenness is likely to be lower in disturbed areas than in undisturbed patches (D. Armstrong 1993). Species richness varies greatly with taxonomic group. Within historic times, Colorado has been home to some 130 species of mammals (4 of which have been introduced: 2 of them deliberately, 2 of them inadvertently), 428 species of birds, 50,000 to 100,000 insects, and 3,000 kinds of plants. For comparison, the approximate number of mammals in adjacent states is, for Wyoming, 115 (Long 1965; T. Clark and Stromberg 1987); Nebraska, 85 (J. K. Jones 1964; J. K. Jones, Armstrong, et al. 1983); Kansas, 84 (Cockrum 1952; E. Hall 1955; Bee et al. 1981); Oklahoma, 108 (Caire et al. 1989; L. Choate and Jones 1998); New Mexico, 151 (Findley et al. 1975; J. Frey and Yates 1996; Findley 1987; J. Frey 2004); Arizona, 138 (Cockrum 1960; Hoffmeister 1986); Utah, 126 (Durrant 1952; D. Armstrong 1977a). As a general rule, the more heterogeneous the landscape in a given area, the higher the species richness.

Individual organisms have genetic information in the nuclei of their cells that tells them how to make a living: how to survive and how to reproduce. No species has genetic information adequate to provide the know-how to operate in all environments. Because they have finite information, species reach distributional limits in the landscape. The limit at a particular time and place may be biotic or physical or some combination of factors. Often we do not know why a particular organism occurs one place but not another, although sometimes we can speculate. The range of tolerance of most species is fairly restricted. Brush mice (*Peromyscus boylii*) in Colorado live almost exclusively under the cover of oakbrush, whereas piñon mice (*Peromyscus truei*) are strongly associated with juniper trees. On the Eastern Slope, north of the Palmer Divide (between Colorado Springs and Castle Rock), both oakbrush and juniper trees occur, but neither of these mice is found. Perhaps they cannot (and could not) get to the suitable habitat because of the intervening ponderosa pine woodland on the Palmer Divide. Perhaps the seemingly suitable habitat is not really suitable at all because it is too cold. We simply do not know.

A few species (such as coyotes, striped skunks, and mule deer) are notorious for being broadly tolerant of a wide range of habitats. The deer mouse (*Peromyscus maniculatus*) is another species that occurs just about everywhere. However, the deer mouse may be scarce or absent where one or more of its larger, more specialized relatives occurs. Further, on closer analysis, it seems that deer mice do particularly well in disturbed areas. The disturbance may be of human origin (a highway margin, a vacant lot, or an overgrazed pasture) or it may be a natural disturbance (e.g., a floodplain or an avalanche chute). Any kind of disturbance seems to favor deer mice.

Because all species reach limits, it is possible to map (at least crudely) distributions of species. Biogeographers can then analyze distribution maps to reveal patterns. Patterns may indicate the history of the system or they may suggest physical factors controlling the distribution of organisms. Biogeographers frequently describe large-scale patterns of distribution in terms of biotic provinces (Dice 1943). D. Armstrong (1972) analyzed Colorado's mammals in an analogous way, identifying three major faunal areas (provinces), each subdivisible into smaller units, termed "faunal districts."

Not surprisingly, faunal areas correspond with physiographic units. The Great Plains Faunal Area is subdivisible north-south by the divide between the South Platte and Arkansas rivers, forming faunal districts marked by different subspecies within a number of mammalian species and by the presence of some species only in one watershed or the other. The Colorado-Wyoming border (Northern High Plains Faunal District) and southeastern Colorado (Raton Faunal District) both are distinctive. The latter area is strongly enriched with species of southwestern affinities, species that also extend northward along the foothills of the Eastern Slope; the northern high plains carry some foothills and mountain species eastward.

The Rocky Mountains are a coherent faunal unit, although dissected by valleys and canyons of the master streams. Major valleys of the Western Slope are distinctive from the Rockies as well as from each other. The Grand Valley and Dolores–San Juan faunal districts exhibit strong resemblance to areas downstream on the Colorado Drainage—the Four Corners area generally (see D. Armstrong 1972). The San Luis Valley, a high, cold desert, is unique in Colorado, but it has strong faunal affinities with both southwestern and southeastern parts of the state, indirectly through the Rio Grande Valley of New Mexico. The Wyoming Basin shows faunal affinities to the northwest, to adjacent Utah and Wyoming and beyond. Generally, environmental change is rapid in Colorado, and faunal turnover is more than 80 percent along particularly dramatic boundaries, such as the abrupt transition from the Great Plains to the Rocky Mountains along the Front Range.

Spector (2002: 1481) defined "biogeographic crossroads" as "regions where biogeographic assemblages intersect." Because the mammalian fauna of Colorado is complex and includes species with a spectrum of biogeographic affinities, the state has been called a "crossroads," but that is perhaps too simple a metaphor. Some three-fourths of Colorado's mammalian species do not cross the state—they simply stop here. For a quarter of the state's species, the Southern Rocky Mountains represent a sort of "remote parking lot," where species from the north or the mountainous West occupy an island of suitable habitat surrounded by an impassable "sea" of grasslands and sagebrush. Another quarter of Colorado's mammals are stuck in "dead ends" of brush-covered roughlands along the foothills of the Eastern Slope, in western valleys, or in the semidesert San Luis Valley. Remember, species occur where they do because they could get there, and once there, they could make a living—maintain homeostasis and reproduce.

Ecology is about patterns in space, and patterns imply processes in time. The ecological patterns that we discern today are but an interim report on processes as old as the planet. Chapter 3 includes a brief account of some episodes in the ongoing history of mammals in Colorado, a story already a quarter of a billion years long (and a story that is now strongly influenced by humans).