California

This chapter presents information on that part of California to the west of the crests of the Peninsular Ranges, Transverse Ranges, Sierra Nevada, and Cascades. This portion of California, which makes up 70% of the state, is referred to as cismontane California or, more simply, westside California. Portions of California excluded from this chapter include the northern steppe to the east of the Cascades and Sierra Nevada, as well as the Mojave Desert—these areas are discussed in the Great Basin chapter. The Colorado Desert, to the east of the Transverse and Peninsular ranges of southern California, is discussed in the Southwest chapter. For some considerations of animals or plants, we also discuss species found in eastside California or discuss the diversity of the state as a whole.

The state of California encompasses 411,015 square kilometers and is 1,326 kilometers long from corner to corner (Donley et al. 1979; Kreissman 1991); westside California covers 287,560 square kilometers of this area (Raven 1977). Westside California is an ecological island: its complex geology and topography, biogeographic history, and Mediterranean climate combine to make the state's animals and plants distinctive (Bakker 1972). Many groups of westside California's native animals and plants exhibit both a high level of uniqueness or endemism and a high total species richness, yet some groups are relatively poor in numbers of species compared with other regions of the United States. Like true island species, many of California's endemic animals and plants do not fare well against the competition of invading nonindigenous species (see chapter on Nonindigenous Species; Bury and Luckenbach 1976; Moyle 1976a; Bradford et al. 1993).

From east to west, westside California stretches from the crests of the Cascades, Sierra Nevada, Transverse Ranges, and Peninsular Ranges to the Pacific Ocean. The Cascades are not a continuous range in California but are variously elevated volcanic flows and cones punctuated by two impressive volcanic peaks, Mt. Shasta (4,305 meters) and Mt. Lassen (3,187 meters), which is still active. The Sierra Nevada is a more impressive, continuous barrier, with boreal conditions extending its full length from southern Plumas County south to Tulare County. The Transverse and Peninsular ranges of southern California are not as high or as continuous as the northern California mountains, but there is still a clear dividing line between the coastal Mediterranean climate and the more rigorous interior continental climate.

Between the dividing mountain crests lies the Central Valley (the combined valleys of the Sacramento and San Joaquin rivers), and beyond it the Klamath Mountains in the north and the complex Coast Ranges to the south. Immediately west of the Coast Ranges lies a relatively narrow Coastal Plain and the Pacific Ocean. In southern California, the Transverse Ranges interrupt the Coast Ranges and form the southern limit of the Central Valley. Only a narrow strip of westside California occurs south of Los Angeles. The often spectacular California coastline is alternately rocky (Fig. 1) and sandy—mostly rocky to the north and more sandy to the south. Where rivers and smaller drainages reach the coast, there may be protected bays, salt marshes, and coastal dunes. Off the coast of southern California lie the Channel Islands, most of which are now a national park.

Fig. 1. Rocky coastline, Carmel, California.

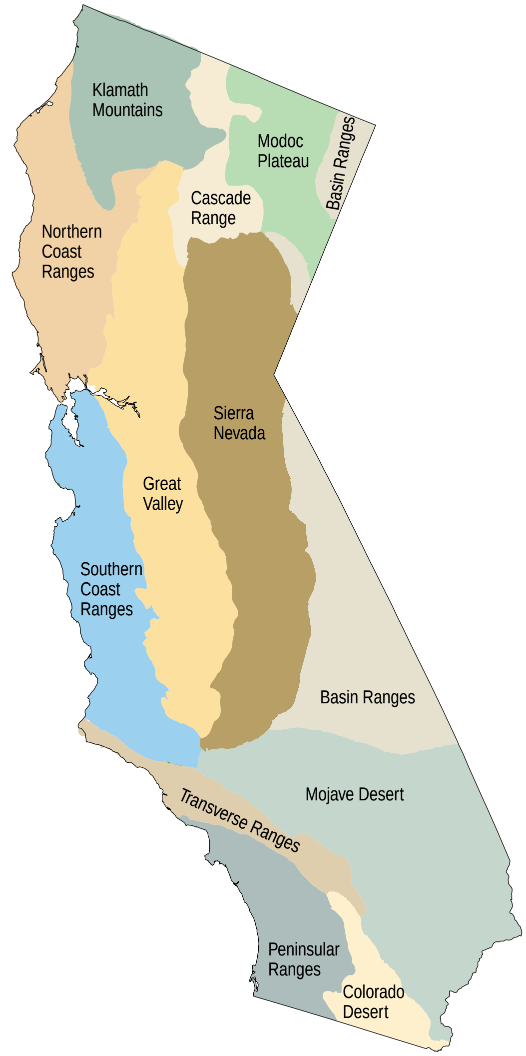

Fig. 2. Physiographic regions of California (after Jenkins 1952).

Environments and History

With 12 physiographic regions (Jenkins 1952; Fig. 2) from high mountains, foothill woodland, chaparral, moist forests, and an alternating rocky and sandy coast, California has high topographic diversity, including the highest land in the conterminous 48 states (Mt. Whitney—4,406 meters). Huge differences in daily and annual temperatures, precipitation, and evaporation have led to strongly differing vegetation patterns (Major 1977) and centers of plant endemism (Stebbins and Major 1965).

Climate

Westside California has a Mediterranean climate, typified by winter and spring precipitation and summer drought (Sprague 1941; Bailey 1966; Gilliam 1966; Major 1977; Mallette 1981). In the Sierra Nevada below about 1,000 meters elevation, precipitation usually falls as rain, whereas above that elevation it falls as snow in winter. Annual precipitation is greatest along the north coast and at middle elevations (2,000 to 2,500 meters) on the west slope of the Sierra Nevada (as much as 1,500 to 2,800 millimeters per year). The least amount of precipitation occurs at low elevations in southern California and in rain shadows along the eastern slopes of the southern Coast Ranges (as little as 140 to 275 millimeters per year). Along the coast, dense fog is common during spring and summer. Moisture-laden offshore breezes emanate from the Pacific High, an offshore high pressure zone, and then move across coldwater upwelling zones to form these fogs (Gilliam 1966), which pour through gaps in the Coast Ranges and bring as much as 200 millimeters of additional moisture in the form of *fog drip* (Azevado and Morgan 1974) along the coast. Coast redwood is limited to this fog belt along the coast from Point Sur north to extreme southern Oregon (Griffin and Critchfield 1972). Most of westside California is dry from May through August, but summer thunderstorms produce small amounts of precipitation at higher elevations in the Sierra Nevada.

Topographic Features

Most of westside California's topographic relief may be explained by the juxtaposition of the Farallon and North American tectonic plates along the western edge of the state (Howard 1979). The crustal movements of these plates give rise to earthquake fault zones (including the well-known San Andreas Fault), volcanoes, and mountain building through faulting or crustal folding (Howard 1979).

Westside California's topographic relief can be divided into nine subregions: the Sierra Nevada, Cascade province, Klamath Mountains, Central Valley, San Francisco Bay and delta, Coast Ranges, California Channel Islands, Transverse Ranges, and Peninsular Ranges. The subregions do not necessarily coincide with vegetation provinces or ecoregions.

The most notable topographic feature of westside California is the Sierra Nevada, a mountain range that extends roughly 650 kilometers from southern Plumas County to north-central Kern County (Storer and Usinger 1964; Howard 1979). The Sierra Nevada is a large granite block that faulted and tilted up along its eastern edge, primarily during the Pliocene and Pleistocene, beginning about 5 million years ago. From the west, the range rises gradually (2%–3% slopes) over its 70- to 90-kilometer east–west breadth but rises dramatically and precipitously along its eastern escarpment (Storer and Usinger 1964; Howard 1979).

Running north from the Sierra Nevada toward the Oregon Cascades (see chapter on Pacific Northwest) is a portion of the Cascade province that consists largely of dissected lava flows of early Tertiary origin and is punctuated by Mt. Lassen and Mt. Shasta, two volcanic cones that rise dramatically above the surrounding landscape (Howard 1979).

The Central Valley, drained by the San Joaquin River in the south and the Sacramento River to the north, lies between the Sierra Nevada and the Coast Ranges. It is a mostly flat plain, 60–120 kilometers wide, which extends about 680 kilometers from Shasta County south to Kern County (Howard 1979). Its elevation ranges from about sea level to a few hundred meters. The soils of the Central Valley consist largely of alluvial sediments derived from various Sierra Nevada uplifts and subsequent erosions (Howard 1979). Where the San Joaquin and Sacramento rivers join and flow westward toward the Golden Gate and the Pacific Ocean, an alluvial delta with alluvial, sandy, or peat soils has formed, braided with sloughs that form numerous islands.

In the northwest corner of California, extending into extreme southwest Oregon, is the Klamath Mountain block, which includes several subsidiary ranges—the Marble, Salmon, Scott, Scott Bar, and Siskiyou mountains; the Trinity Alps; and Mt. Eddy. This block consists mainly of ancient metamorphic and plutonic rocks and is the oldest geomorphic feature in westside California (Hickman 1993). The Klamath Mountain block extends about 200 kilometers south of the Oregon boundary and abuts against the largely sedimentary northern Coast Ranges near the upper headwaters of the South Fork of the Trinity River.

The Coast Ranges are a series of large mountain ranges oriented north to south and extending from the southern limit of the Klamath Mountain block for roughly 720 kilometers south to the Cuyama River, which forms the San Luis Obispo County–Santa Barbara County boundary. These ranges are complex, primarily folded fault blocks composed largely of sedimentary formations with some volcanic intrusions such as Mt. Konocti (1,310 meters) and Mt. Diablo (1,173 meters). Lying between these ranges are north–south-oriented valleys filled with recent alluvial soils. The Coast Ranges, with a few exceptions, lie below 2,000 meters.

The San Francisco Bay and delta include the Sacramento River–San Joaquin River delta, several water bodies and associated wetlands (including San Francisco Bay, San Pablo Bay, and Suisun Bay) that lie between the delta and the Pacific Ocean, and the adjacent low hills. All of the water bodies are tidally influenced well into the delta, and there is a gradual gradation from the seawater that occurs at the entrance of the Golden Gate upstream to the brackish waters of the delta and the fresh water to the east. The hills surrounding the bay are primarily of recent alluvial origin, but other formations are present, including sandstones and serpentine outcrops (Howard 1979).

California has relatively few offshore islands. The Channel Islands occur off the coast of southern California and comprise four northern islands (Anacapa, San Miguel, Santa Cruz, and Santa Rosa) off Santa Barbara and Ventura counties, and four southern islands (San Clemente, San Nicolas, Santa Barbara, and Santa Catalina) off Los Angeles and San Diego counties. The islands are low and generally rolling, with maximum elevations of no more than a few hundred meters, although some islands have steep cliffs. Most of the islands are now included in Channel Islands National Park.

The Transverse Ranges are mainly oriented east to west. These granitic ranges lie between the southern terminus of the Coast Ranges and the Los Angeles basin and trough (Jaeger and Smith 1966), from near the coast inland to the western and southern edges of the Mojave Desert. They include the San Gabriel Mountains, San Bernardino Mountains, Mt. Pinos, and the Santa Ynez, Topatopa, Santa Susanna, Santa Monica, and Liebre mountains. The mountains of the Transverse Ranges are geologically complex, and some reach elevations of more than 3,000 meters, such as Mt. San Gorgonio (3,506 meters) and San Antonio Mountain, which is also called Mt. Baldy (3,068 meters).

The Peninsular Ranges include several more or less north–south-oriented, largely granitic ranges that lead toward the Sierra Juarez of Baja California Norte, Mexico, and that separate the narrow strip of westside California between Los Angeles and the Mexican boundary from the Colorado Desert to the east (see chapter on Southwest). The Peninsular Ranges include the Laguna, San Jacinto, Santa Ana, Santa Rosa, and Vallecito mountains (Jaeger and Smith 1966). Exceptionally high Peninsular Range peaks include Mt. San Jacinto (3,286 meters) and Santa Rosa Mountain (2,452 meters). The low-elevation gaps and passes that occur between the various Peninsular Ranges have allowed some desert animals and plants to extend their ranges almost to the relatively arid southern coast.

Faunal and Floral History

During the Tertiary (65 million to 1.6 million years ago) the area that is now California slowly changed from wet tropical conditions to a more arid environment (Axelrod 1977; Wilken 1993). At that time, westside California had an impressive vertebrate fauna that included such species as sabertooth cats, mammoths, camels, giant bison, rhinoceroses, ground sloths, and ancestors of modern horses and pronghorns (Stirton 1951).

Fossil plant remains tell us that 75 million years ago (near the beginning of the Tertiary), the westside California flora was composed of three major floral elements—the Neotropical-Tertiary Geoflora, the Arcto-Tertiary Geoflora, and the Madro-Tertiary Geoflora (Raven 1977; Raven and Axelrod 1978). As conditions became more arid during the Tertiary, elements of the Neotropical-Tertiary Geoflora disappeared from California; today their relatives are found in the humid tropics of Mexico and Central America. Elements of the other two geofloras evolved in California and became mixed in various ecosystems and habitats with Arcto-Tertiary elements and their derivatives, which tend to be found at higher elevations and at locations with higher precipitation. Madro-Tertiary elements and derivatives tend to be found at lower elevations and at locations with lower precipitation (Axelrod 1977; Raven 1977; Raven and Axelrod 1978; Wilken 1993).

The uplift of the Sierra Nevada was a major geologic event, separating much of westside California from the Great Basin steppe to the east (Hinds 1952). This uplift, which began in the Pliocene (5 million years ago) and accelerated during the Pleistocene (1 million years ago), formed a significant topographic barrier and made considerable changes in the climate on both sides of the mountains (Gilliam 1966; Howard 1979). Species adapted to arid conditions were largely isolated to the east in the range's rain shadow, whereas species adapted to Mediterranean climates were confined to the west side.

The ancestors of California's present plants and animals were largely in place before the Pleistocene ice ages (up to 1 million years ago), when most of westside California did not experience ice sheet advances, and only the high Sierra Nevada experienced valley glaciers, as in Yosemite Valley (Hinds 1952).

Stebbins and Major (1965) analyzed the genetic variability and origins of modern California's endemic plants and divided them into paleoendemics—those species of ancient origins—and neoendemics—those species that have evolved relatively recently in California or in nearby regions. Predictably, paleoendemics are concentrated in the ancient Klamath Mountain block of northwestern California and the low deserts of southern California, and neoendemics are concentrated in relatively young geological formations in the central portion of westside California.

Human History

Human occupation of California has increasingly altered the state's natural resources since the first human occupation of the land 11,000–12,000 years ago (Eargle 1986). The number of Native Americans at the time of European or European-American contact is estimated at 300,000. Today the human population of the nation's most populous state is nearing 32 million and is likely to continue increasing.

Before European contact, more than 100 Native American tribes inhabited California (Rawls 1984). They modified local landscapes by burning vegetation and by hunting and gathering. Tribes in the northwest part of the state were culturally similar to those of the Pacific Northwest. The northeast part of the state was thinly populated, and life there was difficult because of the harsh climate. Peoples of the Central Valley lived a relatively sedentary, peaceful life. Their staple food was meal made from acorns of the valley oaks. Southern California was the most populous part of the state, especially along the coast, where people survived primarily on marine resources.

Although the first Spanish explorers reached California in 1542, and Sir Francis Drake landed near San Francisco Bay in 1579, European colonization did not begin until the Spanish Franciscan missionaries arrived in 1769 (Rawls 1984). Over the next few decades, the Franciscans built 21 missions along the coast from San Diego to San Francisco. These missions served religious and secular purposes: to protect Spanish interests in the area, as well as to convert the natives to Christianity and make them "useful" citizens of the Spanish empire. Native Americans were relocated near the missions and forced to work. Nearly two-thirds of the native population died as the result of introduced diseases (Rawls 1984).

The mission period ended in 1821, when Mexico became independent from Spain. In the years that followed, the Mexican government made many private land grants in California, and Mexican landowners emigrated to Alta (upper) California. Many of the remaining native people worked as bond laborers on Mexican haciendas (Eargle 1986). Spanish and Mexican exploration and colonization in the eighteenth and nineteenth centuries brought ranching and agriculture and the first of a stream of nonindigenous plants and animals to California.

In the early 1800's American trappers arrived in the state, attracted by the wealth to be had from selling sea otter and beaver pelts. Both animals were trapped to near extinction. By 1841 settlers from the eastern United States were arriving in California via the Oregon Trail. Mexico ceded title to California to the United States in 1848; in the same year, gold was discovered at Sutter's Mill, resulting in a flood of prospectors, miners, farmers, merchants, and their families. The European–American population of California grew from 15,000 in 1848 to 380,000 by 1860 (Eargle 1986).

The remaining Native American population suffered greatly from this influx of settlement and development. Whole tribes were exterminated or displaced by settlers who considered them an impediment to development, and during the mid-nineteenth century, many were sold into slavery. Reservations were set aside as early as 1853, but only in the latter part of the nineteenth century were tribal lands secured by the federal government and aid made available for the remaining native peoples in California (Eargle 1986).

Experience with hydraulic gold-mining techniques, combined with the region's rainless summer climate pattern, quickly encouraged industrious settlers to control and divert the rivers for agricultural uses. By 1867 miners had constructed 6,780 kilometers of water ditches and canals (Kahrl 1978). A little more than a hundred years later, almost all of the Central Valley, the large coastal valleys, and the Imperial-Coachella Valley were under irrigation (Donley et al. 1979). In addition, most of the larger rivers and streams—except the Smith River, which drains to the Pacific near the well-watered California–Oregon border—were dammed and regulated.

Through the last half of the nineteenth century and until the 1930's, native populations of many game animals were greatly reduced by subsistence and market hunting to support the growing human population. Populations of native species—from elk, deer, ducks, and geese to frogs and fishes—were shot, gigged, and netted, and sold fresh, dried, or canned to the growing urban populations. Populations of many game species declined until fish and game laws, habitat protection, and game management practices were introduced to protect fragments of the once amazing array of native wildlife. As trade and commerce grew in California, cities also grew, and forests were exploited to supply sawmills with the timber necessary for local construction and also for timber export around the Pacific Rim.

Today, almost all of California's rivers are dammed and fed into federal and state water distribution systems, providing water for the state's intensive agriculture and extensive urbanization. The Central Valley rivers are diked to provide flood control for the farms and cities that now occupy land that was once seasonally flooded. Twentieth-century urban development has claimed much of the southern coast and the area around San Francisco Bay. Millions of hectares of native grasslands, marshes, and seasonal wetlands in the Central Valley and delta—habitats formerly home to native herbivores and large migratory waterfowl populations—have been converted to agriculture. Grizzly bears no longer occur in the valleys and the foothills of the region, and anadromous fisheries of the watersheds draining the Sierra Nevada have much-reduced runs of salmon and other native fishes. As water supplies were acquired by large development interests with the political and financial ability to move water to the semideserts of southern California, the growth of cities and agriculture greatly accelerated, resulting in the loss of the incredible richness of the Central Valley.

As the population increased, so did the harvest of Sierra Nevada and Coast Range forests. Early logging for homesteads and mining activities expanded to accommodate construction of railroads and cities. By the late 1800's, however, some people began to fear that some of the world's most majestic forests and scenic places would be completely destroyed and therefore advocated the establishment of parks on the forested slopes and glaciated valleys of the Sierra Nevada, beginning with Yosemite in 1890 (Fig. 3), and in the coast redwood forests, including California Redwood Park (Big Basin Redwood State Park) in 1902 and Muir Woods National Monument in 1908. Although early timber harvest was extensive, improved logging equipment, better roads, tractors, and trucks

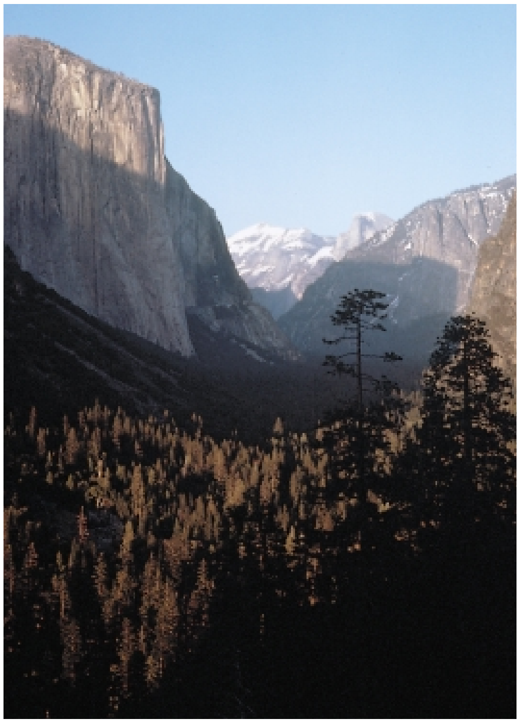

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Fig. 3. El Capitan and Half Dome in Yosemite National Park.

combined to feed the more demanding needs of the building boom after World War II. From 1950 to 1975, approximately 5.3 billion board feet of lumber were produced annually from California forests (Donley et al. 1979).

Status of Ecosystems

Many ways have been proposed to divide westside California into ecological subgroupings or ecosystems (Van Dyke 1919; Dice 1943; Munz and Keck 1949, 1950, 1959, 1968; Küchler 1977; Bailey 1995). The complex patterns of vegetation have been variously classified; Munz and Keck (1959, 1968) identified 29 plant communities in 11 vegetation types. Küchler (1977) classified California's natural vegetation into 54 communities with nine formations. More recently, Bailey (1995) divided westside California into five provinces.

We follow Hickman's (1993) divisions, which refer to all of terrestrial westside California as the Californian Floristic Province and divide the region into six smaller subregions that combine the major topographic features discussed previously. Each of the regions is divided at least once, and several have a further hierarchical geographic division so that, in all, 27 subdivisions are recognized. Even within each subdivision, though, there are hundreds of distinctive communities or formations with characteristic plants and animals, each based on local climate, soils, elevation, and exposure (Munz and Keck 1959, 1968; Barbour and Major 1977). The California Native Plant Society's Inventory of Rare and Endangered Vascular Plants of California is the most comprehensive source of available information and is regularly updated (Skinner and Pavlick 1994). The society's new publication on California vegetation (Sawyer and Keeler-Wolf 1995) begins to address the relative status of plant communities in California and provides systematic methods for their description.

The most human-altered ecosystems in California are those that have been affected by grazing and agriculture, followed by those susceptible to urbanization and timber harvest. Noss and Peters (1995) report significant reductions in the native vegetation of several westside California plant communities and formations (Table 1). Endangered plant communities in southern California include grasslands, coastal sage–scrub, riparian woodlands, and estuarine wetlands (Schoenherr 1990). In most instances, except coastal redwood forest, native vegetation has been replaced by nonindigenous vegetation, croplands, or development.

Table 1. Human-caused reductions in westside California plant communities and formations (after Noss and Peters 1995).

Community/formation	Vegetation reduced (percent)
Native grasslands	99
Needlegrass steppe	99.9
Southern San Joaquin Valley alkali sink scrub	99
Southern California coastal sage–scrub	70–90
Vernal pools	91
Wetlands	91
Riparian woodlands	89
Coast redwood forest	85

Awareness of the relationship among habitat conversion and fragmentation, and the endangerment of habitat-limited, narrowly distributed, or ecologically specialized plants and animals has led to an increased effort by public entities and private developers to deal with land-use issues on bioregional and ecosystem bases. For example, the interagency California Natural Areas Coordinating Committee divided the state into 11 bioregional planning areas in 1990 (Fig. 4), and in 1991 California adopted a bioregional strategy for resource conservation of biodiversity; this strategy involves both California and U.S. agencies (California Governor Pete Wilson, press release, Sacramento, 1991).

Much of the high-elevation forests in the Sierra Nevada, Cascade Range, and Klamath Mountains, and in the drier southern California mountain ranges, were only lightly developed and were eventually included in the national forest system, which is now composed of some 9,161,910 hectares, about one-fifth of California. Much of the land considered to be of

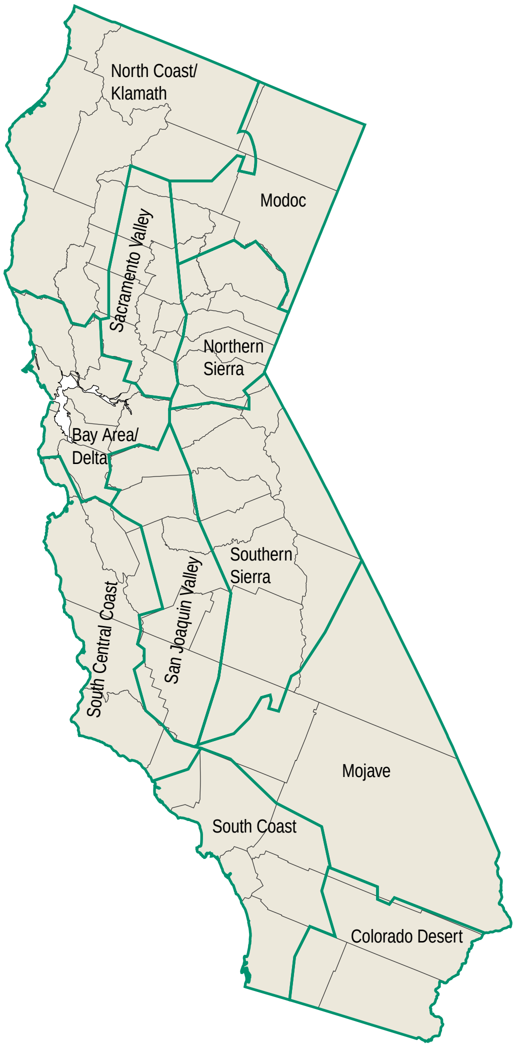

Fig. 4. Bioregional planning areas in California.

lesser economic value in the last century has now become the relatively unaltered wilderness and natural areas conserved within national parks, national forests, and Bureau of Land Management wilderness areas.

Ecological Provinces

Northwestern California

Northwestern California has the wettest, most consistent climate in the state. It is composed mainly of the coastline and several metamorphic mountain ranges, including the Klamath Mountains and the north Coast Ranges. The coastal region, from the Oregon border south to Bodega Bay, is dominated by areas of coastal prairie (Fig. 5), some coastal marsh, closed-cone pine and cypress forests on poor soils, and grand fir–Sitka spruce forests on better soils (Hickman 1993). In California, serpentine soils are common in isolated patches where intrusions of molten material forced their way into the Earth's crust. In these areas, the reddish or greenish rock usually weathers into infertile soils that are high in magnesium and poor in phosphates, potassium, and calcium and are often too thin to hold moisture. Only the hardiest plants can live on these serpentine soils, where they benefit from the absence of competing plants and the absence of many harmful soil organisms (Bakker 1972; Fig. 6).

The closed-cone pines and cypresses form unique communities scattered along the coast, mountains, and islands (Fig. 7). Many of the closed-cone pines and cypresses are endemic (8 of the 10 species of cypress), including Santa Cruz, Modoc, Tecate, Monterey, and Sargent cypresses, as well as knobcone pine, bishop pine, and Monterey pine, a species that is widely planted in reforestation projects all over the world. All of these species are dependent on fire for regeneration and are relicts of a previously more widespread ecosystem that retreated when the climate changed in the Tertiary (Vogl et al. 1977).

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Fig. 5. Coastal prairie, Point Reyes National Seashore.

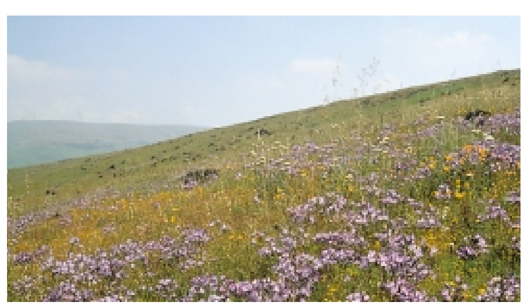

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Fig. 6. Serpentine grassland, Santa Clara County.

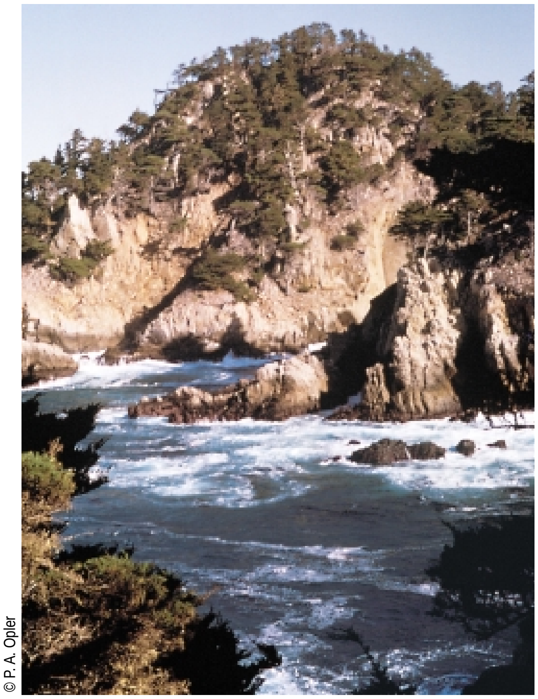

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Fig. 7. Monterey cypress in Point Lobos State Preserve, Monterey County.

Most of the cypress and closed-cone pine forests in California were part of Spanish and early American ranches and have been grazed by domestic livestock. Because the trees are generally dwarfed and gnarled in form, they have not been logged except occasionally for fenceposts and firewood. The most significant human effects on these forests have come from suppression and alteration of fire (Vogl et al. 1977; see box on Torrey Pine).

Many of the cypress groves are associated with chaparral, rock outcrops, or serpentine soils. Cypress seeds are sealed inside their cones with resin; they do not germinate in litter but require bare mineral soils. Cypresses are intolerant of shade and do not reproduce well in the absence of fire. Although cypress trees are usually killed by fire, their cones open when heat from the fire melts the resin. During the following months, the seeds drop, creating dense stands of seedlings. Recently though, some cypress groves have become smaller, possibly because these cypress species could be continuing the natural decline they have experienced since the Tertiary by becoming more restricted in their range following every unfavorable event (for example, fire suppression and ecological changes caused by grazing). In addition, fire suppression over the last century has altered fire frequencies and intensities in the groves, creating less favorable conditions for cypress reestablishment (Vogl et al. 1977).

The closed-cone pines are generally small in stature and, like the cypresses, are associated with chaparral, fire, and shallow, acidic, nutrient-poor soils, often serpentine or sandstone. These pines are short-lived (50–100 years), and their seeds can only germinate on bare mineral soils. Like the cypresses, the closed-cone pines require fire for successful reproduction. Their cones remain attached to the parent tree for years and are sealed shut with resin, rarely opening unless the resin is melted by fire (Vogl et al. 1977). Knobcone pine is the most widespread of the closed-cone pines, ranging nearly the length of the state.

The Klamath Mountains are geologically old and support mixed evergreen forests of Douglas-fir, ponderosa pine, and sugar pine, with mountain hemlock, white fir, and chinquapin found at higher elevations. Serpentine soils are common in the Klamath Mountains. On the west side, Douglas-fir–hardwood forests grow at low elevations, giving way at higher elevation to white fir–Douglas-fir forests, white fir–California red fir forests, and finally to mountain hemlock–California red fir at the highest elevations. East and south of the highest ridges, the climate is drier and more continental. At low elevations, forests are dominated by ponderosa pine, which is replaced by white fir–pine forests at higher elevations, then red fir–white fir forests, and finally mountain hemlock–red fir, with whitebark pine occurring at the highest elevations. The Klamath Mountains have a high floristic diversity, in part because they have acted as refugia supporting many endemics and relict species, including Pacific silver fir, subalpine fir, Alaska-cedar, Brewer spruce, Engelmann spruce, and foxtail pine. The complex vegetation patterns in the Klamath Mountains seem based primarily on differences in soils and secondarily on elevation and soil moisture (Sawyer and Thornburgh 1977).

The northern Coast Ranges occur immediately south of the Klamath Mountains. Coast Range forests do not include hemlock and have noble or red fir replacing grand fir, with rhododendron replacing chinquapin in the understory. Hardwoods increase in frequency on the drier slopes inland. The outer northern Coast Ranges, those farthest to the west, receive a great deal of rain (Hickman 1993).

Riparian areas and north-facing slopes of the Coast Range fog belt support redwood forests (Fig. 8), which thrive where coastal fog is frequent. Redwood is a California endemic and is the tallest (112 meters) and fastest-growing tree in the world (Zinke 1977); one of these trees may live more than 2,000 years (Bakker 1972). Although redwoods were common in the Tertiary over much of North America, they are now restricted to the fog belt of maritime central and northern California. Proximity to the sea moderates temperatures, and fog helps prevent evapotranspiration (moisture loss from leaves). Fog drip contributes considerable


Courtesy M. Madej, USGS

Fig. 8. Coast redwood forest.

moisture to the soil during the otherwise dry summer season (18–30 centimeters per year; Zinke 1977). The continuous moisture enables redwood forests to be home to a number of amphibians, including ensatinas, ocelot-spotted giant salamanders, tailed frogs, and seep salamanders, as well as the more common banana slugs (Bakker 1972).

Redwoods have thick, nonresinous bark, and mature trees are able to withstand fires. Redwood seedlings are tolerant of shade and germinate on logs and root wads rather than in the duff that accumulates under mature trees. Redwoods also sprout from basal buds if the main trunk is damaged or killed by fire (Veirs 1982). Redwoods are also very resistant to feeding by herbivorous insects. Douglas-fir is often a codominant in redwood forests, becoming established after fires, and tanoak, California bay, madrone, and western hemlock are common understory trees where enough light penetrates the canopy (Zinke 1977; Fig. 9).

Redwood is a valuable timber tree because of its size and because of the wood's unique resistance to rot. More than 85% of the old-growth coast redwood forests has been logged, but much of the original distribution of about 810,000 hectares remains in second-growth redwood forests of varying ages. Second-growth redwood forests support most of the same native vascular plants as old-growth forests, but habitat for species that depend on old-growth forests—such as spotted owls, marbled murrelets, some arthropods, mollusks, and canopy lichens—has been greatly reduced (U.S. Fish and Wildlife Service 1995a). Logging of redwood continues, although most old-growth stands are now protected in state parks and in Redwood National Park.

Drier slopes of the Coast Ranges support mixed-evergreen and mixed-hardwood forests, whereas montane forests of subalpine fir and pines are found at higher elevations. Vegetation on the highest peaks is similar to that found at high elevations in the Sierra Nevada; peaks


Courtesy M. Madej, USGS

Fig. 9. Coast redwood forest with rhododendron understory.

above 1,500 meters are treeless and experience heavy winter snows. Summers are hot and rainfall is low in the inner northern Coast Ranges, especially on eastern slopes in the rain shadow of the peaks. Serpentine soils are common, and dry eastern slopes support chaparral and pine–oak woodland. (Hickman 1993).

Cascade Ranges

The Cascades are volcanic mountains to the east of the Northwest province. The foothills, ranging in elevation from 100 to 500 meters, support a mosaic of chaparral and blue oak–foothill pine woodland. The southern foothills form an ecotone with the grasslands on the north and east end of the Central Valley. The high Cascades, above 500 meters, support forests of ponderosa pine. At higher elevations the vegetation is montane in character, with fir–pine and lodgepole pine forests. True mixed-conifer forests predominate on slopes between 500 and 2,000 meters, with sugar pine and white fir more common on moist sites and ponderosa pine and incense-cedar common on drier slopes. Alpine vegetation occurs at the summits of Mt. Shasta and Lassen Peak. Mudflows and avalanches are regular natural disturbances on these peaks, periodically destroying large areas of forest (Rundel et al. 1977).

Sierra Nevada

The Sierra Nevada province includes the long, north–south-oriented mountain range that borders the Central Valley on the east and forms a formidable topographic barrier between the Great Basin and westside California. The foothills of the Sierra Nevada, between 500 and 800 meters in elevation, support blue oak, foothill digger pine woodlands (Fig. 10), and chaparral along the entire length of the range. Above 500 meters, high Sierra Nevada forests vary with elevation. In the lower montane zone, the drier slopes are forested with ponderosa pine, whereas moister slopes support white fir and giant sequoia. Slightly higher, in the upper montane zone, forests of red fir, Jeffrey pine (Fig. 11), and lodgepole pine dominate (Rundel et al. 1977). In the montane zones of the Sierra Nevada, natural fire regimes have been altered by fire control and suppression, and species composition and vegetation structure have changed significantly, as demonstrated in forests protected from timber harvest in the Sierra Nevada (see box on Fire and Fuel in the Sierra Nevada).

Most trees of the Sierra Nevada are common in mountain ranges across the West, but giant sequoia is a California endemic. Although coast redwoods are taller, giant sequoias are the most massive plants on earth, and they may live more than 3,000 years (Bakker 1972). Closely related to coast redwood, giant sequoia is scattered in some 75 disjunct groves throughout the middle elevations of the central Sierra Nevada. The unusual distribution of this species is believed to be due to changing climates in the Holocene, and giant sequoias are probably more abundant now than they were 10,000 years ago (Anderson 1994). At the time of European settlement, giant sequoia populations seem to have been increasing or at least stable (Stephenson 1994).

Seedlings are intolerant of shade and need bare mineral soil to establish. Individual treefalls provide such conditions, but not enough to sustain populations. Giant sequoias are quite resistant to fire and insects; in fact, successful regeneration of the species seems to require locally intense fires that kill the forest canopy, followed by one or more wet summers to aid seedling establishment. Most living sequoias occur in even-aged groups that probably correspond to localized *hot spots* in past fires. Successful management of giant sequoias requires reintroducing fires in which local patches burn intensely within a mosaic of frequent, gentle surface fires (Stephenson 1994).

Giant sequoias are usually dominants in mixed-conifer stands; associated tree species include California white fir, sugar pine, and incense-cedar. Red fir is an important associate at higher elevations, whereas ponderosa pine and California black oak are common associates at lower elevations. Some giant sequoia groves were logged in the late nineteenth century, but most are now protected in national parks (Bakker 1972).

The subalpine zone of the Sierra Nevada is forested by mountain hemlock and whitebark pine, and many of the peaks are high enough to have treeless alpine zones; Mt. Whitney, for example, is more than 4,400 meters high (Fig. 12). The Tehachapi Mountains are a small region of foothill and montane vegetation below 2,000 meters in elevation, at the south end of the Sierra Nevada. These mountains support a unique mixture of vegetation types found in the neighboring provinces, including pinyon–juniper woodland, prairie, and mixed woodlands (Hickman 1993).

Led by the U.S. Forest Service, with the cooperation of other federal and state agencies and the University of California, the Sierra Nevada Ecosystem Project is nearing its conclusion. This bioregional program, which is driven by federal legislation, attempts to describe resource conditions in the Sierra Nevada ecosystem by using existing information; it also attempts to anticipate the direction of future change and the effect of potential resource use on the natural resources and human communities in the area.

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Fig. 10. Digger pine woodland, Contra Costa County.

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Fig. 11. Jeffrey pines, Mono County.

Fig. 12. Subalpine vegetation, Sierra Nevada.

Central Valley

The Central Valley extends 640 kilometers from north to south through the central region of California. Bounded on the east by the Sierra Nevada foothills and on the west by the Coast Ranges, the valley floor averages 64 kilometers in width and encompasses nearly 42,000 square kilometers. The Klamath Mountains form the valley's northern end and the Tehachapi Mountains form its southern end. The valley is divided into three major regions: the Sacramento Valley, which drains southward; the San Joaquin Valley, which drains northward; and the delta and Suisun Marsh areas where the Sacramento and San Joaquin river systems meet. Much of the Central Valley is now agricultural land, but fragmented native ecosystems still exist. The Central Valley once supported extensive prairie (Fig. 13), marshes, riparian woodlands, and valley oak savannas.

Native grasslands in the Central Valley were composed mainly of drought-resistant perennial bunchgrasses, such as needlegrasses, blue wild rye, various bromes, melicgrass, and deergrass (Bakker 1972). However, the native California prairie has almost disappeared, either converted to agriculture or to nonindigenous annual grasslands. Around the middle of the nineteenth century, heavy grazing by cattle and sheep caused native perennials to be replaced by fast-growing annual grasses, which are able to take advantage of spring rains and produce seeds before the dry heat of summer. The native perennial grasses, which are more palatable to livestock than the annuals, were damaged by grazing and trampling during the Mexican Rancho period. Native annuals such as six-weeks fescue, three awns, and lovegrass, whose ranges had been restricted by the dominant perennials, became more prominent and were soon followed by nonindigenous, weedy species such as wild oats, soft chess, and goatgrasses. The disappearance of perennial grasses caused both the extirpation of pronghorns and the near-disappearance of Tule elk from the Central Valley (Bakker 1972). Tule elk, a small, endemic California subspecies, now inhabits California only in managed (usually transplanted) herds in parks and preserves. Pronghorns, however, are still common elsewhere in the West and the Great Plains.

Fig. 13. California poppies blooming at Shotgun Pass, Merced County, in native prairie in the Central Valley.

The Sacramento Valley is composed of five drainages: the Butte, Colusa, Sutter, Yolo, and American river basins. The San Joaquin Valley consists of the San Joaquin basin in the north and the Tulare basin, which forms a closed drainage system at the southern end of the valley. The delta consists of a network of sloughs and islands at the confluence of the Sacramento and San Joaquin rivers. The islands, diked and reclaimed in the 1800's, contain rich peat soils that support a thriving agricultural industry. The Suisun Marsh is an estuarine wetland system that forms a transition zone between the fresh water of the delta and the marine environment of the San Francisco Bay estuary. Within the last 50 years, public works projects designed to respond to the water demands of agriculture and large metropolitan areas have produced a great network of artificial lakes and rivers interconnected by a system of Central Valley aqueducts. The federally administered Central Valley Project and the associated State Water Project are the most important of these systems. Their primary function is to transport water from major sources in northern California to arid regions in the south. This reliable water source, the rich soils, and the ideal climate have made California the nation's leading agricultural state for the last 50 years.

Wetlands in California historically have hosted one of the largest concentrations of wintering waterfowl and other migratory birds in the world. In the mid-1800's, an estimated 2 million hectares of wetlands were present in California, and early explorers reported vast concentrations of waterfowl and other marsh and shorebirds (California Department of Fish and Game 1983). About 1.6 million of these hectares were in the Central Valley. Since then, more than 95% of the historical wetlands in

California have been destroyed or modified (Gilmer et al. 1982). Of about 116,000 hectares that remain in the Central Valley (Heitmeyer et al. 1989), two-thirds are privately owned and managed for duck hunting; the remaining one-third is divided between state and federal ownership and is managed by the California Department of Fish and Game as Wildlife Management Areas (15,282 hectares) or by the U.S. Fish and Wildlife Service as national wildlife refuges (20,337 hectares). Most of these wetlands are seasonal and intensively managed.

Closely associated with the historical wetlands were extensive riparian forests that flourished among wetlands and along waterways (Warner and Hendrix 1984). Recent estimates indicate that only about 11% of the original riparian forest remains in the Central Valley (Katibah 1984). Destruction of riparian forests throughout the Central Valley has had a detrimental effect on species such as the yellow-billed cuckoo and Bell's vireo, which depend on these forests for breeding or wintering habitats (Warner and Hendrix 1984).

About every three to five winters, approximately 38,500 hectares of additional wetland habitat are created, when bypasses (diked agricultural lands) channel Sacramento River overflows to the delta (Kahrl 1978). Major losses of natural wetlands occurred when these flooded areas were converted to cultivation of rice, which has been an important crop in California since 1912. Because rice is grown in flooded fields, marsh soils are ideal for its production. If rice fields are flooded for fall waterfowl hunting they provide considerable benefits to waterbirds, because of the increased availability of waste grain and invertebrates. The total area of harvested rice increased through the 1980's as world markets expanded. For example, in the Sacramento Valley, where rice is primarily grown, land used for this crop has recently increased from about 81,000 to nearly 243,000 hectares. However, if farmers switched from rice cultivation to other agricultural crops, the carrying capacity of the Central Valley for wintering waterbirds could greatly decrease.


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Fig. 14. Vernal pool vegetation: California goldfields, Butte County.

The San Joaquin Valley has experienced major wetland losses caused by the conversion of natural ecosystems to the cultivation of cotton and a variety of row crops. A notable exception to this trend has been the Grasslands, a 26,325-hectare area of private duck clubs that have preserved much of the property's high-quality wetlands. The Grasslands represents the largest tract of waterfowl habitat in the San Joaquin Valley.

Vernal pools, called *hog wallows* in the Central Valley, are unique wetlands found mostly on protected areas in the San Joaquin Valley (Bakker 1972). Vernal pools are small depressions with hardpan floors that fill with water during winter rains and evaporate through the spring. Most pools are between 1 to 2 square meters in area, though they vary considerably in size. These pools were more widespread before the advent of agriculture and urbanization, but they still are scattered throughout the Central Valley grasslands, mostly on old terrace soils (Holland and Jain 1977). Vernal pools support specialized invertebrate and plant communities and are veritable islands of unique vegetation. Of the 101 plants found in vernal pools in one study (Holland and Jain 1977), 70% were native annuals, and only 7% were introduced (nonindigenous) annuals; 55 plants were endemic to California, and another 14 were near-endemics. High species diversity occurs between pools, but less diversity occurs within a single pool. No trees, shrubs, or stem succulents are associated with vernal pools.

Because California vernal pools are a relatively recent phenomenon in geologic time, most of their endemic plants are relatively young species (Stone 1990), many with close ecological and evolutionary relations with highly specialized insects, particularly bees (Thorp 1990). The soil and water of vernal pools are very alkaline, and the pH of the water increases as it evaporates in the spring. As the pools dry, annual plants bloom in concentric rings determined by their proximity to the standing water (Figs. 14 and 15). Within the standing water, one might find the plants hogwallow starfish, Howell's quillwort, marsilea ferns, pygmy epilobium, monkeyflower, or mouse-tail, whereas around the pool margins, foxtail, common stickyseed, annual hairgrass, hedge-hyssop, toad rush, leafybract dwarf rush, and smooth tidytips can be found. Sharp ecotones exist between the pool flora and the annual grassland on the mounds between them. On the mounds one might find brome grasses, fescues, wild oats, and occasionally the native perennial purple needlegrass. Because the soil of these pools is replete with salts and other solutes (alkali), and because of their ephemeral nature, vernal pools have successfully resisted invasion by nonindigenous species, unlike nearby marsh habitats.

Water of sufficient quantity and quality is a major limiting factor for wetlands and wildlife populations in the Central Valley. Historically, legislation governing the allocation of surface water by the Central Valley Project and the State Water Project assigned higher priority to agricultural and municipal needs than to fish and wildlife requirements. About 87% of the water provided by these systems is used for irrigation.

Fig. 15. Vernal pool vegetation: meadow foam, Butte County.

Migratory birds of special interest that breed in the valley include Swainson's hawk, yellow-billed cuckoo, and tricolored blackbird. Wetlands in the Central Valley are critical habitat for the threatened giant garter snake, a species of limited distribution that is being studied.

Central Western California

The central western coast is divided into three regions: the central coast, the San Francisco Bay area, and the south coast. The central coast, right along the ocean, includes true coastal vegetation, coastal sage–scrub in the south, and salt marsh and coastal prairie around San Francisco Bay. Inland from the immediate coast, the San Francisco Bay area supports wet redwood forest in riparian areas and seaward slopes, and dry oak–pine woodlands and chaparral farther inland and on dry slopes. The southern Coast Ranges, which extend along the coast from Santa Clara County to Santa Barbara County, have many small serpentine outcrops. The northern ends of the ranges are forested with redwood and mixed hardwoods near the coast. Farther south, southern oak and blue oak–foothill pine woodland dominate along the coast, with chaparral occurring farther inland.

Oak woodlands are one of the most common and characteristic vegetation types in California, covering 3 million hectares of rolling foothill topography (Huntsinger et al. 1991; Fig. 16). The term *oak woodland* encompasses a variety of environmental conditions and vegetation, representing a group of variable communities geographically located between grassland or scrub and montane forests, with their boundaries often obscured by a zone of chaparral. Open stands of deciduous white oaks (that is, valley oak, blue oak, and Oregon oak) are typical of huge areas, but evergreen black (or red) oaks (that is, coast live oak and interior live oak) are often present and sometimes dominant (Griffin 1977). Oregon oak is important in northern oak woodlands, blue oak and valley oak in central woodlands (Fig. 17), and Engelmann oak in southern woodlands. In coastal foothills, coast live oak is prominent, whereas interior live oak is more common inland. The scrub oaks of chaparral, such as leather oak, which is limited to serpentine soils, and Nuttall's scrub oak, are true shrubs. Nine of California's oak species are endemic, including all the species just mentioned, and many oaks hybridize with each other, making classification difficult in some cases. Tanoak is actually a separate genus and is not a true oak, though it occurs with oaks in woodlands and chaparral. Chaparral often forms a mosaic with grassland and woodland communities on poorer, shallower soils (Griffin 1977).

Oak woodlands often have an understory of grasses and forbs, which now include many nonindigenous species, and have been used for livestock grazing since the time of the Mexican Ranchos. They still provide about one-third of the total rangeland forage supply for California's livestock industry. Oaks are not usually logged, except for firewood. The acorns

Fig. 16. Blue oak woodland, Lake County.

Fig. 17. Valley oaks in fog, Santa Clara County.

they produce, though, were the staple food for Native Americans, who may have actively managed them by setting grass fires. They are also an important food for wildlife. Most (82%) of California's oak woodlands are privately owned (Huntsinger et al. 1991) and are still used for livestock grazing and recreational hunting (Morrison et al. 1991). Since the mid-nineteenth century, oaks have increased in both density and extent at low elevations, probably partly in response to climatic warming, changes in grazing pressure and woodcutting practices, and cessation of regular burning by Native Americans (Byrne et al. 1991).

Southwestern California

This portion of California is made up of several geographic units and a multitude of complex ecological systems and communities (Jaeger and Smith 1966). The area includes the Channel Islands, the Transverse Ranges, the Peninsular Ranges, intervening valleys, and coastal lowlands. The coast is highly urbanized, and most natural vegetation and habitat have been lost. The many endemic plants and animals of this area are threatened or extirpated by urban development. However, some native vegetation remains, consisting mostly of coastal sage–scrub and chaparral.

The Transverse Ranges are unusual in that they are oriented east to west. They include the San Bernardino, San Jacinto, Santa Monica, Santa Ynez, Topatopa, Santa Susanna, and the Liebre and Sierra Pelona ranges. The mountains become hotter and drier to the east, where they border the Mojave Desert. Chaparral dominates the vegetation at lower elevations, grading into southern oak forest, then dry montane forest with white fir, Jeffrey pine, sugar pine, and lodgepole pine at the highest elevations. The Peninsular Ranges are farther south and include the Santa Ana, Cuyamaca, Santa Rosa, Laguna, Jacumba, and San Jacinto ranges (Hickman 1993). The coastal sage–scrub, which is restricted to coastal plateaus and lower slopes of the coastal ranges, changes in character from north to south; evergreen species are more common in the north, whereas many species in the south are drought-deciduous or succulent. Most of the plants grow actively only during the cool, wet winters.

Coastal sage–scrub occupies drier, usually lower elevation sites than the chaparral and tends to be shorter; on sites that can support chaparral, sage–scrub eventually succeeds to chaparral following disturbances. Sage–scrub habitat also adjoins the annual grasslands, and islands of sage may be included within the grasslands. Usually, though, a bare zone nearly a meter wide occurs between scrub and grassland wherever they meet; scientists suspect that this is due to inhibitory compounds produced by the sagebrush plants (Mooney 1977). Dominant species in most sage–scrub sites are California sagebrush, white sage, black sage, purple sage, California buckwheat (also see Fig. 18), and mahogany sumac. Farther south, where conditions are drier, such distinctive species as California buckeye (Fig. 19), California adolphia, golden-spined cereus, and Shaw's agave join the sages (Mooney 1977).

Chaparral is a word of Spanish derivation that originally referred to a thicket of shrubby evergreen oaks but is now applied to dense brushland in general. It is the most extensive vegetation type in California, covering about 5% of the state (Hanes 1977), but it reaches its maximum development in southern California, where it ranges in elevation from 300 to 3,000 meters. Chaparral develops on alluvial fans and


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Fig. 18. Wild buckwheat, Granite Creek, Madera County.


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Fig. 19. California buckeye, Mariposa County.

washes adjacent to coastal sage–scrub and riparian woodland. In northern California, chaparral is scattered, ringing the Central Valley and generally occurring on drier, south-facing slopes of the inner ranges and coast ranges (Fig. 20). Chaparral consists of dense shrubs with distinctive sclerophyll leaves, which are small, stiff, thick, and usually evergreen. Chaparral occurs in areas with cool, wet winters and hot summers with prolonged drought.

Fire has shaped chaparral communities for more than 2 million years. Most fires in California natural areas are in these communities, occurring every 10 to 40 years (Hanes 1977). Chaparral shrubs have adapted to fire by producing seeds at an early age, by producing fire-resistant seeds that can live in the soil for decades, or by sprouting from a lignotuber or root-crown burl after the main-stem is destroyed. As California's human population has grown, this fire-adapted vegetation is now interspersed with housing developments in many areas, and fires in this urban–wildland interface are dangerous to human life and costly in terms of property loss.

Chamise chaparral, the most common chaparral type in California, is so named because it is dominated by chamise. It occurs on hot, dry, infertile south- and west-facing slopes and is 1 to 2 meters tall, with little or no understory and few associated species, such as manzanitas, different kinds of ceanothus, giant wild-rye, California buckwheat, Nuttall's scrub oak, sugar bush, white sage, and Our Lord's candle. Shrubs recover slowly after fire, and ephemeral annuals may occupy spaces between shrubs in the first few seasons following a fire. Because the shrubs hold the soil on steep slopes, landslides and erosion are common following fires.

Ceanothus chaparral is successional to other communities in southern California, but it is common as a climax community in northern California. It grows on moister sites than chamise, rarely above 1,200 meters. Several species in ceanothus chaparral—including hoaryleaf ceanothus, hairy ceanothus, and blue blossom (also see Fig. 21)—may be codominant with manzanitas. Ceanothus chaparral may also form the understory for deciduous oak woodland or ponderosa pine forest. The crowns are not as dense as those of chamise and reach a height of 1–3 meters at maturity. Some species are short-lived and between fires may die out of a stand. Associated species are usually sprouters, including chamise, Nuttall's scrub oak, toyon, and sugar bush, and elements of coastal sage–scrub also occur in ceanothus chaparral, such as California buckwheat and California sagebrush (Hanes 1977).

Scrub oak chaparral occupies wetter north-facing slopes below 900 meters but is more

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Fig. 20. Coastal chaparral, Contra Costa County.

common above 900 meters in elevation in southern California. In the north, it occurs above chamise chaparral where soil is sufficiently deep. The dominant species is Nuttall's scrub oak. The canopy is so short (2–4 meters tall) that the trees' lowest branches nearly touch the ground. Scrub oak chaparral has the greatest species richness of all the chaparral communities; woody vines and ferns are common on its deep litter. Scrub oak chaparral develops rapidly after fire because it usually occurs on more mesic sites and because many of the species sprout then (Hanes 1977).

Manzanita chaparral occurs on deeper soils and at higher elevations than chamise or ceanothus, thus it obtains most of its moisture from fog drip, freezing precipitation, and snow. It forms very dense stands from 1 to 2 meters tall. Only about half of the manzanita species are sprouters, so many of them must seed after fire. Manzanitas are long-lived, and several species may reach tree size (Hanes 1977).

Montane chaparral occurs at higher elevations in scattered thickets in the Cascades and Sierra Nevada. It is often seral or an understory to coniferous forest and rarely exceeds 2 meters in height; usually it is less than 1 meter tall. Associated shrub species include manzanitas, huckleberry oak, bush chinquapin, and many species of ceanothus.

Red shank chaparral occurs in only four locations in southern California and Baja California: the San Jacinto and Santa Rosa mountains, and in the interior valleys of Riverside and San Diego counties. It is dominated by red shank and grows between 600 and 1,800 meters in elevation on granitic soils. Individual shrubs are 2–3 meters tall and grow in relatively open sites (Hanes 1977).

Serpentine chaparral is associated with serpentine soils from San Luis Obispo County northward and is characterized by a dwarfed stature due to the poor soils on which it grows. Chamise and toyon are the dominant shrubs; whiteleaf manzanita and musk brush are endemic members of this community. Sargent cypress, interior silk-tassel, and leather oak are also characteristic of serpentine chaparral, which can be associated with foothill

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Fig. 21. Blooming deer brush, a ceanothus species, Butte County.

woodlands or montane coniferous forests. The shrubs are 0.5 to 2 meters in height, compact, and close to the ground. Their leaves are often reduced, curled, or thickened (Hanes 1977; Fig. 22).

Desert chaparral is associated with desert scrub communities in the inner Coast Ranges and Transverse Ranges. It is more open than most chaparral communities and does not burn as often as these other forms. Woodland chaparral has two phases, one of large woody shrubs associated with tree communities and the other a live oak chaparral dominated by Nuttall's scrub oak, interior live oak, and canyon live oak.


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Fig. 22. Serpentine chaparral, Lake County.

Fire has shaped nearly all of California's vegetation communities. From the closed-cone pines and cypresses on the northwest coast to the chaparral-covered hills above Los Angeles, fire has been a constant in the seasonally dry climate. Before European settlement, most fires were probably started by lightning, though Native Americans also deliberately used fire to create both habitat for animals and travel routes, and to select for useful plants (Martin and Sapsis 1995). In presettlement times, fire burned 5.5%–13% of California's total area each year (Martin and Sapsis 1995).

Fires that occurred during the settlement period (1800's) tended to be large and destructive in terms of life and lost resources because they were indiscriminately set and could not be effectively suppressed. These fires helped convince followers of the early conservationist movement in the late 1800's that fire was the enemy; thus, most forestry practices in the early 1900's excluded fire (Martin and Sapsis 1995). From about 1910 until the 1960's, fire in California was aggressively suppressed with increasing effectiveness. But although humans were able to suppress the less intense fires, we have not reduced the number or magnitude of large and disastrous wildland fires; if anything, these have increased in frequency since fire suppression began (Martin and Sapsis 1995).

The state of California now has the best wildland fire suppression capability in the world, with 20,000 firefighters and support staff available within 72 hours, aircraft, and an incident command system (Irwin 1995). But fires still occur, and though only 3% of fires do excessive damage, all are costly. The Tunnel fire near Oakland in October 1991 killed 25 people, injured 150, destroyed 3,810 dwellings, and burned 1,500 acres at an estimated cost of $1 billion (Sapsis et al. 1995). In recent decades, more people have moved out of California's large cities and into the urban fringes, where human housing is mixed with native vegetation that is adapted to periodic fire. Often such communities are not designed with the likelihood of fire in mind, exacerbating the problem (Irwin 1995). Thus, fires in this wildland–urban interface are difficult to suppress and tend to be costly.

Since the 1960's, fire itself has been used as a tool to control fuel buildups and to mitigate the effects of fire. Prescribed fire techniques were pioneered in California (Green 1981), particularly in chaparral. Prescribed fires are deliberately set by land management professionals under a predetermined set of weather and fuel conditions that are predicted as closely as possible so that the fire can be controlled to produce the desired effect. The usual goal is a slow-burning surface fire, which reduces fuels within a prearranged area. Because the dead fuels carry the fire, chaparral younger than 25 years old is difficult to burn. Topography, temperature, relative humidity, condition of the fuels, timing, and especially wind are key factors in the success of a prescribed burn. Most of these factors can be predicted and many are related to one another; topography helps determine wind direction, and temperature and relative humidity help determine the flammability of fuels (Green 1981).

Prescribed fire is not used as widely as it could be, in part because of concerns for air quality (Hurley 1995). Though a prescribed fire generally produces less smoke than a wildfire, air quality restrictions and complaints from the public have curtailed some prescribed burning in wildland–urban interface areas. Also, prescribed burning is inherently risky; though it is possible to predict many conditions of fuels and weather, it is always possible, however unlikely, that a prescribed fire could escape control or at least have different effects than those expected. Because suppression is generally funded first and is extremely expensive, fuel mitigation is often underfunded (Irwin 1995). Prescribed fire, though, is important in order to restore California ecosystems to a healthier, more natural state and to protect property in the wildland–urban interface.

Channel Islands

The California Channel Islands are a group of eight islands lying from 19 to 97 kilometers off the southern California coast, in the nearshore section of the Pacific Ocean known as the southern California bight. These islands are generally segregated into the four adjacent northern islands of Anacapa, Santa Cruz, Santa Rosa, and San Miguel, and the southern four, more widely scattered islands of Santa Barbara, San Nicolas, Santa Catalina, and San Clemente. Four additional islands range south to Punta Eugenia, Baja California, and are known as the Mexican Channel Islands. The islands are owned and managed by a variety of federal, Mexican, state, and private agencies.

Fire and Fuel in a Sierra Nevada Ecosystem

Early travelers and photographers in the mid-1800's recorded the forests of the Sierra Nevada as parklike, with little undergrowth and wide expanses of meadows. The forests were a mixture of conifers dominated by ponderosa pine, with some incense-cedar and California black oak at lower elevations and increasing numbers of sugar pine and white fir at the higher elevations. Beneath the larger trees, the forest floor was carpeted with needles, forbs, and grasses. The understory, where present, consisted of young trees and some chaparral shrubs. These open conditions were attributed to low-intensity surface fires set by lightning and augmented by Native Americans.

Lightning fires have unique spatial and temporal distribution patterns in relation to topography and vegetation. The ecological role of fire is a manifestation of those patterns. The simultaneous occurrence of a lightning strike, flammable fuel, and conducive weather determines the frequency, size, and intensity of a fire. The prevalence of lightning strikes and fires shows conclusively that fire is an integral and pervasive part of Sierra Nevada ecosystems rather than an external disturbance (van Wagtendonk 1994).

Nearly a century of fire control in the Sierra Nevada has led to conditions that now threaten the very forests they were designed to protect. Suppression of naturally occurring surface fires has allowed the forest floor to become a tangle of understory vegetation and accumulated debris. Open forests and meadows have been invaded by trees and chaparral. Thickets of shade-tolerant incense-cedar and white fir have increased and have deflected succession away from the less shade-tolerant ponderosa and sugar pines.

As undergrowth has increased, fuel volumes have expanded, and a continuous ladder of fuel extends from the ground to the forest canopy. The understory is now so thick with dead trees, branches, needles, and other debris that inevitable wildfires will soon reach catastrophic proportions. Today, millions of hectares of forest and grasslands in the Sierra Nevada face abnormally high risks of wildfire because of these altered conditions. This situation is worsened by the increasing numbers of vacation homes and other human developments within the forest and foothill vegetation.

The cycle can be illustrated by examining simulated fuel accumulation rates during periods before and after the initiation of fire suppression, by using graphs generated by the FYRCYCL model based on data collected in Yosemite National Park (van Wagtendonk 1985; Figure). As long as fires are suppressed, this new, longer cycle of extremely intense wildfires will continue.

If natural conditions and processes are to be restored and perpetuated in the Sierra Nevada, fire must be reintroduced. In large wilderness areas and parks, naturally occurring lightning fires should be allowed to burn under prescribed conditions. Where this is not possible because the area is too small or because other human factors (such as the presence of human dwellings, timber harvest areas, and so forth) preclude the implementation of a program to monitor wildland fires, surrogates for fire must be found. Prescribed burns, mechanical manipulation, and artificial cutting are possible options. In any case, it is important that naturally managed ecosystems not be denied ecologically significant processes such as fire.

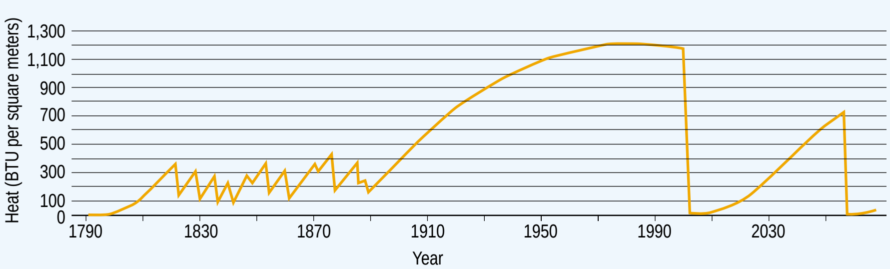

Figure. Simulated fire cycle from Yosemite National Park as generated by the model FYRCYCL. Starting in 1790 with open ground, as might be expected following a stand-replacing fire, a forest began to grow and fuels accumulated. By 1820 enough fuel had accumulated to carry a fire, and lightning strikes occurred when weather conditions were conducive to burning. The resulting fire reduced fuels. According to the model, during the next 70 years, lightning-caused surface fires occurred in a cycle averaging one every 7 years. In 1890 a policy of total fire suppression was implemented, and all subsequent fires were extinguished. Without the frequent surface fires, fuels will have accumulated to such a volume by the years 2000 and 2055 that when fires do occur, they will be intense crown fires that exceed suppression capability. The amount of fuel on the ground is measured in units of heat per square meter.

See end of chapter for references

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The eight U.S. California Channel Islands range in size from 249 square kilometers (Santa Cruz Island) to 2.6 square kilometers (Santa Barbara Island). In addition to Santa Cruz Island, three other islands exceed 100 square kilometers in size—Santa Rosa (217 square kilometers), Santa Catalina (194 square kilometers), and San Clemente (145 square kilometers; Philbrick 1967). Because the islands were never connected to the mainland in their geologic history, they are rich in endemic plants and animals. Furthermore, the islands are near an area of cold-water upwelling where the Pacific Current meets the warm waters of the bight. As a consequence, they have an extremely rich marine flora and fauna.

The four northern islands are most likely a geological extension of the Santa Monica Mountains, separated from the mainland by a deep ocean trench. During the Pliocene they were joined into one large island called Anacapia. The four southern islands, also known as Catalinia (Weaver and Doerner 1967), are more scattered and include islands farther from the mainland. They seem geologically related to the Palos Verdes Peninsula, which was itself an island at various times in the Cenozoic, at the edge of the Greater Los Angeles basin (Weaver and Doerner 1967). San Clemente Island is the largest island that is far from the mainland, and it is perhaps not surprising that it has the largest number of endemic plants—40 species, subspecies, and varieties (Raven 1967). All the Channel Islands have varied in size during sea-level shifts that have occurred since their formation (Valentine and Lipps 1967; Weaver and Doerner 1967). Today, their terrestrial fauna and flora most closely resemble those of adjacent southern California, although some elements are more related to today's biota of central coastal California (Raven 1967).

The Channel Islands are rich in endemic species, subspecies, and varieties of animals and plants. Most of the species did not evolve on the islands alone—they are relict populations of species that once occurred on the mainland during the Tertiary and Pleistocene but which became extinct there because of harsher climatic conditions or competition (Axelrod 1967; Powell 1985). Approximately half of the endemic species occur on more than one island. Genetic divergence of island populations continues, however, and there are distinct subspecies and varieties of many taxa endemic to single islands (Raven and Axelrod 1978).

The islands were used for ranching, farming, and military activities beginning in the mid-1800's. Grazing by sheep, cattle, goats, donkeys, and pigs has limited certain species to tiny inaccessible pockets on canyon walls and coastal bluffs (Raven 1963). The accompanying soil compaction and erosion have changed community dynamics, and many habitats are now dominated by nonindigenous Mediterranean annual grasses and herbs.

Conservation is now a major land-use priority on the Channel Islands. Anacapa, Santa Rosa, San Miguel, and Santa Barbara constitute the Channel Islands National Park, and Santa Cruz is owned by The Nature Conservancy. There are large areas in conservation reserves on San Nicolas and San Clemente islands, which are owned by the U.S. Navy, and also on Santa Catalina, a privately owned island managed largely by the Catalina Island Conservancy.

The Channel Islands are rich in endemic plants; Raven (1967) cites 76 endemic plant species, subspecies, and varieties. One tree genus in the rose family, Catalina ironwood (Fig. 23), is entirely endemic to the Channel Islands and is found on the four largest islands. More than 40 species of plants, and a number of additional subspecies and varieties, are endemic to the islands, including island live oak, wild lilacs, wild cherries, native sages, and several woody shrubs such as manzanitas.

Five endemic Channel Island plants are listed as endangered on the U.S. list of endangered and threatened plants and wildlife (U.S. Fish and Wildlife Service 1994a): San Clemente Island broom, San Clemente Island bush-mallow, San Clemente Island Indian paintbrush, San Clemente Island larkspur, and Santa Barbara Island liveforever. Three additional plants from the southern Channel Islands and 16 plants from the northern Channel Islands have been proposed as endangered (U.S. Fish and Wildlife Service 1995b,c). The proposed listings summarize the status and population trends of each plant and detail the detrimental effects on each caused by intentionally introduced grazing mammals and rooting pigs (U.S. Fish and Wildlife Service 1995b,c). Thus, about a third of the Channel Islands' endemic flora is listed as endangered or is likely to be listed soon.

Notable invertebrates of the Channel Islands include several genera of snails (see box on Channel Islands and California Desert Snail Fauna), including island snails, cactus snails, and a shelled slug, as well as the Avalon hairstreak, a species of butterfly found only on Santa Catalina Island. The Avalon hairstreak has one of the smallest ranges of any North American butterfly (Gall 1985). The status of Channel Islands insects has been the topic of a symposium (Menke and Miller 1985), and Miller (1985) lists the Channel Islands' endemic arthropods. Powell (1985) described the patterns of apparent endemism in the

Torrey Pine

Torrey pines occur naturally only in two limited coastal California sites and are the rarest species of North American pines. The first population was discovered on the coast at the mouth of the Soledad River near San Diego. This population, now within the Torrey Pine State Reserve, includes an estimated 4,000–5,000 trees, mostly larger, reproductive individuals, some of which were planted by concerned caretakers. In 1988, following a damaging wind storm and several seasons of drought, this mainland stand was severely attacked by bark beetles, and hundreds of trees were killed. The beetles were controlled by trapping using a chemical attractant, which probably saved the bulk of the mainland trees (Berson 1992).

The second population occurs on Santa Rosa Island (now a part of Channel Islands National Park) and was described (Brandegee 1888) as a stand of about 100 trees with plenty of vigorous young trees (Fig. 1). This stand was probably limited by the species' sensitivity to the occasional fires that burned through the island vegetation (S. Veirs, U.S. Geological Survey, Davis, California, unpublished fire history; Fig. 2). Sheep were introduced to the island by Europeans about 1840, and they controlled fires by consuming most of the island's vegetation. The sheep were removed early in the twentieth century and were replaced by cattle. In the continued absence of fire, the stand has increased to 4,200 individuals, including many seedlings and young trees (Veirs, unpublished data; Fig. 3).

Courtesy S. Veirs, USGS

Fig. 1. Torrey pines on Santa Rosa Island.

Courtesy S. Veirs, USGS

Fig. 2. Scars from surface fires at the base of a Torrey pine on Santa Rosa Island. The tree is about 275 years old and its scars record fires that occurred in 1756, 1773, 1803, 1814, 1837, and 1840; there have been no surface fires recorded in the last 150 years, since the introduction of sheep to the island.

The native populations of Torrey pines are at considerable risk because of their small numbers and limited natural distribution. Natural influences, including drought, insects, and fire, pose serious hazards and probably account for the present limited distribution of this species. Torrey pines are relicts of the Pleistocene flora of California; this relict flora has apparently been pushed to the brink of extinction by natural processes—probably climatic changes—over the past 10,000 years (Vogl et al. 1988). Careful monitoring, understanding, and management are essential to perpetuating the native populations of Torrey pines.

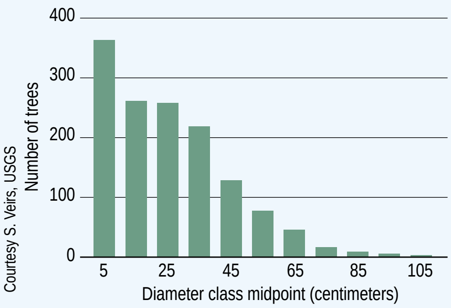

Fig. 3. Numbers of Torrey pines on Santa Rosa Island by size class; note that there are many more small trees than large ones (seedlings omitted.

See end of chapter for references

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islands' butterfly and moth faunas and analyzed the species richness. Generally, an island's fauna is proportional to its size, except that islands closer to the mainland have a richer fauna than those more distant (Powell 1985).

The endemic vertebrate fauna includes the Channel Islands gray fox, a species protected by the state of California and which is found on the six largest islands, each with its own subspecies (von Bloecker 1967); an island subspecies of spotted skunk found on Santa Rosa and Santa Cruz; and the island night lizard, a genus and species endemic to San Clemente, San Nicholas, and Santa Barbara islands (Savage 1967). The Santa Cruz Island gopher snake, a candidate for federal protection, occurs on Santa Rosa and Santa Cruz; each of these islands also has a distinct subspecies of deer

Courtesy G. Davis, USGS

Fig. 23. Channel Island scrub-jay on Catalina ironwood; both species are Channel Island endemics.

mouse. The San Clemente sage sparrow and the San Clemente loggerhead shrike are both on the U.S. list of threatened and endangered wildlife (U.S. Fish and Wildlife Service 1994b).

Six species of pinnipeds feed in the waters surrounding the islands: California sea lions, northern elephant seals, northern sea lions, harbor seals, northern fur seals, and Guadalupe fur seals. These species have breeding grounds and rookeries on the sand beaches of the islands, most notably on San Miguel, San Nicolas, and San Clemente. Populations of these species are recovering from the near extinctions at the turn of the century that resulted from hunting and from pesticide poisoning of their food base.

Some of the richest marine communities in the world are found in the waters of the Channel Islands. Intertidal areas are dominated by algae and invertebrates. Nearshore waters support forests of giant kelp, one of the fastest-growing algae in the world and home to more than 1,000 species of fishes, other algae, plants, and a wide variety of invertebrates. The outer waters are traversed by migrating gray whales, humpback whales, blue whales, and other whales, as well as dolphins and large fishes; all these species compete for traveling space with commercial freighters, private fishing vessels, and recreational boat traffic.

The marine communities of the Channel Islands have been heavily exploited for their fishes, shellfish, marine invertebrates, and kelp. These organisms are largely unprotected by federal and state laws, and serial depletion of one species after another has been a long-term trend evident in commercial harvest records since World War II (see box on California Abalone). Conservation efforts now focus on the establishment of marine reserves in and around the islands managed by the National Park Service.

Intertidal, Beach, and Dune Communities

Intertidal, beach, and dune communities may be divided into northern and southern biotic units at Point Conception, Santa Barbara County. Major habitat types are rocky intertidal, sandy beach intertidal, dune (including coastal dunes), and salt marsh.

The California outer coast is 1,326 kilometers long, with an additional 365–370 square kilometers of salt marshes and somewhat extensive areas of brackish marshes. Major California estuaries, from north to south, are the adjacent Humboldt and Arcata bays (Barnhart et al. 1992), Bodega Bay, Tomales Bay, Drakes Bay, San Francisco Bay (together with adjacent San Pablo and Suisun bays; Josselyn 1983), Morro Bay, and San Diego Bay (Macdonald 1977; Zedler 1982). San Francisco Bay accounts for about 90% of California's remaining salt marshes (Macdonald 1977).

The habitats and biota of the outer coast have been dealt with by researchers emphasizing the central coast (Ricketts et al. 1952), Bodega Head in Sonoma County (Barbour et al. 1973), southern California estuarine species (MacGinitie and MacGinitie 1949), and the ecology and systematics of marine invertebrates of the central California coast (Light et al. 1961). Seashore plants, including both marine and strand species of northern and southern California, respectively, are summarized by Dawson (1966a,b) and Barbour and Johnson (1977).

The status and trends of intertidal species of the outer coast's rocky and sandy shores are influenced by several natural and human-related factors. Some species, such as abalones (see box), clams, and sea urchins (see chapter on Marine Resources), are harvested for human consumption, whereas several species in the lower intertidal zones are preyed on by southern sea otters, an endangered species (Riedman and Estes 1990; Estes et al. 1995; see boxes on Sea Otters in the Pacific Northwest chapter and in this chapter). Episodic changes in sea temperatures and the related occurrence of coastal fogs triggered by El Niño events may cause periodic die-offs of intertidal species, but most recover after cooler sea temperatures return (see chapter on Marine Resources).

The trends of most species associated with estuarine habitats in California have been declining disastrously (Macdonald 1977; Harvey et al. 1992). There has been a tremendous loss of habitat due to the filling of much of California's estuarine habitats, especially in San Francisco Bay (Harvey et al. 1992; Monroe et al. 1992), in the vicinity of Los Angeles, and in San Diego Bay (Zedler 1982); estuarine wetlands have been almost completely replaced by landfills, marinas, docks, and other development (Zedler 1982; Monroe et al. 1992). As a result, several endangered species—including the salt marsh harvest mouse, California clapper rail, light-footed clapper rail, and salt marsh bird's-beak—are protected by the U.S. Fish and Wildlife Service (1994a; Fig. 24). The Belding's savannah sparrow is listed as endangered under California law. Coastal wetland-dependent species listed as sensitive or of special concern by the state or federal government include 1 plant, 7 insects, 2 reptiles, and 14 birds. Each of these species depends on different habitat types or combinations within salt-marsh ecosystems.

The Humboldt Bay estuarine ecosystem and its biota have been summarized by Barnhart et al. (1992), and the biotic resources of San Francisco Bay and southern California coastal marshes have been summarized by Josselyn (1983) and Zedler (1982), respectively.

Emerging Diseases in Southern Sea Otters

The southern sea otter is a large mustelid that spends its life in the nearshore marine community along the California coast. Prized for its fur, this subspecies was thought extirpated until a remnant population of approximately 50 animals was discovered near Big Sur in the early 1900's. The slowly recovering population was listed as threatened by the U.S. Fish and Wildlife Service in 1977. Although the sea otter's range has expanded to cover more than 320 kilometers of the central California coast and the population is now about 2,500 animals, the rate of recovery has been slower than biologists expected (Riedman and Estes 1990; Riedman et al. 1994). Concern that excess mortality was hindering recovery prompted the U.S. Fish and Wildlife Service to ask the U.S. Geological Survey's National Wildlife Health Center to perform an intensive necropsy survey of wild southern sea otters beginning in 1992.

The necropsies we performed from 1992 through 1995 yielded unexpected results (Figure). In particular, we found that the frequency and variety of infectious diseases were unusual for wildlife species. Forty percent of the sea otters examined died from parasitic, fungal, or bacterial infections. Traumatic injuries are generally common in wildlife, and injuries such as shark attack or shooting were also common (21%) in southern sea otters. Eleven percent of the otters were emaciated at death with no specific cause identified for this debility. In 10% of the sea otters, we diagnosed a variety of other problems, such as gastrointestinal or urinary tract obstructions or tumors. For 18%, we could not ascertain the cause of death.

Peritonitis induced by acanthocephalan parasites was the most frequent (15%) cause of death by infectious disease we identified in the otters. Peritonitis occurs when acanthocephalan parasites that inhabit the intestine migrate aberrantly through the intestinal wall, perforate the intestine, and allow bacteria to enter the abdominal cavity. Although this parasite (*Polymorphus* sp.) has been present in the sea otter population for many years (Hennessy and Morejohn 1977), the infection and mortality rates observed in the 1990's appear unprecedented. The invertebrate intermediate hosts that transmit this parasite are largely unconfirmed, and the roles of other hosts, such as birds, are unexplained.

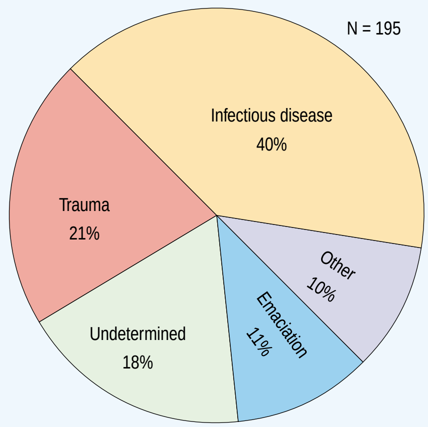

Figure. Causes of mortality in southern sea otters from 1992 through 1995.

Another parasitic disease, protozoan encephalitis, was newly identified in this survey, indicating that it may be an emerging disease. We are investigating the identity of the causative parasite; the ubiquitous organism *Toxoplasma gondii* was isolated from several otters, but the results are confounded by evidence that another protozoan may also be involved. Fatal toxoplasmosis is more common in animals and humans that have impaired or immature immune systems than it is in healthy organisms.

Before our study, coccidioidomycosis, or San Joaquin Valley fever, had been described in a sea otter only once, in 1976 (Cornell et al. 1979), but one or more cases were diagnosed during each year of our survey (Thomas et al. 1996). This fungal disease affects humans and animals in the deserts of the lower Sonoran life zone of the southwestern United States, so its prevalence in the marine environment is puzzling. The fungus *Coccidioides immitis* thrives in arid and semiarid soil. Inhalation of the airborne fungal spores may produce respiratory disease, or the spores may disseminate to many organs in susceptible individuals. The cases of San Joaquin Valley Fever in sea otters coincide with a human epidemic of the fever that began in California in the fall of 1991. The human epidemic was tentatively attributed to unusual weather and environmental conditions rather than to human-related factors, a hypothesis supported by the coincident occurrence in sea otters.

Researchers continue to monitor southern sea otter abundance and distribution to assess the population's progress toward recovery goals. The emergence of several diseases as important causes of death raises concern about the otters' immune status and resistance. By elucidating factors in the individual disease cycles we are trying to determine both an explanation for the emergence of these diseases and a means of controlling them. The challenge remains to identify not only the overt but also the underlying factors that may have more far-reaching effects in the marine environment.

See end of chapter for references

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Beaches and dunes, which are separate but usually connected sandy coastal habitats (Barbour and Johnson 1977), are limited to 305 kilometers of California's coastline, whereas the more limited occurrence of major dunes along the California coast is described by Cooper (1967), who does not include many smaller dunes in his discussion. The Antioch Dunes National Wildlife Refuge is a unique dune system found along the tidal Sacramento–San Joaquin River (Cooper 1967).

Beaches, as defined by Barbour and Johnson (1977), are limited to the salt spray-saturated zone below the highest high-tide line, typically seaward of the foredune crest. Beaches have a very limited flora of salt-tolerant plants that includes European beachgrass, maritime sea-rocket, silverweed cinquefoil, coastal sand verbena, and iceplant as dominants, and pink sand verbena and beach saltbush as subdominants (Barbour and Johnson 1977).

California Abalone

The recent demise of abalone in southern California evokes memories of the fate of bison in the United States in the nineteenth century. Once so abundant their disappearance was unimaginable, the abalone that supported huge commercial and sport fisheries 30 years ago are now on the brink of extinction.

Abalone are marine snails, with some 70 modern species occurring globally. Fossil abalone first appear in Cretaceous rocks dating from about 70 million years ago, in what is now California (Lindberg 1992). Humans have exploited abalone for food, tools, and jewelry for millennia (Shepherd et al. 1992). Five of the eight eastern Pacific abalones were abundant enough to support multimillion-dollar fisheries through most of the twentieth century. However, abalone populations in southern California recently collapsed under a flawed management approach (Davis et al. 1992; Richards and Davis 1993; State of California 1995). This situation has caused worldwide concern because abalone management practices in Australia, New Zealand, South Africa, and elsewhere were based on the same assumptions and strategies as in California (Shepherd et al. 1992). In the mid-1990's, California fisheries for four abalone species were closed to prevent harvest-induced extinctions, but even that drastic action may have been too late to save the white abalone (Davis et al. 1996). The story of these populations, the fisheries they supported, and efforts to restore them is a harbinger for coastal marine fisheries. The lessons learned in efforts to restore and sustain California abalone can be applied profitably to coastal resources worldwide.

Biology

Abalone cling to rocks, from wave-swept intertidal ledges down into the twilight zone of deep reefs at 65 meters, wherever they can catch drifting fronds of kelp and other algae. In California, species separate themselves roughly by depth and latitude (Haaker et al. 1986). Black abalone live in tidal pools from Oregon to the southern tip of Baja California. Green abalone, pink abalone, and white abalone prefer southern climes, with each species occupying increasingly deeper waters, respectively, from Point Conception into Baja California. Red abalone, the largest species, occupies the broadest range, from tidal pools in Oregon to deep reefs as far south as Bahia Tortugas, Baja California. Flat abalone, pinto abalone, and threaded abalone are relatively rare and are only incidentally involved in California fisheries.

Abalone have separate sexes. To reproduce, they broadcast sperm and eggs into the sea, relying on high gamete densities for successful fertilization, a reproductive strategy requiring densely aggregated adults for success. The larvae are free-swimming for only a few days before settling to the bottom as juveniles. California abalones mature between 3 and 7 years of age and may live for 35 to 54 years, commonly reaching sizes of 15–25 centimeters in length and 1–2 kilograms. Fecundity increases exponentially with size. Newly mature females produce only a few hundred thousand eggs each year, whereas older individuals produce 10–15 million eggs (Hahn 1989).

Management Strategies

California's management strategy to sustain exploited abalone populations was based on a surplus yield model. It was implemented through minimum harvest sizes, based on growth rates and size at maturity. Under this scheme, abalone were permitted to reproduce for the first few years of maturity and then were harvested. Since no relationship between spawning stock and recruitment had been defined, fishery managers assumed cohorts of young abalone could sustain harvests with no other constraints (Tegner et al. 1989). Closed seasons protected spawning aggregations. Other regulations, such as bag limits on sport fishers and limited entry to the commercial fishery, attempted to allocate limited resources equitably.

In northern California, an additional management measure protects more brood stock of red abalone, thus assuring a sustained fishery. Only sport breath-hold diving or shore-picking in the intertidal zone is allowed. Zoning use in this way separates commercial and sport fishing and protects a large spawning stock of big abalone. The inherent depth limit imposed by breath-hold diving creates a refuge at greater depths, thereby protecting sufficient brood stock to replenish the harvest in adjacent shallow waters. This refugia-based red abalone fishery is the only sustained abalone fishery in California today.

Serial Depletion

Truly sustainable fisheries are based on sustained populations of target species. The frontier approach to fishery management practiced in many areas today produces a pseudo-sustained fishery. This approach unrealistically assumes the availability of an endless supply of new, unexploited populations, but it has the virtue of economic expediency.

Following a fishing hiatus during World War II, southern California abalone fisheries grew rapidly. Soon, readily available and well-known abalone populations along mainland shorelines were exhausted. Then lightweight, mobile, inexpensive diving gear, fast boats, modern navigational aids, and improved knowledge of abalone and the coastal environment made available virtually all of the pristine abalone habitat on offshore reefs. After 25 years of apparently sustained fisheries, abalone landings began declining in the 1970's. A careful examination of this harvest shows it was not truly sustained but rather the result of serial depletion (Dugan and Davis 1993; State of California 1995). Fishery landings and fleet income were sustained at the expense of a series of abalone populations in different areas. Only after landings of pink abalone and red abalone declined in the 1970's did the fishery shift to green and white abalone in shallow and deep water, respectively. When white and green abalone populations collapsed, harvest shifted to intertidal black abalone. Then, as the remnants of the black abalone population succumbed to disease, the diving fishery shifted to red sea urchins. Income to the diving fleet during this period remained relatively stable. The fishery had been sustained, but the productivity of the exploited populations was destroyed in the process.

The success of serial depletion in sustaining fishery income obscured the need to restore severely depleted stocks and to protect more reproductive capacity of abalone populations. Denial that abalone populations were imperiled obstructed efforts to improve management. The virtual absence of fishery-independent information made it difficult to assess population status and gave fishery landings data more credibility than they warranted. These gaps in accessible information delayed remedial actions, making restoration more costly and perhaps impossible for some species.

Current Population Status

Few fishery-independent data exist for abalone in California. Since 1982 the National Park Service and the California Department of Fish and Game have jointly monitored population dynamics of nearly

100 marine taxa, including the five common abalones, in Channel Islands National Park (Davis et al. 1994). Other population trends must be inferred from fishery landings, with considerable uncertainty and ambiguity.

Black abalone populations in California survived with harvests of 2,000 metric tons per year for the last third of the nineteenth century. Large populations accumulated after harvest ceased in 1900, with densities often exceeding 125 abalone per square meter on the Channel Islands (Richards and Davis 1993; Figure). When harvest resumed in 1968, annual landings quickly rose to 870 metric tons. By the mid-1980's black abalone were found primarily on offshore islands and inaccessible sections of the coast north of Santa Barbara. A withering foot disease caused massive deaths in these remnant populations, beginning in 1985 on the Channel Islands and spreading to the mainland (Haaker et al. 1992). Relict populations of apparently disease-resistant individuals survive on the islands at less than 1% of their former abundance.

White abalone occurred at average densities of 10,000 per hectare in the early 1970's (Tutschulte 1976). Ten years later, densities at the historical center of their abundance were 10 per hectare. By the early 1990's densities were only 1 per hectare, and the species was in danger of extinction (Davis et al. 1996).

In Channel Islands National Park, exploited pink abalone population densities fell from 250 per hectare to less than 14 per hectare in the 1980's, while a population protected in an ecological reserve remained relatively stable at about 400 per hectare (Davis et al. 1992). Red abalone population densities in the park dropped from more than 1,000 per hectare to less than 10 per hectare in the 1980's. Fishery landings reflected these population trends. Pink abalone landings fell from 48 metric tons to 7 metric tons, and red abalone landings dropped from 235 metric tons in 1980 to 120 metric tons in 1986. There are no recent fishery-independent data for green abalone populations.

Fishery Status

California abalone fisheries landed more than 4,000 metric tons per year during the 1950's and 1960's, split roughly equally among sport and commercial interests (State of California 1995). After harvest started in 1968, black abalone landings peaked quickly at 870 metric tons in 1973 and stabilized at 225 metric tons in the early 1980's. Then, reflecting the rapid population collapse, landings dropped to less than one metric ton in 1993, when the fishery was closed to protect disease-resistant stock for use in restoration efforts. Landings of black, white, pink and green abalones fell in the 1990's to less than 4% of the early 1970's landings, from 882 metric tons to 32 metric tons. The California Fish and Game Commission closed the pink, green, and white abalone fisheries in 1996 to prevent extinction of reproductive stocks (State of California 1995).

For more than 20 years, sport and commercial abalone fisheries generated $15–$20 million per year for the state's economy. The abalone population trends of the 1980's, caused largely by a flawed harvest scheme, must be reversed if the productivity of these fisheries is to be restored.

Courtesy G. E. Davis, USGS

Figure. Intertidal black abalone on Santa Rosa Island, California, before the catastrophic population collapse in the late 1980's.

Only red abalone still support fisheries in California. The sport-only red abalone fishery in northern California annually produces about 1,000 metric tons (Tegner et al. 1992). Although generally stable, continued productivity of that fishery is now threatened by poaching, induced by the extremely high value of individual abalone ($32 per pink abalone to $100 per white abalone). Abalone fisheries in southern California are now concentrated on a small population of red abalone around San Miguel Island, in western Channel Islands National Park and National Marine Sanctuary. This population is located at the edge of the southern-flowing California current, and recruitment to this population may be provided from unharvested populations to the north. Annual commercial red abalone landings have apparently stabilized at about 170 metric tons, less than 15% of the 1,200 ton landings of 30 years ago.

Restoration Plans

Restoring populations of slow-growing, long-lived abalones to levels that can sustain productive fisheries will take decades and will require active intervention. Closing the Orange County shoreline to abalone harvest in 1977 and waiting 15 years for populations to recover spontaneously was ineffective (Tegner 1992). Abalone are not unusual in this respect. Recent analysis of 128 marine fish stocks revealed that only 3 species might be able to recover spontaneously from severe harvest-induced reductions (Meyers et al. 1995). Active brood-stock husbandry now seems to offer the only promising abalone restoration approach (Tegner 1992, 1993).

Formal comprehensive plans have not yet been made to restore the productivity of California abalone populations. Limited research on recruitment dynamics, larval and juvenile stocking feasibility, and brood-stock husbandry are under way. White abalone stocks are so low that extremely expensive, large-scale surveys of deep reefs are needed just to find enough individuals for captive breeding and rearing programs and to test new strategies, such as aggregating adults in refugia (Davis and Haaker 1995).

See end of chapter for references

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Fig. 24. A tidal salt marsh in southern San Francisco Bay provides habitat for the endangered California clapper rail.

Human foot traffic has eliminated the strip of vegetation (primarily the nonindigenous American sea-rocket and silver bur ragweed) found just above the highest high-tide line from most California beaches. As a result, the globose dune beetle, a restricted denizen of that narrow habitat, has been eliminated from most California beaches, although it may be common on only a few relatively undisturbed Channel Island beaches (Doyen 1976; J. Doyen, University of California [retired], El Cerrito, California, and P. A. Opler, U.S. Geological Survey, Fort Collins, Colorado, unpublished data).

Beach and dune habitats in California are negatively affected by human foot traffic and by off-road vehicles, but they are also severely affected by the presence of nonindigenous plants, many of which were planted intentionally for "beach stabilization." Additionally, development, primarily residential, has eliminated huge areas of formerly extensive sand dune systems; the San Francisco, Monterey, and El Segundo dunes have been almost entirely replaced by development. The native animals and plants of other extensive dune systems, such as the dunes at Point Reyes National Seashore (Fig. 25), have been almost completely replaced by introduced European beachgrass and iceplant (Slobodchikoff and Doyen 1977; Doyen, personal communication). At the Oso Flaco dunes south of San Luis Obispo, almost all life forms have disappeared under the onslaught of off-road vehicles (Powell 1981).

Above the high-tide line are dunes and deflation plains that form the habitat of several nesting birds, numerous native plants, and many insects (Powell 1981; Doyen, personal communication) and other invertebrates. Many of these species are restricted to such beach dune habitats. The endangered California least tern and the threatened western snowy plover (Page and Stenzel 1981; Page et al. 1991; Page and Gill 1994) are two federally listed birds that nest in this habitat (U.S. Fish and Wildlife Service 1994a; also see box).

Status of Species

Plants

The pioneering botanical work of Willis Linn Jepson (Jepson 1925) was the first comprehensive treatment of the higher plants of California. The revised Jepson flora of California plants (Hickman 1993) includes 5,800 species in 173 families and 1,222 genera; about 24% are endemic. Much of the California flora is specifically adapted to the state's Mediterranean climate, and many of the dominants in the plant communities are endemic.

Completely new plant species may yet be identified in more remote and undeveloped parts of California. For example, in 1993 a new genus, Shasta snow-wreath, was discovered near Redding in northern California (Taylor 1994), and two plants that had been believed to be extinct were rediscovered (Corbin et al. 1993).

With development and exploitation of grasslands and other vegetation easily converted to human use, native vegetation has been disappearing. Indeed, most of the plant communities with the largest numbers of rare plant occurrences in California are those that are poorly represented in parks and preserves (Skinner and Pavlick 1994), largely because of their locations and their relatively high value in the 1800's and early 1900's. Today, of some 6,300 native vascular plant taxa (including subspecies and varieties), some 857 (13.6%) are considered rare or endangered in California and elsewhere, and 34 (0.05%) are considered extinct (Skinner and Pavlick 1994).

Invertebrates

California has a rich terrestrial and aquatic invertebrate fauna that features a high level of endemism and a number of species and groups


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Fig. 25. Coastal dunes, Point Reyes National Seashore.

with specialized life histories or behaviors. A conservative estimate of the state of California's insect fauna is 27,000 to 28,000 species (Powell and Hogue 1979). This does not include other arthropods such as mites, spiders, harvestmen, and crustaceans, nor does it include mollusks or other invertebrate phyla. The total count of invertebrates for California is probably in excess of 50,000 species. The exact distribution and population status are not known for most described species. At least several hundreds of undescribed invertebrates also inhabit California.

Unlike much of the eastern United States, where between-habitat diversity of invertebrates is relatively low, California's between-habitat diversity is high. Even though the number of insects found in a single habitat might be relatively low, after visiting several habitats one would soon appreciate that California has a vast array of invertebrates (Powell and Hogue 1979). For example, in the Sierra Nevada, one might find no more than 30 species of butterflies at a single locality on a very good day but would find more than 60 species at three or four sites at different elevations or in different plant communities, and more than 100 different species of butterflies at these localities over the course of a year (Swengel 1995; Opler, unpublished data). In lowland and coastal areas, one would have to make visits almost year-round to find most of the moth species at a single locality (for example, Opler and Buckett 1971; Powell 1995).

Land Snails

California's native land snail fauna is large and diverse, reflecting the geological and ecological diversity of the state. The state's known fauna is composed of about 200 species, and new species continue to be discovered and named (for example, see Roth and Hochberg 1988, 1992). Several genera are endemic or nearly endemic to California or have undergone their greatest diversification in the state.

Land snails are abundant in most terrestrial ecosystems, although they are often inconspicuous because of secretive habitats, seasonal inactivity, or—for some species—their very small size. Most feed on fungi, decaying plant or animal material, or green plants, but a few are predators of snails and other invertebrates. Land snails are fed on by a variety of amphibians, reptiles, birds, and mammals. California does have nonindigenous garden pests, such as the brown gardensnail and several nonindigenous slug species, but the native fauna is essentially harmless.

California includes portions of four molluscan faunal provinces (Pilsbry 1948): the Oregonian province includes humid coastal areas of northwestern California through Oregon and Washington to Alaska; the Southwestern province as defined by Bequaert and Miller (1973) includes the Mojave and Colorado deserts of southeastern California and extends to Arizona, New Mexico, and adjacent parts of Mexico; the Rocky Mountain province is along the eastern border of California north of the Mojave Desert but contributes relatively little to the faunal diversity of the state; and the Californian province occupies the remainder of the state. These provinces are not precisely or consistently defined and serve here only to broadly describe the diversity and affinities of the molluscan fauna.

Because land snails are highly dependent on ambient moisture for their activities, their richness in California, where most regions are at least seasonally dry, may seem surprising. Land snails have adapted to these conditions by finding shelter and becoming dormant within deep plant litter, rockslides, or fissures in soil and rock, emerging only when rains supply sufficient moisture. In very arid areas, conditions for such shelter may be in short supply and widely scattered. These small, scattered refuges, together with the poor dispersal ability of snails, have promoted speciation in many groups and are partly responsible for the high species richness of California's snail fauna.

The shoulderband genus of snails, with 52 species recognized, constitutes perhaps the most remarkable and distinctly Californian genus of snails (Turgeon et al. 1988). This group extends into northern Baja California Norte and southwestern Oregon but is otherwise restricted to California. Shoulderbands are found in a range of habitats, including moist areas on the northwest coast and dry hills in the Mojave Desert.

Many populations of native land snails have been lost because of urban and agricultural development. The species most vulnerable to extinction are the highly localized endemics, but this localization can also simplify their protection. Many species occur on public lands where, if land managers are aware of their presence and habitat needs, protective measures can ensure their persistence (Fig. 26). In many instances, overall ecosystem management will enhance native land snail populations. For example, restoration of native plant communities in the Channel Islands National Park should also restore native land snails. Releases of nonindigenous predatory snails—such as the decollate snail—to control brown garden snails, are an additional threat to the native fauna.

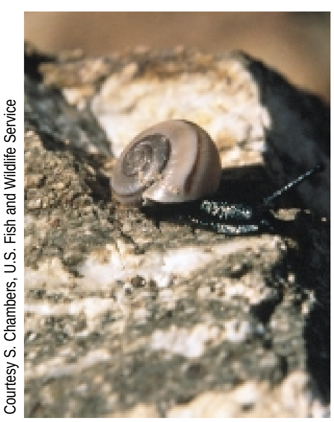
Courtesy S. Chambers, U.S. Fish and Wildlife Service

Fig. 26. The Coachella desert snail (Deep Canyon, Riverside County, California).

Patterns of Insect Diversity

As elsewhere in the United States, the richest habitats for insects in California occur in areas with at least moderate topographic relief

Channel Islands and California Desert Snail Fauna

The land snail faunas of the Channel Islands and the California deserts include many helminthoglyptid species (desert snails, shoulderbands, island snails, and allies). These are relatively well known, and their classifications are well documented and easy to describe. These regions provide only two examples of the diversity of California's land snail fauna. Snails and slugs found elsewhere in California are equally deserving of attention and conservation.

Channel Islands Snails

Southern California's Channel Islands are sometimes separated into two groups. The northern group (including San Miguel, Santa Rosa, Santa Cruz, and Anacapa islands) has been considered a westward extension of the Santa Monica Mountains on the mainland, although existence of a Pleistocene or Holocene connection to the mainland is now doubted (Junger and Johnson 1980). The southern group (Santa Barbara, San Nicolas, Santa Catalina, and San Clemente) is generally more remote from the mainland than the northern group.

The San Miguel shoulderband is endemic to the northern group of islands. This species has its closest known affinities with two coastal species from north of Point Conception in Santa Barbara and San Luis Obispo counties: the surf shoulderband and the endangered Morro shoulderband (Roth 1973; U.S. Fish and Wildlife 1994). Even without an earlier land bridge connection to the mainland, the ancestors of these snails could have reached these islands through over-water dispersal. Many land snails of arid or semiarid areas have features (reviewed by Chambers 1991) that permit them successful island colonization by dispersal on floating rafts of woody debris.

The southern group of islands is occupied by a much more diverse fauna that includes island snails and cactus snails. The island snails are single-island endemics on these islands and on Guadalupe Island, Baja California Norte, except the San Nicolas island snail, which also occurs as fossils on San Clemente Island (Roth 1975a,b). The cactus snails (formerly included with island snails by Pilsbry 1939) are made up of four living species. The plain cactus snail and the wreathed cactus snail are extant, single-island endemics that occur on San Clemente Island. The Catalina cactus snail has also been reported by Pilsbry (1939) from the Palos Verdes Peninsula, Los Angeles County, which is the only report of the genus outside of the southern group of Channel Islands. The co-occurrence of species of these two groups on each of these islands is another notable feature of their land snail fauna.

The Santa Barbara shelled slug has been found living only on Santa Barbara Island, although fossil shells have been found on San Nicolas Island (Roth 1975a; Hochberg 1979). The only other occurrences of this small group are the Guadalupe shelled slug of Guadalupe Island, Baja California Norte, and forms of limited known occurrence on the mainland of Baja California Norte (Roth 1975b).

An extremely curious element of the snail fauna of these islands is the Catalina mountain snail, which is endemic to Santa Catalina Island. This population occurs several hundred miles away from the nearest living related populations in southeastern Arizona and Baja California Sur. Because the original collector (Henry Hemphill in 1905) was not known for his care in handling specimens, and because subsequent workers failed to locate the species on Santa Catalina Island, this seemingly anomalous record was doubted for many years. Hochberg et al. (1987) provide a fascinating account of their rediscovery and verification of the identity of the species, along with documentation of its likely status as a relict of the group's formerly wider distribution.

The high incidence of endemism of land snails in the Channel Islands has probably resulted from the low frequency of interisland dispersal and the age of the islands. Formerly larger island areas during periods of lower sea levels (Roth 1975b) may have contributed to the high diversity seen today in the southern group of islands.

California Desert Snails

A diverse helminthoglyptid fauna has evolved in the Mojave and Colorado deserts of southeastern California (Pilsbry 1939; Bequaert and Miller 1973). Most distinctive are two desert snail groups limited to these California deserts and extending only to western Arizona and northern Mexico. Species of these groups mainly occupy rockslides in the bordering mountain ranges and the smaller, isolated ranges that are scattered throughout these deserts. Some of these ranges support endemic desert snails.

Two additional groups endemic to the northern Mojave Desert are each represented by a single species. The El Paso shoulderband is endemic to the El Paso Mountains, and the Argus desert snail is endemic to the Argus and Slate mountains (Pilsbry 1939).

The land snails of this desert fauna have probably evolved from ancestors that were more widespread during prolonged periods of moister climate (Wells and Berger 1967). They have probably survived in this most inhospitable (for snails) dry climate by remaining inactive deep within rockslides between rains. Isolated because of poor dispersal capabilities and lack of refuge from desiccation between rockslide areas, they have differentiated into the relict fauna observed today.

The shoulderband group is also represented by several localized species in the Mojave Desert. Endemic species occur in the El Paso (mimic shoulderband) and Panamint mountains (Panamint shoulderband). Two additional species occur near the Mojave River, which receives flow from snowmelt from the San Bernardino Mountains. Other desert shoulderbands occur at the edges of the deserts, such as near the San Gabriel (Soledad shoulderband) and Tehachapi mountains (Mojave shoulderband).

See end of chapter for references

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and with the richest array of native woody vines, trees, and shrubs. Such localities are often found along or adjacent to streambeds or valleys at low to moderate elevations in mountainous areas.

Notable invertebrate habitats in California that are either unique or limited elsewhere in the United States include coast redwood forests, serpentine grasslands, coastal and riverine dunes, chaparral, evergreen oak woodland, and coastal sage–scrub. The uniqueness and local nature of many of California's insects have resulted in either the extinction or endangerment of many species and subspecies. Fifteen of 27 U.S. insects listed as endangered or threatened under the U.S. Endangered Species Act are from California (U.S. Fish and Wildlife Service 1994b; Table 2).

Table 2. California invertebrates listed as endangered or threatened on the U.S. list of endangered and threatened wildlife (U.S. Fish and Wildlife Service 1994a).

Species	Status
Mollusks	
Morro shoulderband snail	Endangered
Insects	
Ash Meadows naucorid	Threatened
Bay checkerspot butterfly	Threatened
Delhi Sands flower-loving fly	Endangered
Delta green ground beetle	Threatened
El Segundo blue butterfly	Endangered
Kern primrose sphinx moth	Threatened
Lange's metalmark butterfly	Endangered
Lotis blue butterfly	Endangered
Mission blue butterfly	Endangered
Myrtle's silverspot butterfly	Endangered
Oregon silverspot butterfly	Threatened
Palos Verdes blue butterfly	Endangered
San Bruno elfin butterfly	Endangered
Smith's blue butterfly	Endangered
Valley elderberry longhorn beetle	Threatened
Crustaceans	
Shasta crayfish	Endangered
California freshwater shrimp	Endangered

Most listed California insects are subspecies of butterflies that occur in extremely localized habitats within 80 kilometers of the coast (Arnold 1983; Opler 1991; New 1993). The population structure and detailed status of six listed California butterflies were described by Arnold (1983), and the population size of the Lange's metalmark butterfly at the Antioch Dunes National Wildlife Refuge 80 kilometers east of San Francisco has been estimated during most years for more than 12 years. Management actions taken to improve the number and density of butterfly host plants at the refuge have been rewarded by fairly dramatic increases in the population size of the Lange's metalmark (Opler and Robinson 1986).

One of the longest continuously monitored populations of any animal is that of the Bay checkerspot butterfly, another listed species, on Jasper Ridge above the campus of Stanford University in central California. More than 120 insects and many other westside California invertebrates are species of special concern that are being monitored by The Nature Conservancy on behalf of the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1994b).

There have been no specific studies of invertebrates of old-growth forests in westside California, but a literature survey, review of museum material, and interviews with expert entomologists indicate that many arthropods are found primarily in north coast Douglas-fir and coast redwood old-growth forests (U.S. Fish and Wildlife Service 1995a; Opler, U.S. Geological Survey, Fort Collins, Colorado, and J. Lattin, Oregon State University, Corvallis, unpublished manuscript).

Some California habitats dominated by nonindigenous plants are virtually devoid of native insects, and presumably of other native invertebrates as well. Examples are urban environments dominated by plantings of nonindigenous ornamental trees, shrubs, and grasses; Coast Range, Sierra Nevada, or Transverse Range foothills dominated by Mediterranean grasses such as wild oats; or coastal strand and dunes taken over by European beachgrass (Slobodchikoff and Doyen 1977).

Fishes

The fish fauna of westside California is composed of 100 species (Moyle 1976a). The losses of fishes and fisheries represent national and global declines as well, because 31 of the 52 (60%) native westside California fish species are endemic (Table 3), and most of the remainder are confined to the Pacific coast. A report on the status of the California fish fauna (Moyle et al. 1995:1) addresses this regrettable situation:

> In the event these fishes are lost from California, they will be globally extinct; there are no populations in some distant or remote location that can be used to resurrect the local populations. These fishes represent millions of years of evolutionary response to the fluctuating and often harsh aquatic environments of the state. As a result, there is an extraordinary diversity of form and function among the native fishes. They are found in habitats ranging from tiny desert springs, to rivers that have huge fluctuations in flow, to high mountain streams, to shallow alkaline lakes, to salty estuaries. Although the native fishes are admirably suited for surviving the vagaries of nature, they have done poorly when forced to compete with humans for the waters which are their homes.

Table 3. California fishes of conservation concern, including endemic species (modified from Moyle 1976b; U.S. Fish and Wildlife Service 1994a,b). Status codes are C = full species endemic to California, to California and adjacent state, or to Baja California; E = presumed extinct in California; FE = federally endangered; and FT = federally threatened.

Species	Status
Arroyo chub	C
Blue chub	C
California killifish	C
California roach	C
Clear Lake splittail	C, E
Delta smelt	C, FE
Green sturgeon	C
Hardhead	C
Hitch	C
Kern brook lamprey	C, E
Klamath largescale sucker	C, E
Klamath River lamprey	C
Klamath smallscale sucker	C
Little Kern golden trout[a]	FT
Longjaw mudsucker	C
Lost River sucker	C, E
Marbled sculpin	C
Modoc sucker	C, E
Pit sculpin	C
Pitt–Klamath brook lamprey	C
Riffle sculpin	C
Rough sculpin	C
Sacramento blackfish	C
Sacramento perch	C
Sacramento splittail	C
Sacramento squawfish	C
Sacramento sucker	C
Santa Ana sucker	C
Shortnose sucker	C, E
Thicktail chub	C, E
Tidewater goby	C, FE
Tule perch	C
Unarmored three-spined stickleback[a]	FE

[a] Subspecies.

Although water diversion and use have seriously affected waterfowl, the native freshwater fishes and fisheries in California have been more seriously affected. Unique local populations and species are being extirpated or becoming extinct on a regular basis, and major fisheries have greatly declined (Moyle 1976a; Moyle and Williams 1990). The disappearance of native fishes and fisheries reflects the degree to which California's streams have been dammed and diverted, the poor condition of many watersheds that support the streams, and the detrimental effects of the many nonindigenous fishes and invertebrates that have been introduced into California's waters.

At present, 9 of the 116 fish taxa (species and subspecies) are extinct in California, 16 are formally listed as threatened or endangered, 25 probably qualify for listing as threatened or endangered, and 27 others require special management to prevent further declines that might put them in jeopardy (Moyle and Yoshiyama 1994; Moyle et al. 1995). In short, 67 (57%) of the taxa are either extinct or on the road to extinction if present trends continue. Not surprisingly, valuable fisheries for native fishes are also in decline, as salmon, steelhead, and other fish populations dwindle. Many of these fisheries are increasingly dependent on hatchery production, but the added fish production has not halted the declines, it has only slowed them down and may make recovery more difficult. The problems with fishes and fisheries can be seen by examining the status of anadromous fishes, Sacramento–San Joaquin estuarine fishes, Sierra Nevada fishes, and southern California fishes.

Anadromous Fishes

California supports the southernmost populations of 13 species of native anadromous (sea-run) fishes, plus 2 nonindigenous species (striped bass and American shad). All these species are in decline (Moyle 1994), which has resulted in major economic losses related to fisheries. The most visible declines are those of coho salmon, chinook salmon, and steelhead. Coho salmon were once abundant spawners in most coastal streams north of Monterey Bay; they have suffered a 90% decline in abundance over the past 50 years, and their populations have disappeared from about half the streams in which they once spawned (Brown et al. 1994). The principal causes of coho salmon decline seem to be loss of spawning habitat and juvenile rearing habitat in streams as the result of logging, road building, urbanization, and other factors.

Chinook salmon are the most abundant salmon in California and show remarkable adaptations to local conditions for spawning. In rivers of the Central Valley, for example, four distinct runs exist, maximizing the ability of the salmon to take advantage of unique conditions. In the nineteenth century, the annual runs of these fishes were 2–3 million per year in Central Valley rivers alone. Today, the Central Valley chinook runs are around 130,000 fishes per year (and declining), about 90% of which are fall-run chinook, a run supported mainly by fish hatcheries (Fisher 1994). The winter run is formally listed as endangered, and the spring and late fall runs qualify as such (Moyle et al. 1995). The single biggest cause of chinook salmon declines is that dams have cut off access to most of their historical spawning grounds. Their continuing decline in recent years is due to many factors, including habitat degradation and diversion of water from the Sacramento–San Joaquin estuary.

These same factors have contributed to the continuing decline of steelhead in the Central Valley, which now number only about 35,000 fishes annually, 90% of them of hatchery origin (California Department of Fish and Game 1990; Mills et al. 1996). In coastal streams, steelhead are still widely distributed as far south as Malibu Creek in Los Angeles County, but their numbers are greatly reduced, especially in southern California, where the populations are genetically distinct from more northern populations (Moyle et al. 1995). Steelhead co-occur in many streams with coho salmon and have declined for similar reasons. A number of Pacific salmon are on the threatened and endangered species list (see chapter on Marine Resources for current listings).

Sacramento–San Joaquin Estuary Fishes

The Sacramento–San Joaquin estuary is one of the most modified estuaries in North America, and its fishes and fisheries have suffered as a consequence (Herbold et al. 1992). Declines in striped bass, chinook salmon, steelhead, and American shad have been noted for the past 30 years, but the declines of other species, such as the endemic delta smelt and the longfin smelt, have only been noted more recently (Moyle et al. 1992). The decline in the fish populations has largely been linked to ever-increasing freshwater diversions from the estuary, but also to recently introduced nonindigenous species, pesticides, and other factors. The crisis in fish population declines, including two endangered species, led to the development of a 1994 Delta Native Fishes Recovery Plan by the U.S. Fish and Wildlife Service and an agreement (December 1994) on new estuarine standards among California and federal agencies, urban and agricultural water users, and environmental groups.

Sierra Nevada Fishes

The Sierra Nevada is the backbone of California and is the source of much of its agricultural and urban water. Sierra Nevada lakes and streams support 40 kinds of native fishes but are best known for 7 native trouts (California golden, Kern rainbow, Little Kern golden, Eagle Lake rainbow, Paiute cutthroat, steelhead, and Lahontan cutthroat; Moyle et al. 1995). Five of these forms would probably be extinct today (three are still listed as threatened species; U.S. Fish and Wildlife Service 1994a) if drastic action had not been taken by fisheries agencies to protect and improve their habitats, move fishes to new locations, and remove competing nonindigenous trouts from their streams.

The western Sierra Nevada also was once a major spawning region for anadromous fishes, primarily chinook salmon, steelhead, and Pacific lamprey, but these species are now relatively unimportant there. Overall, 22 of the 40 native fishes are threatened, declining rapidly, or otherwise in need of special protection (Moyle et al. 1995). As a consequence, the sport fisheries of the Sierra Nevada consist primarily of introduced nonindigenous fishes in reservoirs and streams.

Southern California Fishes

Nowhere in California is the fish fauna in more trouble than in the urbanized coastal areas of southern California (Swift et al. 1993; Moyle et al. 1995). Although only three of the native fish species (unarmored threespine stickleback, tidewater goby, southern steelhead) are listed as endangered, strong cases can be made for listing all of the native forms as endangered, including arroyo chub, Santa Ana sucker, and Santa Ana speckled dace. Indeed, a strong case can be made for designating the native aquatic ecosystems as endangered, if such a delineation were possible. The declines are all linked to the region's expanding human population; specific causes of the declines include dams and diversions, watershed urbanization, channelization of streams for flood control, pollution, and heavy recreational use of stream corridors.

Accounts similar to the decline of fishes, fisheries, and suitable fish habitat in southern California could be written for other regions of the state (for example, the Sacramento, Klamath, and Pit rivers). Widespread decline of native fishes (including economically and culturally important species) is associated with major alterations of aquatic habitats (Moyle 1995) and has occurred in the entire state. There are many indications that such trends can be halted and perhaps reversed when private landowners and public land users form cooperative alliances with public agencies and environmental groups to find solutions to the problems. To function well, such alliances require strong leadership, economic incentives, and good scientific information. In the long run, however, conservation of the fish fauna of California has to be part of a statewide strategy for the conservation of aquatic biodiversity (Moyle and Yoshiyama 1995).

Amphibians

For the past 5 years, considerable attention has been focused on the apparent decline of many amphibian species in North America and in other parts of the world (see reviews in Blaustein 1994). Although, as with the fishes, much of the overall decline of amphibians can be directly attributed to extensive habitat alteration and loss, a small component of amphibian population extinctions in seemingly pristine areas is currently unexplained (Blaustein and Wake 1995). California is one of the few places where such unexplained declines have been observed and are being studied (for example, Fellers and Drost 1993; Bradford et al. 1994; Jennings 1995). We describe here the present status of California's declining amphibian fauna and the species most at risk of extinction.

California currently has 77 amphibian species, which include all known species, subspecies, and undescribed forms. At least 43 (56%) are endemic or nearly so (Stebbins 1985; Jennings 1995; Fig. 27; Table 4). New species continue to be discovered and described (Wake 1994). Historically, only a handful of species were commercially exploited to the point of localized extinction (for example, see Bury and Stewart 1973; Jennings and Hayes 1985). However, a recent survey of the status of the state's native amphibian fauna revealed that 18 of 45 (40%) salamanders and 15 of 28 (54%) frogs are already protected or are in need of protection at the state or federal level (Jennings and Hayes 1994a; Table 4). Four salamanders and frogs are introduced forms that became established in the state during the twentieth century. The current status of native true toads and frogs is of particular concern, because during the past 25 years, 4 of 10 (40%) of the toad species and 7 of 8 (88%) of the frog species have disappeared from 45% or more of their historical California ranges (Table 5). The decline is especially significant in southern California, where all of the native frogs are either extirpated or on the verge of extinction (Jennings and Hayes 1994b; Jennings 1995).

The reasons for the decline and loss of certain native amphibians in California are varied. For example, all of the salamanders (Fig. 28) and some of the frogs (such as the California red-legged frog, foothill yellow-legged frog, and Yavapai leopard frog) have declined because of outright habitat loss from agriculture, livestock grazing, urbanization, placer mining, road construction, and large water-development projects (Jennings and Hayes 1994a). Some of the aquatic habitats relied on by these organisms have also been extensively altered by human-induced hydrological alterations and by nonindigenous vegetation (such as water hyacinth and saltcedar), so that they now support largely nonindigenous aquatic faunas. Virtually all of the major river systems and native grasslands of California have been changed by human activities to the point that they can no longer support several imperiled amphibians, such as Colorado River toads in the Colorado River Valley and California tiger salamanders in the Central Valley (Jennings and Hayes 1994a).


Courtesy M. R. Jennings, USGS

Fig. 28. Adult male Santa Cruz long-toed salamander, Santa Cruz County.

Additionally, the introduction of a wide variety of nonindigenous predatory fishes, bullfrogs, and crayfishes into natural and artificial waterways has resulted in the extirpation of much of the local native amphibian fauna through predation on vulnerable eggs, larvae, and juvenile life stages (Hayes and Jennings 1986; Bradford 1989; Bradford et al. 1993; Jennings and Hayes 1994b; Rosen and Schwalbe 1995). Predation on amphibians has been exacerbated by the extensive transplantation of trout into the originally fishless lakes of the Sierra Nevada, as well as the interbasin transfer of water that has occurred throughout California since the 1930's. The interbasin transfer of water has resulted in the establishment of many nonindigenous species in locations far from the area where they were originally introduced (Moyle 1976a).

Besides the human-related factors just listed, some amphibian declines and extinctions can be attributed to natural disasters such as flooding, drought, and fires (both natural and human-caused). For example, a pair of 500-year floods (that is, floods of a magnitude that usually occur only once every 500 years) in 1968–1969 effectively eliminated many native frog populations in southern California (Jennings and Hayes 1994b). In the Sierra Nevada foothills, 5 years of drought from 1988 to 1992 resulted in the extirpation of most of the remaining California red-legged frog populations (Jennings and Hayes 1994a; Jennings 1996; Fig. 29) and negatively affected many high-elevation populations of Yosemite toads as well (Sherman and Morton 1993). Sweet (1991) documented the

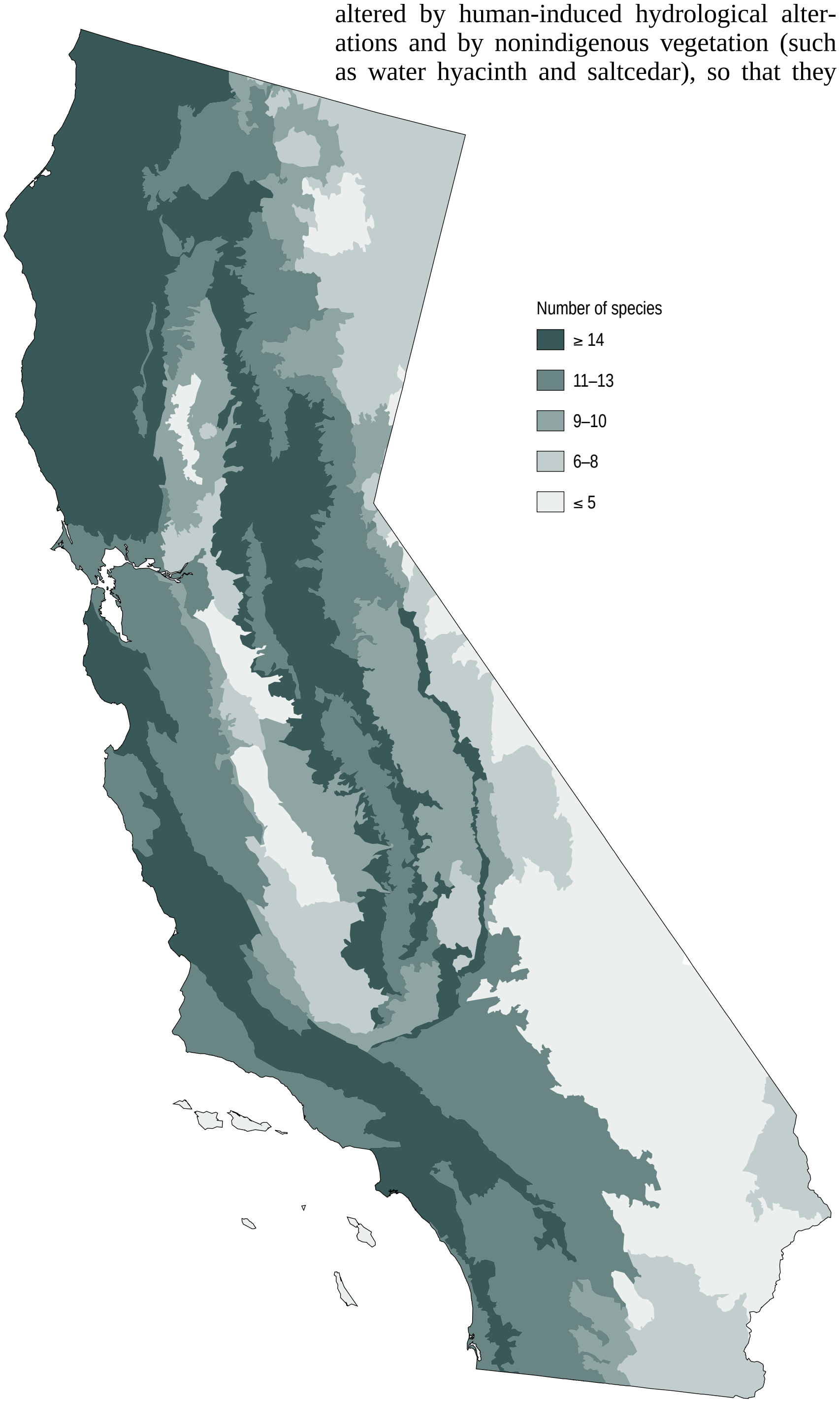

Fig. 27. Potential species richness of amphibians (total of 46 species) in California; 5-quantile classes by U.S. Department of Agriculture ecological subsection. Each class contains an equal number of data records. Note the concentrations of amphibians along the coast and in the mountains. Maps provided courtesy of the California Wildlife Habitat Relationships Program, Wildlife Management Division, California Department of Fish and Game, Sacramento.

Table 4. California amphibians, including endemic species and those of conservation concern (modified from Stebbins 1985; Jennings 1987; and Jennings and Hayes 1994a). Status codes are C = full species endemic to California, to California and a small part of an adjacent state, or to Baja California; E = presumed extinct in California; I = introduced; FE = federally endangered; FT = federally threatened; PE = proposed endangered; PT = proposed threatened; N = none; ST = state threatened; and SC = state species of special concern.

Species	Status
Salamanders	
Arboreal salamander	C
Black salamander	C
Black-bellied slender salamander	C
Breckenridge Mountain slender salamander	C, E, PE
California giant salamander	C
California slender salamander	C
California tiger salamander	C, PT[a]
Channel Islands slender salamander	C
Clouded salamander	N
Coast Range newt[b]	C, SC[c]
Del Norte salamander	SC
Desert slender salamander	C, FE
Dunn's salamander	N
Fairview slender salamander	C
Gabilan slender salamander	C
Garden slender salamander	C
Guadalupe slender salamander	C
Hell Hollow slender salamander	C
Inyo Mountains slender salamander	C, PT
Kern Canyon slender salamander	C, ST
Kern Plateau slender salamander	C
Large-blotched ensatina[b]	C, SC
Limestone salamander	C, ST
Monterey ensatina[b]	C
Mount Lyell salamander	C, SC
Northern rough-skinned newt[b]	N
Northwestern salamander	N
Oregon ensatina[b]	N
Owens Valley web-toed salamander	C, SC
Pacific giant salamander	N
Painted ensatina[b]	N
Red-bellied newt	C
Relictual slender salamander	C, SC
San Gabriel slender salamander	C
Santa Cruz long-toed salamander[b]	C, FE
Santa Lucia slender salamander	C
Shasta salamander	C, ST
Sierra Nevada ensatina[b]	C
Sierra newt[b]	C
Siskiyou Mountains salamander	ST
Southern long-toed salamander[b]	N
Southern seep salamander	C, PT[d]
Tehachapi slender salamander	C, ST
Tiger salamander	I?
Yellow-blotched ensatina[b]	C, SC
Yellow-eyed ensatina[b]	C
Frogs and toads	
African clawed frog	I
Arizona toad[b]	N
Arroyo toad[b]	FE
Black toad	C, ST
Bullfrog	I
California red-legged frog[b]	C, FT[e]
California toad[b]	C
California treefrog	N
Cascades chorus frog[b]	N
Cascades frog	SC, PE
Coast chorus frog[b]	N
Couch's spadefoot	SC
Foothill yellow-legged frog	C, SC, PT, PE
Great Basin spadefoot	N
Great Plains toad	N
Mountain yellow-legged frog	C, PT, PE[f]
Northern leopard frog	PE[g]
Northern red-legged frog[b]	SC
Oregon spotted frog	PE[h]
Pacific chorus frog[b]	N
Red-spotted toad	N
Rio Grande leopard frog	I
Sierra chorus frog[b]	C
Sonoran Desert toad	E, PE
Southwestern chorus frog[b]	N
Tailed frog	SC, PT
Western spadefoot	C, PT
Western toad[b]	N
Woodhouse's toad[b]	N
Yavapai leopard frog	E, PE
Yosemite toad	C, PT

[a] This salamander was found to be warranted but precluded from listing by the most recent ruling of the U.S. Fish and Wildlife Service (1994c).

[b] Subspecies.

[c] Southern California populations only (Jennings and Hayes 1994a).

[d] This salamander was recently petitioned to the U.S. Fish and Wildlife Service for listing under the Endangered Species Act (H. H. Welsh, U.S. Forest Service, Redwood Sciences Laboratory, Arcata, California, personal communication).

[e] A final rule for listing this frog as threatened was recently published by the U.S. Fish and Wildlife Service (1996).

[f] Southern California populations of this frog have been petitioned to the U.S. Fish and Wildlife Service for listing under the Endangered Species Act (M. C. Long, Eaton Canyon Nature Center, Pasadena, California, personal communication).

[g] Some populations in the Lake Tahoe basin are known to have been introduced (Bryant 1917; Jennings and Hayes 1994b).

[h] This frog was petitioned for listing under the Endangered Species Act by the Board of Directors of the Utah Nature Society (U.S. Fish and Wildlife Service 1989). Although a ruling has been made on this petition, the status of peripheral populations (such as those in California) is still under review (M. P. Hayes, Portland State University, Portland, Oregon, personal communication).

Table 5. Percentage of reduction of historical range of selected native California amphibians (data from Jennings and Hayes 1994a; Jennings 1995).

Species	Reduction in range (percent)
Arroyo toad	76
Breckenridge Mountain slender salamander	100
California red-legged frog[b]	75
California tiger salamander	55
Cascades frog	50
Foothill yellow-legged frog	45
Mountain yellow-legged frog	50/99[a]
Northern leopard frog	95
Northern red-legged frog[b]	15
Oregon spotted frog	99
Sonoran Desert toad	100
Western spadefoot	30/80[a]
Yavapai leopard frog	100
Yosemite toad	50

[a] Values are for central/southern California populations, respectively.

[b] Subspecies.

Fig. 29. Adult male California red-legged frog, Pescadero Natural Area, San Mateo County.

Fig. 30. Adult female arroyo toad, San Diego County.

loss of an arroyo toad population in southern California because of a wildfire burning the riparian zone it inhabited (Fig. 30).

In recent years, several kinds of native true toads and frogs have disappeared from seemingly pristine areas such as wilderness areas and national parks (Bradford 1991; Fellers and Drost 1993; Drost and Fellers 1994; Jennings and Hayes 1994a). Such losses are especially troubling since they indicate that even the traditional conservation practice of setting aside large protected areas may be insufficient to keep these amphibians from becoming extinct (Jennings 1995). A number of hypotheses have been put forth in an attempt to explain these declines and localized losses, including acid precipitation (Bradford et al. 1992, 1994), air pollution (T. Cahill, University of California, Davis, personal communication), increased ultraviolet radiation levels (Blaustein et al. 1994a), introduced pathogens (Blaustein et al. 1994b), and pesticides (Stebbins and Cohen 1995). None of these hypotheses, though, can convincingly explain the widespread amphibian declines, and there is great debate among herpetologists over their validity (for example, Pechmann et al. 1991; Blaustein 1994; Pechmann and Wilbur 1994).

In California and over much of the American West, unexplained amphibian declines seem to have the following in common: only true frogs and toads appear to be affected (for example, lists in Hayes and Jennings 1986; Scott 1993), death occurs in the postmetamorphic stages (that is, juvenile and adult frogs and toads), populations are able to successfully reproduce until all adults are extirpated, and die-offs are most pronounced at higher elevations (Carey 1993; Scott 1993). The most likely causes of this kind of mortality are natural or human-induced stressors (Scott 1993), such as increased UV-B levels or air pollution, which weaken the immune systems of host organisms. Disease organisms could either be natural or introduced. Whatever is occurring, it is apparent that mass die-offs of native frogs and toads have been observed in natural areas of California over the past 25 years (Bradford 1991; Scott 1993; M. R. Jennings, U.S. Geological Survey, unpublished data). Clearly, more study is needed to determine the exact causes of these amphibian losses.

Reptiles

California has a diverse nonmarine reptile fauna, including 5 freshwater turtles, 1 tortoise, 38 lizards, and 37 snakes (Stebbins 1985; Jennings 1987; Laudenslayer et al. 1991; Fig. 31). Three turtle species and one gecko are nonindigenous species. The California population of one native reptile, the Sonoran mud turtle, has probably been extirpated (Jennings 1987). Many of California's reptiles are common in much of western North America, but there are 14 endemic species (15%) with restricted ranges that include only some part of California or California and a portion of an adjacent state and Baja California (Stebbins 1985; Table 6). In addition, many species have one or more subspecies with limited ranges that include a portion of California.

Nomenclature of reptiles in California is in flux, and taxonomic relationships are in the process of being revised for a number of groups. Unlike the amphibians, which are threatened by factors that often appear to be systemic in nature, most terrestrial reptiles are threatened only by habitat conversion. Reptile species richness increases from north to south in California, along with an increase in average temperature and aridity (Fig. 31). Only a few species are found in the cool, moist northwestern corner of the state, whereas the southern tier of counties hosts a wide array of species (Stebbins 1985). Eleven taxa of special concern are listed in California's Natural History Diversity Database (California Department of Fish and Game 1996). Although some taxa, like the San Francisco garter snake, have very restricted ranges, limited range per se is not the primary threat to continued existence. In general, habitat destruction is the main cause of reptile population declines in California. This is evident because the distribution of species identified by either the state or federal governments as being at risk occurs primarily in areas where the greatest habitat manipulation has occurred in California: coastal urban development, Central Valley agriculture, and desert livestock and recreational habitat alteration.

Giant Garter Snake

The giant garter snake, which is federally listed as a threatened species in the Central Valley of California, demonstrates the effects of habitat changes on population size and species viability (Fig. 32). Historically, the giant garter snake ranged throughout the San Joaquin and

Sacramento River basins, inhabiting wetland habitats along streams and rivers, and perhaps parts of the major delta marshes as well (Brode 1988). Much of the Sacramento Valley wetland was probably suitable habitat for the giant garter snake when Europeans first arrived in California (Bryan 1923; Hinds 1952). By 1971, though, much of the Central Valley had been drained and converted to dryland agriculture, eliminating almost all the natural habitat of this snake (Brode 1988). In the Sacramento River basin, where rice cultivation has maintained some seasonal wetland habitat, the giant garter snake has occupied the rice fields and associated water delivery systems. Relatively healthy populations can still be found in the Sacramento basin.

The San Joaquin River basin has been more intensively manipulated than the Sacramento River basin. Most of the area was converted to dryland farms such as orchards or cotton, which are unsuitable habitats for giant garter snakes (Hansen and Brode 1980; Brode 1988), and it is not known whether any giant garter snakes remain in the San Joaquin basin. Any populations there must be very small and isolated. In the San Joaquin Valley, no individuals were captured during extensive surveys in 1985–1986, nor were they captured in additional surveys in 1995 (Brode 1988; J. Brode, California Department of Fish and Game, Sacramento, personal communication). Although there is

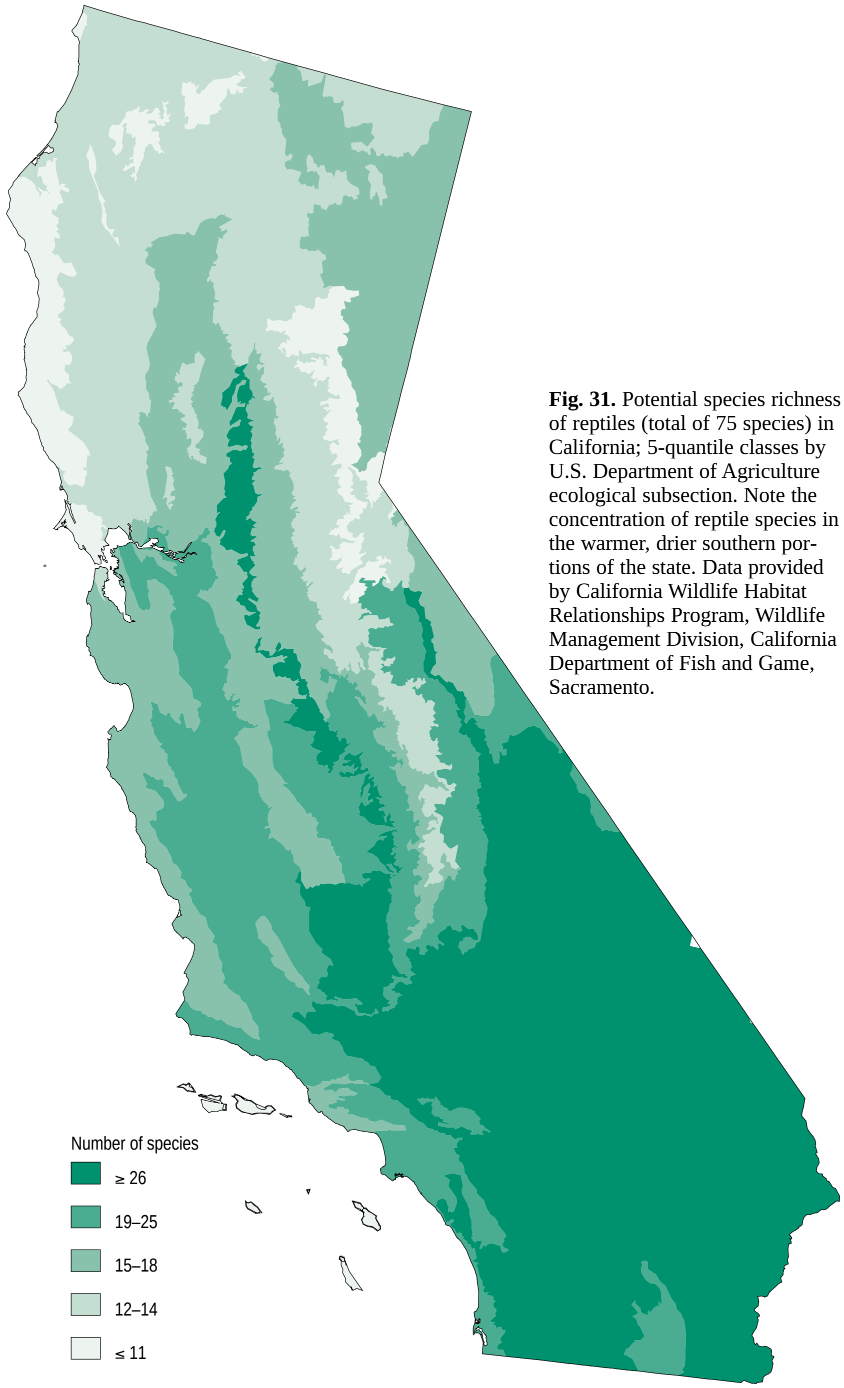

Fig. 31. Potential species richness of reptiles (total of 75 species) in California; 5-quantile classes by U.S. Department of Agriculture ecological subsection. Note the concentration of reptile species in the warmer, drier southern portions of the state. Data provided by California Wildlife Habitat Relationships Program, Wildlife Management Division, California Department of Fish and Game, Sacramento.

Table 6. California reptiles of conservation concern, including endemic species (modified from Stebbins 1985; Jennings 1987; Jennings and Hayes 1994a). Status codes are C = full species endemic to California, to California and an adjacent state, or to Baja California; E = presumed extinct in California; CE = California endangered; FE = federally endangered; FT = federally threatened; and ST = state threatened.

Species	Status
Tortoises and turtles	
Desert tortoise	FT, ST
Western pond turtle	C
Lizards, skinks, and geckos	
Blunt-nosed leopard lizard	C, FE, CE
California legless lizard	C
Coachella Valley fringe-toed lizard	C, CE, FT
Gilbert's skink	C
Granite night lizard	C
Island night lizard	C, FT
Mojave fringe-toed lizard	C
Panamint alligator lizard	C
Switak's banded gecko[a]	ST
Snakes	
Alameda striped racer[a]	ST
California black-headed snake	C
California mountain kingsnake	C
Giant garter snake[a]	ST
San Francisco garter snake[a]	FE, CE
Sharp-tailed snake	C
Sierra garter snake	C
Southern rubber boa[a]	ST
Striped racer	C

[a] Subspecies.

Courtesy T. Graham, USGS

Fig. 32. Giant garter snake, Gilsizer Slough, Sutter County, 1996.

some concern that agricultural pesticides may have played a role in the giant garter snake's decline, habitat alteration has unquestionably been the major factor.

Birds

California is rich in bird species, with 581 recorded as of 1991 (Zeiner et al. 1990a; Laudenslayer et al. 1991). This number includes migrants and species that breed or winter in California, as well as accidental and vagrant species. California birds range in size from the largest flying land bird in North America—the California condor (Pattee and Mesta 1995)—to the smallest bird in the United States, the tiny calliope hummingbird (Small 1994). Nearshore and pelagic marine birds are not considered here; they are discussed in the chapter on Marine Resources and are treated in detail elsewhere (Stallcup 1990). California is an important region for breeding, migrant, and wintering species, each of which we consider separately.

Breeding Birds

California's breeding avifauna consists of 293 species (Fig. 33), of which about 26 are exclusively nearshore and pelagic breeders. Twenty-three of these species breed only in eastside California, further reducing the nonmarine westside California avifauna to about 244 species. Sixteen bird species are either relatively narrow Pacific coast or Californian endemics, whereas only five (2%; California condor, Pacific-slope flycatcher, yellow-billed magpie, coastal California gnatcatcher, and tricolored blackbird) are either entirely limited to California (condor and magpie) or extend only a short distance north or south into Oregon or Baja California, respectively. Two of the five endemics are either ecologically extinct (California condor) or are in need of conservation intervention and management to assure their long-term survival (Table 7).

Unique species of westside California's bird fauna are those which breed primarily in the Central Valley (yellow-billed magpie and tricolored blackbird), in various forms of chaparral or brushland, and in foothill oak woodland. In the montane portions of westside California as well as in moist coastal forests, bird species tend to be widespread in at least western North America, although certain species (mountain quail, white-headed woodpecker, hermit warbler, and gray-crowned rosy-finch) are relatively restricted to the Pacific coast and possibly to small areas away from the coastal states.

Wintering Birds

While there are many more birds that winter in California than breed, there are similar numbers of species (Fig. 33). In addition to the breeding birds, many of which are year-round residents, massive numbers of birds that breed in Alaska, western Canada, and other Pacific Northwest states winter in California because of its relatively mild winter weather and rich food resources. Including birds that winter in the nearshore and pelagic marine zone, California supports 289 wintering species.

Wintering birds include huge numbers of waterfowl in freshwater, brackish, and saltwater environments. California, principally its coastal areas, harbors significant numbers of wintering shorebirds (Gill et al. 1995), gulls, and wading birds, although there are probably more shorebirds that pass through the state as spring and fall migrants. Some shorebird species, such as surfbirds, black turnstones, and black oystercatchers, winter only on the rocky coastline, but most species are found in California's restricted and shrinking estuarine mudflat habitats.

Waterbirds

California has a rich diversity of breeding, migratory, and wintering waterbirds (Cogswell 1977). In westside California, there are at least 64 breeding waterbird species. Sixteen of these species breed in nearshore or pelagic marine environments and are discussed in the chapter

Table 7. California birds of conservation concern (U.S. Fish and Wildlife Service 1994a; California Department of Fish and Game 1995). Status codes are FE = federally endangered; FT = federally threatened; CE = California endangered; and CT = California threatened.

Species	Status
Aleutian Canada goose[a]	FT
American peregrine falcon[a]	FE, CE
Arizona Bell's vireo[a]	CE
Bald eagle	FT, CE
Bank swallow	CT
Belding's savannah sparrow[a]	CE
California black rail[a]	CT
California clapper rail[a]	FE, CE
California condor	FE, CE
California least tern[a]	FE, CE
Coastal California gnatcatcher	FT
Elf owl	CE
Gila woodpecker	CE
Gilded flicker	CE
Great gray owl	CE
Greater sandhill crane[a]	CT
Inyo California towhee[a]	FT, CE
Least Bell's vireo[a]	FE, CE
Light-footed clapper rail[a]	FE, CE
Marbled murrelet	FE, CE
Northern spotted owl[a]	FT
San Clemente loggerhead shrike[a]	FE
San Clemente sage sparrow[a]	FT
Southwestern willow flycatcher[a]	FE
Swainson's hawk[a]	CT
Western snowy plover[a]	FT
Western yellow-billed cuckoo[a]	CE
Willow flycatcher	CE
Yuma clapper rail[a]	FE, CT

[a] Subspecies.

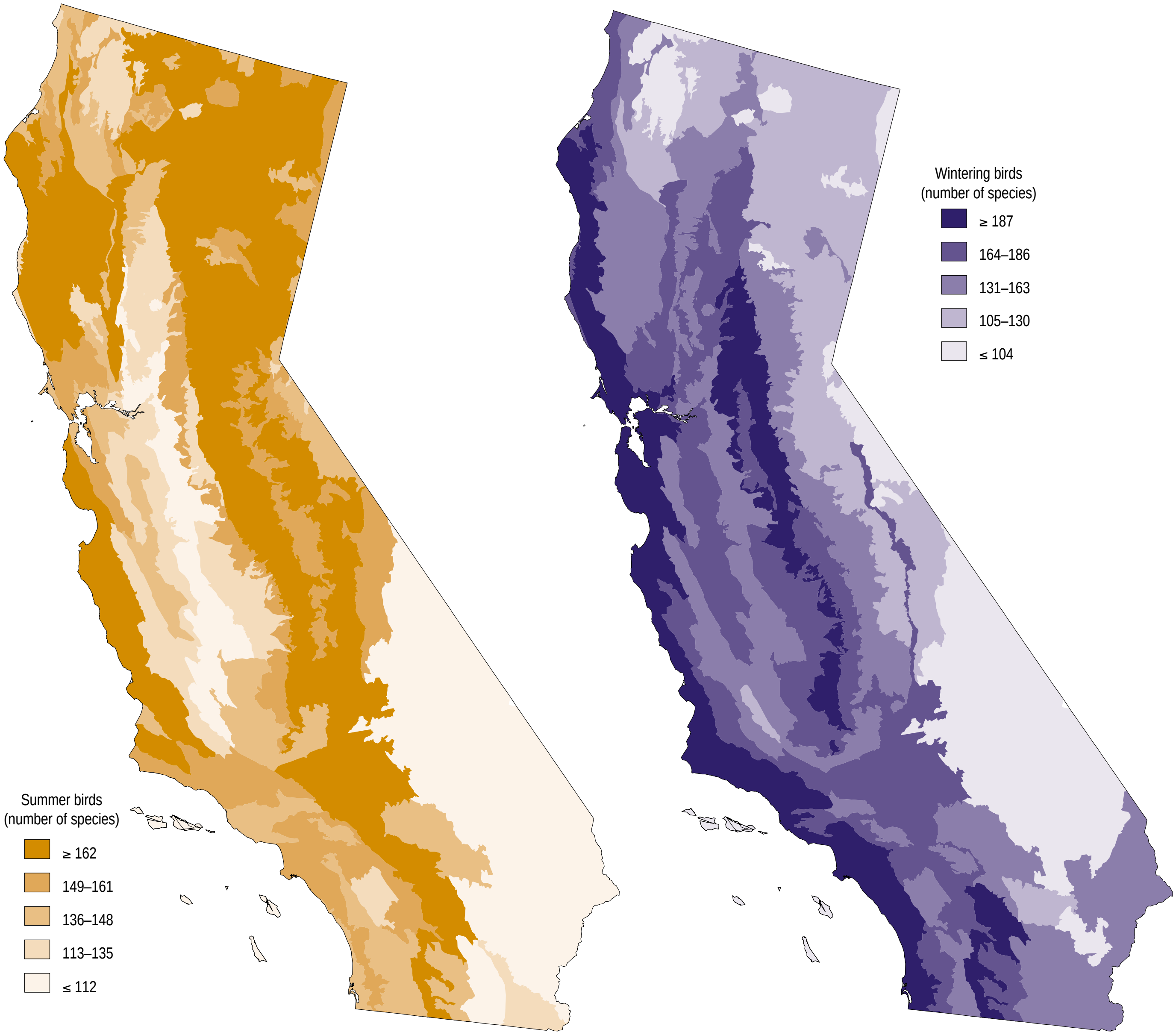

Fig. 33. Distribution of summer birds (mostly breeding; 293 species) and wintering birds (mostly nonbreeding; 289 species) in California by 5-quantile classes by quadrangle. Summer and winter range maps for California Wildlife Habitat Relationships System bird species were intersected with the boundaries of 2,831 1:24,000 scale topographic quadrangles. Each covers approximately 153 square kilometers and is labeled with the number of species that potentially occupy it. Data from California Wildlife Habitat Relationships Program, Wildlife Management Division, California Department of Fish and Game, Sacramento.

on Marine Resources, and 48 are coastal or inland breeders (Cogswell 1977; Stallcup 1990; Table 8). A number of additional waterbirds breed in northeastern or central eastern California (Mono and Topaz lakes), and the Salton Sea east of the Peninsular Ranges (Cogswell 1977). American white pelicans and fulvous whistling-ducks formerly bred in the San Joaquin Valley but no longer breed in westside California.

Westside California is rich in wintering, migratory, and postbreeding waterbirds, with more than 200 recorded species, including some rare visitors or vagrants (Cogswell 1977; Stallcup 1990). Although some species occur in both marine and more inland settings, an arbitrary division was made between marine and coastal or inland waterbirds, with 81 species considered entirely or primarily marine and 120 species being primarily coastal or inland in their occurrence (Table 8). Some terrestrial members of usual “waterbird” groups, such as mountain plovers and long-billed curlews, are arbitrarily grouped as waterbirds.

Several of the westside California waterbirds are on the U.S. list of threatened and endangered wildlife (U.S. Fish and Wildlife Service 1994a). These include the California and light-footed clapper rails, western snowy plover, California least tern, and marbled murrelet.

Table 8. Waterbirds of westside California.

Family or group	Breeding		Nonbreeding[a]	
	Marine	Nonmarine	Marine	Nonmarine
Loons	0	0	4	0
Grebes	0	3	2	4
Albatrosses	0	0	5	0
Shearwaters and petrels	0	0	10	0
Storm-petrels	3	0	8	0
Tropicbirds	0	0	3	0
Pelicans	1	1[b]	1	1
Boobies	0	0	3	0
Cormorants	2	1	2	1
Frigatebirds	0	0	1	0
Herons and allies	0	8	0	12
Storks	0	0	0	1
Ibises	0	1	0	3
Waterfowl	0	14[b]	11	27
Cranes	0	0	0	1
Rails and allies	0	7	0	6
Oystercatchers	1	0	2	0
Avocets and stilts	0	2	0	2
Plovers	0	2	0	9
Probing shorebirds	0	2	4	30
Phalaropes	0	1	1	2
Jaegers and skuas	0	0	5	0
Gulls and terns	3	3	7	18
Skimmers	0	0	0	1
Murres and allies	6	1	12	0
Kingfishers	0	1	0	1
Dippers	0	1	0	1
Total	16	48	81	120

[a] Includes wintering, migrant, or vagrant species.
[b] Includes one species that formerly bred in the San Joaquin Valley.

Waterfowl

As recently as the 1970's, an estimated 10–12 million waterfowl wintered in or migrated through California (U.S. Fish and Wildlife Service 1978). While California's upland birds depend on a variety of vegetation and habitat types, the great majority of the Pacific Flyway's migratory and overwintering waterfowl depend upon habitat in California's Central Valley.

Migratory waterfowl concentrations in the Central Valley are greatest during the fall and winter when migrants join local breeding birds. In recent years, approximately 2.5 million waterfowl wintered in the Central Valley (U.S. Fish and Wildlife Service 1987). This represents approximately 60% of all waterfowl wintering in the Pacific Flyway and about 20% of those wintering in the entire United States (Heitmeyer et al. 1989). Most of the continental populations of northern pintails, white-fronted geese, Ross's geese, cackling Canada geese, and Great Basin Canada geese and the entire populations of Aleutian Canada geese and Tule white-fronted geese winter in the Central Valley (Heitmeyer et al. 1989).

Land Birds

Although many insect-eating land birds leave California in winter, many fruit-eating, seed-eating, and bird of prey species winter in California. Examples of species that are absent or rare in summer but common to abundant in winter include the varied thrush and golden-crowned sparrow. Additionally, birds that breed at high elevations in summer may winter at lower elevations.

The California Fish and Game Commission lists 15 land birds as endangered or threatened under California law (California Department of Fish and Game 1995; Table 7), and there are 5 fully protected bird species in California (California Department of Fish and Game 1988).

Species of concern, also known as species at risk, are species monitored by The Nature Conservancy and are under consideration for possible addition to the list of federal endangered and threatened wildlife (U.S. Fish and Wildlife Service 1994a,b). The species of management concern list, developed and maintained by the Office of Migratory Bird Management of the U.S. Fish and Wildlife Service, identifies "32 species, subspecies, and populations of all migratory nongame birds that, without additional conservation action, are likely to become candidates for listing under the Endangered Species Act of 1973" in California (U.S. Fish and Wildlife Service 1995d).

Similar to the two federal species of concern programs, the California species of special concern is an informal designation used by the California Department of Fish and Game to identify declining and vulnerable species in the state (Remsen 1978). Presently, there are 45 land birds on the species of special concern list in California (California Department of Fish and Game 1992). Many species of special concern also occur on other California or federal species protection or management lists. The California species of special concern list is being revised; 20 land bird species or subspecies that are not mentioned on preceding lists are proposed for addition (S. Laymon, Kern River Research Center, Weldon, California, personal communication). Many species on California's species of special concern list are widespread elsewhere in the United States and are not included in Table 7.

Of the 342 species of land birds that occur in California, 73 (21.3%) are listed as California or federally threatened and endangered species (U.S. Fish and Wildlife Service 1994a; California Department of Fish and Game 1995), California fully protected species (California Department of Fish and Game 1988), federally designated species of concern (U.S. Fish and Wildlife Service 1994b) and species of management concern (U.S. Fish and Wildlife Service 1995d), or California species of concern (California Department of Fish and Game 1992). An additional 19 species show significant population declines (U.S. Geological

Western Snowy Plovers and California Least Terns

Western Snowy Plover

Western snowy plovers are small shorebirds that breed along the Pacific coast of the United States and northern Mexico as well as at interior sites in several western states (U.S. Fish and Wildlife Service 1993). The Pacific coast population was recently listed as threatened (U.S. Fish and Wildlife Service 1992, 1993). This population nests in Washington, Oregon, California, and Baja California, Mexico, and is associated with coastal wetlands and coastal dune habitat (Palacios and Alfaro 1994; Page et al. 1995). As much as half of the Pacific coast population may breed in Mexico (Palacios and Alfaro 1994). This population winters along the coasts of southern Oregon, California, and Baja California, Mexico (Page et al. 1995). Some snowy plovers that nest along the coast of California do not migrate in winter but remain on their breeding grounds (Stenzel et al. 1994; Powell et al. 1995; Fig. 1).

Courtesy A. Powell, USGS

Fig. 1. Western snowy plover nest, with two newly hatched chicks.

The decline and loss of western snowy plover populations along the Pacific coast have been attributed to habitat loss and disturbance caused by urbanization. At northern sites, the invasion of nonindigenous beach grasses has reduced available breeding habitat, including dunes with scant vegetation, dredge-spoil islands, natural salt panne, and salt evaporation pond levees. The greatest loss of plover habitat has occurred along the southern California coast (U.S. Fish and Wildlife Service 1993). In southern California, many of the plover's nesting sites are associated with breeding colonies of California least terns.

Causes of low reproductive success in western snowy plovers include loss and degradation of breeding habitat, inclement weather, human disturbance, and increased numbers of predators associated with urban areas, including domestic and feral dogs, feral cats, red foxes, American kestrels, common ravens, American crows, striped skunks, Virginia opossums, and raccoons. Predators may take adults, chicks, or eggs. Plovers are highly susceptible to human disturbance and, if disturbed sufficiently, may abandon their nests. In addition, eggs have been lost from being trampled and run over by vehicles. At one site in coastal California, humans were directly responsible for the loss of at least 14% of nests over a 6-year period (Warriner et al. 1986). Chicks that become separated from adults through human disturbance or predators may die of exposure. Annual reproductive success for coastal snowy plovers in California has ranged from 0.8–0.9 fledglings per female near Monterey Bay to 0.8–1.1 fledglings per female in San Diego County (Warriner et al. 1986; Powell et al. 1995). Predation rates and levels of human disturbance are probably higher in central and northern California because plovers nesting in southern California benefit from site protection and predator management associated with California least tern colonies.

Western snowy plovers have high breeding-site fidelity, but some movement occurs between sites within and between years (Stenzel et al. 1994; Page et al. 1995; Powell et al. 1995). In addition, there is site fidelity associated with wintering areas (Page et al. 1995; A. Powell, U.S. Geological Survey, San Diego, California, unpublished data). Although some plovers return to their natal site to breed, there are few data on natal site fidelity. Little is known about the genetic makeup of snowy plover populations; however, banding studies indicate little mixing occurs among breeding sites in southern California (Powell et al. 1995).

Regular, standardized monitoring of western snowy plovers along the Pacific coast has not been conducted on an annual basis. However, a 20% reduction in population size was reported from surveys between the late 1970's and late 1980's, and winter numbers obtained from Christmas Bird Counts along the California coast declined significantly between 1962 and 1984 (Page et al. 1995). Other evidence of population decline has come from the documentation of the loss of breeding sites. Before 1970 snowy plovers nested at 53 sites along the California coast; the number of sites available has since been reduced by 62%. Currently, about 78% of the California breeding population is supported at only eight sites (U. S. Fish and Wildlife Service 1993). The breeding range along California's coast has been significantly interrupted by the loss of all historical breeding sites in Los Angeles County and most of Orange County. Loss of habitat in these areas has been attributed to high levels of recreational beach use and the raking of beach sand (for removal of debris) on a regular basis. Only one site in Orange County has supported a few nesting pairs in recent years (Powell et al. 1995).

Breeding populations of western snowy plovers in California continue to decline despite relatively high reproductive success at selected sites (Fig. 2). Numbers of snowy plovers surveyed in California during the middle of the breeding season in 1989, 1991, and 1995 were 1,139, 1,180, and 967, respectively (G. Page, Point Reyes Bird Observatory, Stinson Beach, California, unpublished data). Western snowy plovers have only been afforded protection by the Endangered Species Act for a short time, and populations appear to be steady or in decline.

Management plans for snowy plovers need to include designation of critical habitat, protection of nesting areas from recreational use during the species' breeding season, increased monitoring of populations and their reproductive success, predator management, and education. There is some evidence of higher reproductive success for snowy plovers nesting in areas protected as California least tern breeding habitat, probably because of the limited recreational use and the predator management in these locations. However, many of the largest snowy plover breeding areas in California do not overlap with least tern colonies.

California Least Tern

California least terns (Fig. 3) are migratory and spend the breeding season, from April through August, along the central and southern California coast, as well as along northern Baja California, Mexico. Historically, the breeding range stretched from Monterey County, California, to Cabo San Lucas, Baja California Sur, Mexico (Atwood and Minsky 1983). California least terns nest in colonies on sandy beaches that are usually associated with river mouths or

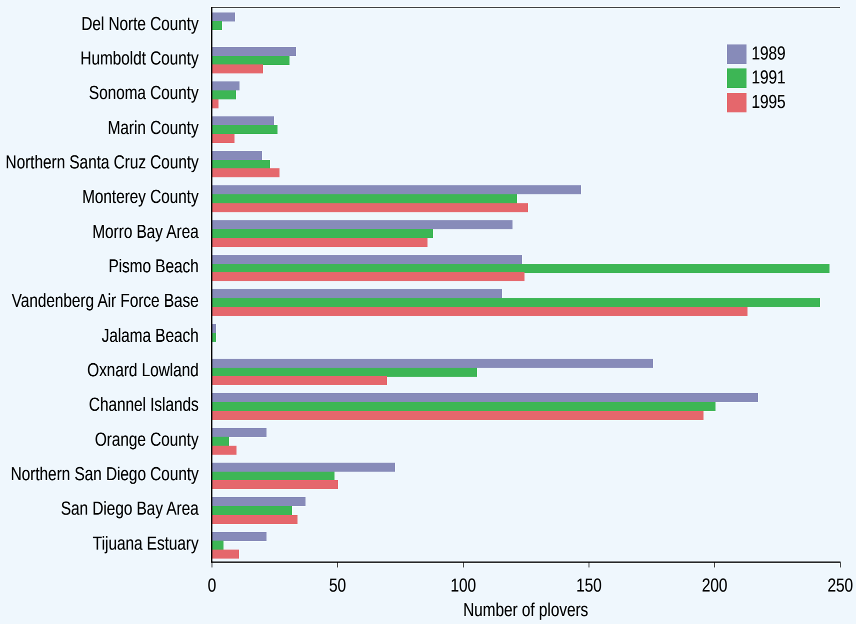

Fig. 2. Populations of breeding western snowy plovers during statewide surveys in California in 1989, 1991, and 1995. Sites are listed from north (top) to south (bottom). Data compiled by Gary Page, Point Reyes Bird Observatory, Stinson Beach, California.

estuaries. Nesting habitat has been degraded by high levels of human disturbance in sandy dune areas as well as by the effects of urbanization, including industrial, recreational, and residential development of the shoreline. Least terns, however, have successfully used created sites for nesting, including areas on dredge-spoil islands, open areas adjacent to airport runways, and industrial ports. Like snowy plovers, least terns are ground-nesting birds. They feed themselves and their chicks with small fish such as anchovies and topsmelts, captured from nearshore waters, estuaries, river mouths, and bays (Massey 1974; Atwood and Minsky 1983).

Low rates of reproductive success of California least terns have been linked to several factors. El Niño events, which cause nearshore water temperatures to rise, have depressed food availability for terns, which may in turn reduce tern productivity. The lowest annual production ever recorded for California least terns occurred after the 1982–1983 El Niño event, when fish populations off the shores of southern California plummeted (Massey et al. 1992). In addition to their vulnerability to catastrophic events, least tern colony sites in California have become restricted to fewer and smaller areas that are often surrounded by highly developed settings, leaving tern colonies susceptible to human disturbance as well as to intense predation. Predators associated with urban landscapes, such as domestic and feral dogs and cats, red foxes, American kestrels, American crows, common ravens, coyotes, raccoons, striped skunks, and Virginia opossums, eat least tern adults, chicks, and eggs.

Contaminants bioaccumulated in fish eaten by least terns may be another contributing factor to least terns' low reproductive success. Preliminary research on contaminants shows elevated levels of PCB's in California least tern eggs collected from sites around San Francisco Bay (Hothem and Zador 1995).

Although California least terns can and do nest again after losing eggs or chicks, some adults may abandon further breeding attempts that season (Fancher 1992). Least terns are fairly faithful to breeding sites and return year after year regardless of past nesting success. In addition, there is some evidence that least terns tend to return to their natal sites to breed (Atwood and Massey 1988). This may have major conservation implications because the average expected breeding life of California least terns is estimated at more than 9 years (Massey et al. 1992). Least terns breed after their second year, and first-time breeders are more likely to nest later in the breeding season (Massey and Atwood 1981).

Between 1978 and 1994, approximately 50 sites in California supported nesting least terns (Fancher 1992; Caffrey 1995). Fewer sites have been used in recent years; for example, only 36 sites were used in 1994 (Caffrey 1995). Furthermore, most California least terns nest at only a few select sites. In 1994, 76% of the population nested at nine sites, all in southernmost coastal California. Four of the nine sites (in Los Angeles, Orange, and San Diego counties) supported 48% of the breeding pairs (Caffrey 1995). In 1970, when California least terns were listed as endangered by the federal government and California, their population in California was estimated at 600 breeding pairs (Fancher 1992).

By 1994 the population had increased to an estimated 2,792 pairs (Fig. 4), which represents more than a fourfold increase (Caffrey 1995). Although the increase in the breeding population has not been consistent from year to year, long-term trends have

Courtesy A. Powell, USGS

Fig. 3. California least tern and chick.

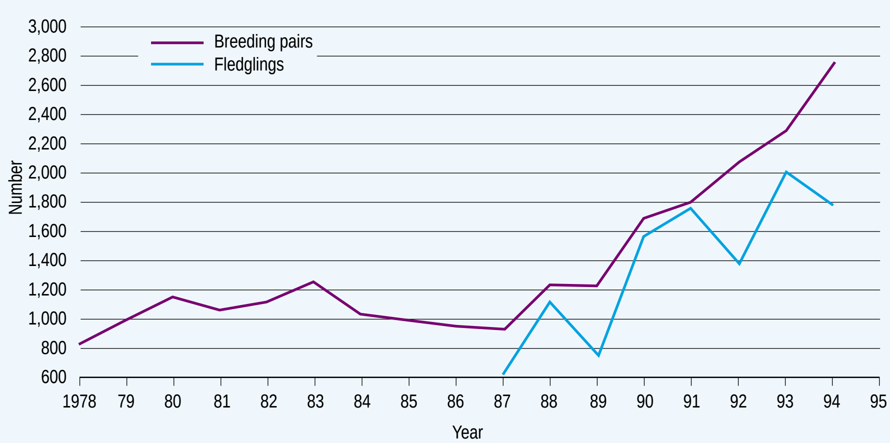

Fig. 4. Populations of breeding California least terns in California. Data compiled by the U.S. Fish and Wildlife Service and the California Department of Fish and Game.

shown steady population growth (Fig. 4). Tern population growth has been sustained even though ratios of fledglings to adults have fluctuated between colony sites and years (Massey et al. 1992; Caffrey 1995). Population growth rates have increased, especially since the mid-1980's, when active management for least terns was initiated.

Management of California least tern colonies has included intensive monitoring of nesting colonies, site preparation to reduce vegetative cover, protection of sites by means of reduced access to humans, and predator management. Although individual nesting sites may not be used every year, and reproductive success varies among sites and years, the population of least terns in California continues to grow. Historical breeding sites should be preserved and managed for least terns because their adaptability to new or different sites depends on past reproductive success, predation pressure, and food supplies.

See end of chapter for references

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Survey Breeding Bird Survey, Laurel, Maryland, unpublished data) but have no protection or management designation. However, this additional number of declining or vulnerable land bird species in California is likely an underestimate because it does not consider species that are underreported or unreported by the Breeding Bird Survey, nor does it account for all of the species that depend upon vulnerable or restricted habitats (for example, riparian obligate species). Finally, this estimate does not include all the species that are proposed for addition to protection or management lists (for example, species of special concern) but have not yet been officially approved.

For a majority of California's land bird species, population trends are unknown. According to the recently analyzed (1966–1994) Breeding Bird Survey data covering 145 of the 342 land bird species in California, for 110 of the 145 species, the population trend is either insignificant (no real change exhibited) or the number of Breeding Bird Survey routes is too small to provide a reliable estimate of the species' statewide population trend (B. Peterjohn, U.S. Geological Survey Breeding Bird Survey, Laurel, Maryland, personal communication). Thus, of California's 342 land bird species, there are only 35 species for which present Breeding Bird Survey population monitoring efforts in California provide a reliable estimate of the species' statewide population trend.

Further analysis of the land bird monitoring situation in California reveals that—excluding the 83 land bird species that are rare visitors to California (and are therefore difficult to monitor), the 20 state or federally listed land birds whose populations are already being monitored, and the 35 species with reliable Breeding Bird Survey population trend estimates—there are roughly 204 land bird species in California that require additional or alternative population monitoring efforts. More conventional monitoring (that is, additional Breeding Bird Survey routes) as well as alternative land bird population monitoring programs (for example, habitat-specific monitoring, night surveys, soaring bird surveys, winter surveys) are sorely needed to accurately assess the status and trends of land bird species in California.

The population trends of many of California's land bird species are estimated from data collected annually by the U.S. Geological Survey's Breeding Bird Survey. To furnish a reliable (statistically sound) analysis of land bird population trends in California, we consider only species that were observed on 33 or more Breeding Bird Survey routes (Peterjohn, personal communication) and whose 29-year (1966–1994) population trend is significantly increasing, decreasing, or stable.

According to the 29 years of Breeding Bird Survey data that are available between 1966 and 1994, 13 California land bird species show significant population increases: red-shouldered hawk, red-tailed hawk, nonindigenous rock dove, white-headed woodpecker, black phoebe, scrub-jay, American crow, common raven, white-breasted nuthatch, northern mockingbird, phainopepla, solitary vireo, and common yellowthroat (U.S. Geological Survey Breeding Bird Survey, unpublished data).

California land bird species that show significant population declines between 1966 and 1994 are American kestrel, band-tailed pigeon, mourning dove, belted kingfisher, olive-sided flycatcher, western wood-pewee, horned lark, northern rough-winged swallow, barn swallow, mountain chickadee, chestnut-backed chickadee, plain titmouse, Bewick's wren, American robin, Wilson's warbler, chipping sparrow, black-chinned sparrow, dark-eyed junco, western meadowlark, Brewer's blackbird, pine siskin, and American goldfinch (U.S. Geological Survey Breeding Bird Survey, unpublished data).

Five land bird species are subject to sport or commercial harvest under regulations of the California Fish and Game Commission: band-tailed pigeon, spotted dove, white-winged dove, mourning dove, and American crow

(Laudenslayer et al. 1991). Populations of both the band-tailed pigeon and the mourning dove have declined significantly from 1966 to 1994, whereas the American crow shows a significant population increase. No Breeding Bird Survey population trend estimates are reported for the spotted dove and the white-winged dove (U.S. Geological Survey Breeding Bird Survey, unpublished data).

Four species of feral introduced land birds are established and successfully breeding in California: rock dove, spotted dove, European starling, and house sparrow (Laudenslayer et al. 1991; Small 1994). The rock dove appears to be thriving in California and shows a significant increasing population trend (U.S. Geological Survey Breeding Bird Survey, unpublished data). Also, two native species, the ruddy ground-dove and the plumbeous solitary vireo, appear to be expanding their ranges into California (Small 1994). In addition, there are 83 land bird species that are occasionally seen in California and are considered rare visitors to the state (Laudenslayer et al. 1991; Small 1994).

A discussion of land bird population trends would not be complete without also mentioning the impact of the brown-headed cowbird on many species of land birds. Cowbird parasitism is the main reason that the least Bell's vireo and the willow flycatcher are endangered in California. The effect of the cowbird has increased dramatically as a result of agricultural rangeland expansion, which creates more foraging habitat for cowbirds as well as habitat fragmentation, both of which enable cowbirds to find a larger proportion of host nests (Palazzo 1994; Laymon, personal communication). Although efforts by California Fish and Game and U.S. Fish and Wildlife Service personnel to trap and remove cowbirds continue in areas throughout the state (Franzreb et al. 1994), the brown-headed cowbird does not yet show a significant population decline in California (U.S. Geological Survey Breeding Bird Survey, unpublished data).

Riparian habitats, mostly composed of willow, alder, cottonwood, and dense undergrowth bordering streams and lakes, are the richest terrestrial habitats for breeding and wintering land birds in California. Riparian habitats, however, have been converted to other uses in California at a faster rate than any other habitat, with the possible exception of perennial grasslands. Only 5%–10% of the original riparian habitat in California exists today, and much of what remains continues to be developed for flood control or is degraded by grazing, logging, water diversions, and the introduction of invasive nonindigenous plants. Riparian habitats support more endangered land bird species than any other habitat type in California. Birds that use or nest in riparian habitat are limited not only by the loss and degradation of this habitat but also by cowbird brood parasitism that is aided by riparian habitat fragmentation. Of the 36 land bird species that rely heavily or depend exclusively upon riparian habitat, 21 have undergone substantial population declines and are either legally protected by state or federal governments or appear on species of concern lists. Nine additional riparian obligate species show signs of population decline (U.S. Geological Survey Breeding Bird Survey, unpublished data) or are suggested for addition to the California list of species of special concern (Laymon, personal communication).

Mammals

There are 181 species of terrestrial and flying mammals that regularly occur in California (Fig. 34), 29 of which are endemics (16%) whose entire ranges are limited to California or to California and portions of another state and Baja California (Burt and Grossenheider 1976; Table 9). Fourteen mammal species are nonindigenous introductions (Ingles 1957; Zeiner et al. 1990b).

Five mammals that occurred in California at the time of European settlement are now extirpated from the state but can still be found elsewhere. The last California grizzly bear was killed in 1922 in Sequoia National Forest (Storer and Tevis 1955). The other four mammals—gray wolf, jaguar, bison, and white-tailed deer—were restricted in range and abundance, and our information about them is sparse and often contradictory (Steinhart 1990). Wolves were recorded with some regularity in the Modoc Plateau region of northeastern California, where they were apparently an extension of Oregon and Nevada populations; the last record for that area is 1922 (Jameson and Peeters 1988). The Modoc Plateau country was also where bison and white-tailed deer populations were found in the early 1800's. Jaguars may have ranged north from Mexico as far as the Monterey Bay area in the early nineteenth century, but they were probably always rare. The last recorded jaguar in California was killed in Palm Springs in 1860 (Jameson and Peeters 1988).

Mammals at Risk

As large portions of many ecosystems have been destroyed, fragmented, or altered by development and subdivision, many populations of native mammals have decreased in direct proportion to the loss in their habitats. Fourteen nonmarine California mammals are on the U.S. list of endangered and threatened wildlife (U.S. Fish and Wildlife Service 1994a) or are listed as endangered or threatened under California law. The federally listed species include the San Joaquin kit fox, Fresno kangaroo rat, giant kangaroo rat, Morro Bay kangaroo rat, Stephens' kangaroo rat, Tipton kangaroo rat, salt marsh harvest mouse, and Amargosa vole; California lists the Mojave ground squirrel, Sierra Nevada red fox, Channel Islands gray fox, wolverine, California bighorn sheep, and peninsular bighorn sheep.

As a further indication of declining or at-risk California mammal populations, 49 additional species or subspecies are listed by the state as mammals of special concern, and the state is reconsidering a further 38 taxa for that status (including those already on the state list; P. Brylski, Santa Barbara Museum of Natural History, California, personal communication). Most of these are federal species of special concern.

Table 9. California mammals of conservation concern, including endemic species (modified from Burt and Grossenheider 1976; U.S. Fish and Wildlife Service 1994a). Status codes are C = full species endemic to California, to California and adjacent state, or to Baja California; E = presumed extinct in California; CE = California endangered; FE = federally endangered; and ST = state threatened.

Species	Status
Agile kangaroo rat	C
Amargosa vole[a]	FE, CE
Broad-footed mole	C
Brush rabbit	C
California bighorn sheep[a]	ST
California ground squirrel	C
California mouse	C
California pocket mouse	C
California vole	C
Channel Islands gray fox	ST
Dusky-footed woodrat	C
Fresno kangaroo rat	C, FE, CE
Giant kangaroo rat	C, FE, CE
Heermann's kangaroo rat	C
Lodgepole chipmunk	C
Long-eared chipmunk	C
Merriam's chipmunk	C
Mohave ground squirrel	C, ST
Morro Bay kangaroo rat[a]	FE, CE
Mountain pocket gopher	C
Mt. Lyell shrew	C
Narrow-faced kangaroo rat	C
Nelson's antelope squirrel	C, ST
Ornate shrew	C
Pacific shrew	C
Panamint kangaroo rat	C
Peninsular bighorn sheep[a]	ST
Red tree vole	C
Salt marsh harvest mouse	C, FE, CE
San Diego pocket mouse	C
San Joaquin kit fox[a]	FE, ST
San Joaquin pocket mouse	C
Sierra Nevada red fox[a]	ST
Sonoma chipmunk	C
Stephens' kangaroo rat	C, FE, ST
Tipton kangaroo rat[a]	FE, CE
Wolverine	ST
Yellow-eared pocket mouse	C

[a] Subspecies.

In earlier times, mammals most at risk were large carnivores such as the grizzly bear, jaguar, and mountain lion, as well as furbearing species including the fisher, marten, red fox, river otter, and wolverine. These species declined as a result of being hunted or trapped; many appear to have recovered significantly under the protection afforded them since trapping days (Schempf and White 1977).

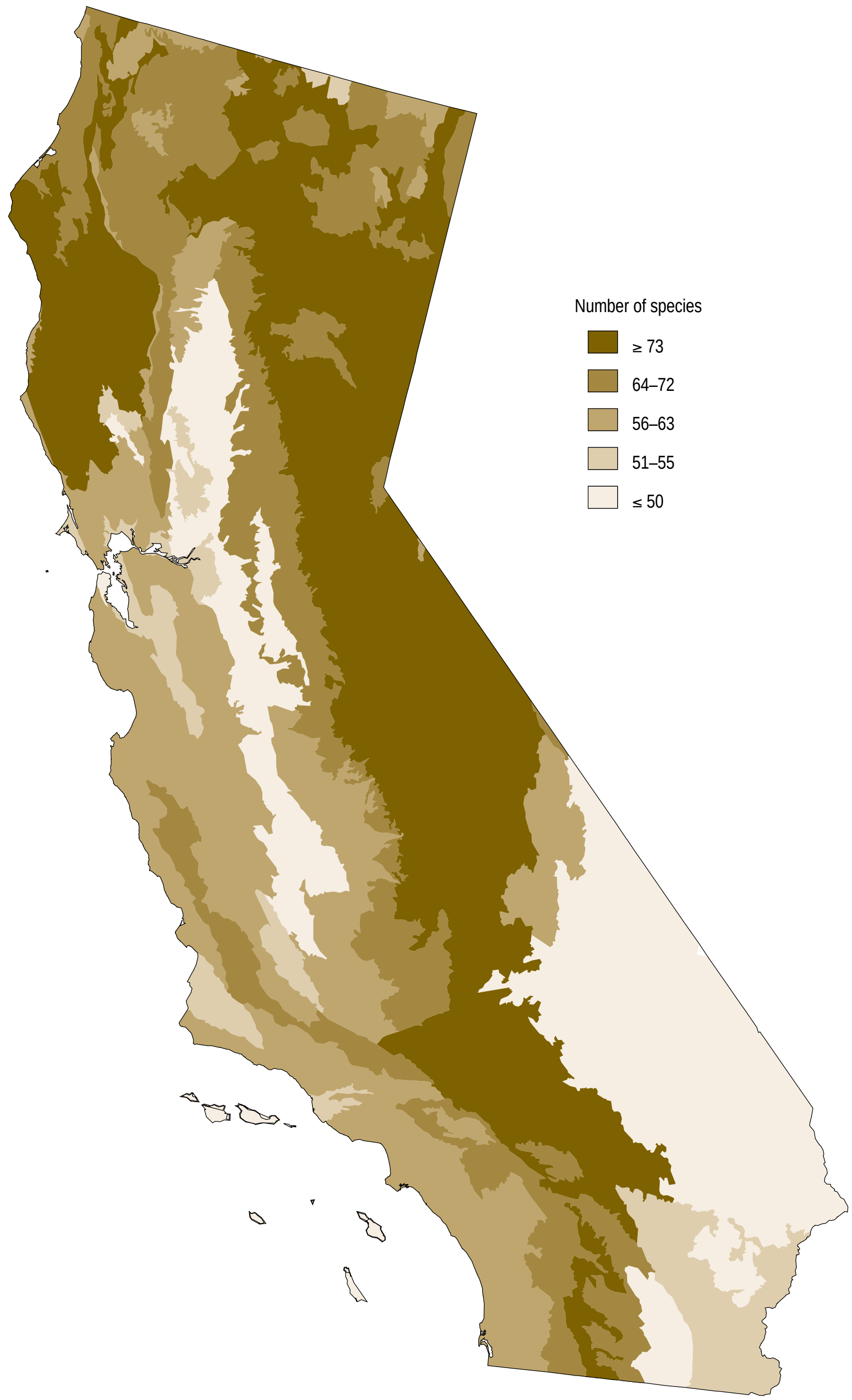

Fig. 34. Potential species richness of mammals (181 species) in California; 5-quantile classes by U.S. Department of Agriculture ecological subsection. Data provided by California Wildlife Habitat Relationships Program, Wildlife Management Division, California Department of Fish and Game, Sacramento.

On the other hand, taxa on contemporary lists are mostly rodents, bats, and other insectivores. These creatures are listed largely because of habitat loss or modification (see chapter on Land Use), and in the case of bats, perhaps because of pesticide poisoning as well (see box on Southwestern Bats in Southwest chapter). Many of the small rodents, especially kangaroo rats, are moderately to highly localized subspecies occupying habitats that have been almost completely converted to agriculture or to housing developments. Most species at risk are not native to montane or desert habitats but occupy the valleys and coastal plains where settlement and agriculture are intense. The most endangered biological communities in California are those of the Central Valley grasslands and the coastal scrub and chaparral communities (Fig. 35).

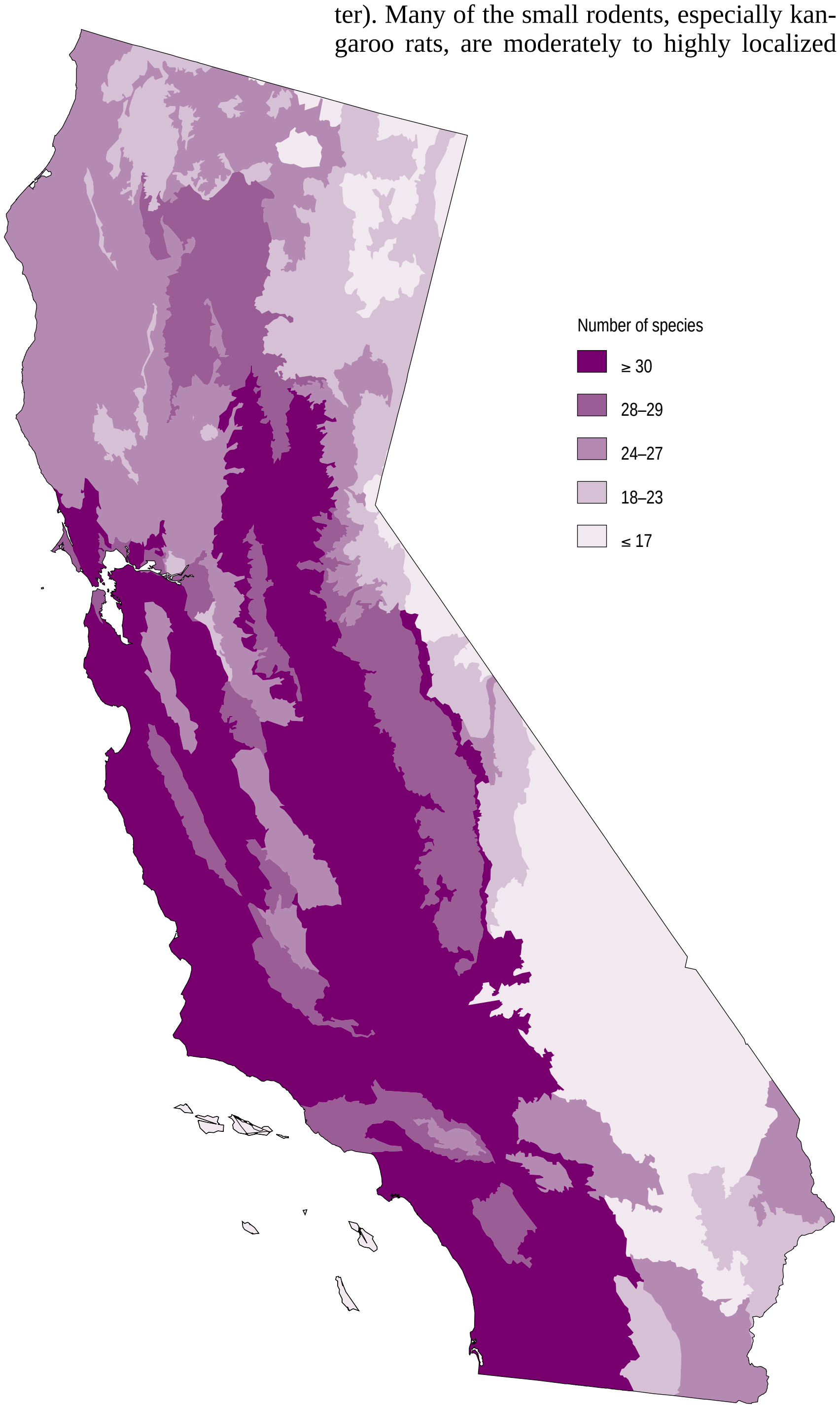

Fig. 35. Species richness of threatened, endangered, and candidate terrestrial vertebrates (94 species) in California by 10-quantile classes; range maps for species were intersected with 1:24,000 scale topographic quadrangles of approximately 153 square kilometers. Each map is labeled with the number of threatened, endangered, or candidate species that potentially occupy the region. Note the concentration of species in urbanized coastal areas and the Central Valley. Data provided by California Department of Fish and Game.

It is important to note that for most California mammals, abundance and distribution records are poor, localized, and often quite old. Many of these species and their distributions were described in the first half of the century, during the "golden age" of trapping.

Nonindigenous Mammals

The nonindigenous mammals of California include the classic human symbionts—house mouse, Norway rat, and black rat; these are virtually restricted to regions of moderate to dense settlement. Several mammals were introduced for fur trapping: Virginia opossums in Palm Springs in 1910, which are now widespread in all but deserts and mountains above about 1,500 meters; muskrats, introduced to the Central Valley and now widespread in waterways there; and nonindigenous subspecies of the red fox, which escaped from fur farms and now occur in small populations over much of western California. All three of these species can be considered pests to varying degrees. Opossums overturn garbage cans and consume the eggs of native birds. Muskrats have compromised the integrity of the artificial water systems of California by their burrowing. Introduced red foxes pose a potential threat to the genetic integrity of the native Sierra Nevada red fox and ravage the nests of endangered coastal shorebirds.

Wild pigs, introduced throughout westside California as game animals (as well as released or escaped domestic forms), are now widely recognized as significant ecological and agricultural pests of western parks and farmlands. Fallow deer, sambar, Axis deer, and Barbary sheep are all introduced game species now highly localized in California. The population of feral goats, also localized, has probably arisen from escaped and released individuals.

Mammals of the Sierra Nevada

In the Sierra Nevada, 84 terrestrial vertebrate species are considered dependent on riparian habitat (including wet meadow or lakeshore) to sustain viable populations; 24% of these are considered at risk. Eighteen species are similarly dependent upon late successional forests; 28% of these are considered at risk. There are

85 species that require west-slope foothill savannah, woodland, chaparral, or riparian habitats (some species are also counted as riparian-dependent) for Sierran population viability; 16% of these species are listed as at risk. This latter number is misleadingly low because many of these species are more widely distributed elsewhere, such as in the Coast Ranges (California Department of Fish and Game 1994; D. Graber, National Park Service, Three Rivers, California, unpublished data).

Seventeen bat species are believed to inhabit the Sierra Nevada. Of these, seven have been nominated for listing under the Endangered Species Act. Three of those and one additional species have been listed as sensitive or of special concern. Concerns began about many bat species when populations using known historical roosts were noticeably smaller or had disappeared entirely. An obvious potential culprit in these declines has been pesticides, because bats are insectivorous. But habitat requirements of most bat species have been based on studies at a very small number of sites. More recent work by E. Pierson (University of California, Berkeley) and others in California suggests that the large, old trees and snags associated with late successional forests may be quite important to long-eared myotis and long-legged myotis, as healthy populations have been found only in late successional forests. The large trees and snags of conifers are riddled with cavities and crevices that provide thermal protection for these bats. The presence of spotted bats, Brazilian free-tailed bats, and western mastiff-bats is correlated with meadows, whereas many, if not most, Sierran bats forage over water, especially in riparian corridors. As bats use lower elevations for part of the year, loss of high-quality riparian habitat there may be a factor in the apparent decline of many species. Relatively high densities of spotted and mastiff-bats have been found only near the substantial cliffs in large river drainages such as the Kings, Kaweah, Merced, and Tuolumne rivers (E. Pierson and W. Rainey, W. Rainey, and E. Pierson and P. Heady, University of California, Berkeley, unpublished reports; Pierson, personal communication).

As in other places in the West, bighorn sheep populations in the Sierra Nevada were decimated following the arrival of Europeans in the mid-nineteenth century (Buechner 1960). Sheep populations in the Sierra Nevada were originally scattered along the crest and east slope from Sonora Pass south, and along the Great Western Divide of what is now Sequoia National Park; there was also a population in the Truckee River drainage (Jones 1950; Wehausen 1988). Likely causes for the precipitous population decline include market hunting, severe overgrazing by domestic stock, and, probably most importantly, the transmission from domestic sheep of respiratory bacteria fatal to mountain sheep.

Bighorn sheep had been extirpated from the Yosemite region before the turn of the century (Grinnell and Storer 1924). By the 1970's, only two populations remained: one near Mt. Baxter (about 220 sheep) and the other on Mt. Williamson (about 30 sheep), west of Independence. The Mt. Baxter herd increased during the 1970's (Wehausen 1980), and from 1979 until 1988 this population was used by the California Department of Fish and Game, in cooperation with the U.S. Forest Service and the National Park Service, to successfully reestablish herds near Wheeler Ridge, Mt. Langley, and Lee Vining Canyon. Some mountain lions were removed from the Lee Vining Canyon area to reduce significant losses while that sheep herd was becoming established. By 1990 the three introduced herds were all increasing, and the overall Sierra bighorn population was at least 300 (Bleich et al. 1990).

Between 1977 and 1987, reports of mountain lion depredation of mountain sheep in Inyo and Mono counties, as well as in California as a whole, increased dramatically (Foley et al. 1996). During that period, 50 mountain sheep from the Mt. Baxter herd were lost to predation on the herd's escarpment base winter range. Losses from mountain lion predation were detected in the other herds as well. During the extended drought of the late 1980's and early 1990's, the herds gradually abandoned their low-elevation winter ranges for much higher elevation sites that, although inferior from the standpoint of forage and protection from cold, were relatively snow-free during the drought and afforded protection from predation. This profound behavior change is attributed to heavy mountain lion predation pressure in the traditional low-elevation ranges (J. D. Wehausen, University of California, Bishop, personal communication). Concurrent with this behavior change has been a steady decline in the bighorn sheep populations. The Mt. Baxter population included 108 ewes in 1978; no more than 20 were counted in 1995. Twelve sheep died in a single avalanche on Wheeler Ridge in 1995, and only 10 ewes remain as a reproductive base. The Lee Vining Canyon population declined from 36 ewes in 1993 to 14 in 1995. Whether because of accidents or an inferior energetic balance, the new situation is distinctly pessimistic. As of summer 1996, the rangewide Sierra Nevada bighorn sheep population had been reduced to about 150 individuals—well below the 250 recorded in the original reintroduction in 1979.

There is no reason to assume that mountain lion populations were smaller before settlement, although they may well have fluctuated significantly over time. But whereas mountain sheep were widespread in the Sierra Nevada at settlement, they only persist in scattered small pockets of high-elevation habitat where snow depths are tolerable and mountain lions are absent.

Information Gaps

In California, the status and trends of vegetation are better known than those of the fauna. Researchers are proceeding to describe regional overviews of the distribution and conservation status of major terrestrial plant species and communities (Davis et al. 1995). In addition, a framework for characterizing communities statewide exists in the new *Manual of California Vegetation* (Sawyer and Keeler-Wolf 1995). California botanists are working together to define future needs in the study of California floristics (Mishler et al. 1995). Rare plant taxa and state and federally listed species are fairly well described and managed. Bioregional conservation and development planning that focuses on plant communities, as demonstrated by the California coastal sage–scrub Natural Community Conservation Planning process, is increasingly recognized as a tool for protecting natural diversity in an increasingly urbanized landscape (State of California 1993; McCaull 1994; Fig. 36). The threats to biodiversity presented by invasion of nonindigenous weeds and altered fire regimes are increasingly well understood, but implementation of effective programs to systematically monitor or manage these threats lags severely (van Wagtendonk 1985; Keeley 1995; Schierenbeck 1995). Land management agencies have begun to inventory and monitor the vegetation under their stewardship. Although much of the systematic monitoring is in relation to consumptive resource uses, such as timber harvest and grazing, some monitoring, including the model broad-spectrum program of the National Park Service at the Channel Islands National Park (Davis and Halvorson 1988), encompass natural communities not now subjected to consumptive uses. Rare plants are tracked by the Rare Plant Program of the California Native Plant Society; Skinner and Pavlick (1994) identify research needed for their perpetuation.

Many of the programs we have mentioned are pilot programs or are still being developed. Actual practices lag far behind. In 1991 only 11% of Bureau of Land Management lands in California had been adequately inventoried for special status plants, and only 6% of those were being monitored (Willoughby 1995). Although the U.S. Fish and Wildlife Service is responsible for enforcing the Endangered Species Act, complete botanical inventories for the agency's refuge lands in California do not exist (Knight 1995). The National Park Service is assembling a national flora of parklands (NPFLORA data base), but the species lists from most parklands in California are old and usually incomplete. The California Department of Fish and Game administers more than 300,000 hectares of land, including 3,665 hectares in 14 ecological reserves managed specifically for native or rare plant populations, but most of these lands have not been thoroughly inventoried, and only a few priority plant populations are monitored (Morey 1995). Lower plant taxa are much more poorly known and less well monitored. Lichens are extremely sensitive indicators of air quality changes, but they are poorly monitored and not widely known.

The status and trends of most of California's more than 50,000 invertebrate species are either unknown or poorly known. In fact, the estimated number probably includes many hundreds of undescribed species. On the other hand, some of California's invertebrates are among the best-monitored animal populations on the continent, and it is not appropriate to assume that the status of any particular species or population is unknown without having sought the information. For example, the Jasper Ridge population of the threatened bay checkerspot butterfly above Stanford University has been monitored in great detail for more than 30 consecutive years (P. R. Ehrlich et al., Stanford University, Stanford, California, unpublished data). To a lesser degree, populations of several other listed butterflies have been closely monitored, some sporadically, for 20 years or more. Populations of other insects, such as the listed California elderberry longhorn beetle, are relatively well surveyed. The status of other insect groups, insects of certain localities or habitats, and some economically important species is well known, but much of the information is scattered in the literature or is unpublished.

Still there is a need for a much greater effort at surveying California's invertebrates that are or may be of conservation concern. The fact that parks or reserves have been established for vertebrates or plants implies neither that the state's invertebrates are equally protected nor that appropriate management actions are being taken on behalf of invertebrates on existing tracts of protected land.

Data for the status of most vertebrate taxa in California are poor and are largely based on surveys conducted in the 1930's. Data for population trends often represent short time periods or exist for only a few locations. Existing status and trend data are largely inadequate for the

Fig. 36. Urbanized landscape, looking across San Francisco Bay to San Francisco and the Bay Bridge.

basic policy and land management decisions essential for protection, listing, delisting, or habitat management. Better surveys and monitoring of density, distribution, and habitat relations—such as those being conducted in the coastal sage–scrub community for amphibians, reptiles, small mammals, and birds, and in the Channel Islands National Park terrestrial and nearshore marine communities—are much needed in many other California habitat types.

Time-series and geographic data for status and trends exist for only a few groups of vertebrates, including the long-term transects of the North American Breeding Bird Survey in California and long-term monitoring of important game species, such as mule deer and waterfowl. Observations of birds, often made by volunteers who contribute to data bases such as the annual Christmas Bird Counts, provide a large, if limited, data set. For other species, range and habitat type maps have been developed by drawing upon the location data from museum specimens and extrapolating this data onto maps (U.S. Geological Survey, Western Ecological Research Center, Davis, unpublished data). These voucher specimens were collected over a period as great as a hundred years, and many or most locations are represented by specimens collected in the early or middle part of this century. Few surveys have been repeated. Recent repeat surveys, such as those for the amphibians in the national parks of California (Drost and Fellers 1994, 1996) and in California in general (Jennings and Hayes 1994a), have been launched as a result of recognition by individual herpetologists of broad species losses and not as a result of systematic assessments of status and trends by government agencies.

Files of national forest, national park, and Department of Fish and Game biologists, some county agencies, and many private land managers and landowners, often contain records of observations of rare or unusual wildlife, many with behavioral or habitat-use information attached. Although this information is of far less value than systematic scientific surveys, long-term studies, or investigations of species–habitat relations, it can be valuable for improving the resolution of distribution information and for making inferences about habitat preferences and other ecological characteristics of the species. At present, there is no efficient way to locate these data.

The California Natural Diversity Database, managed by the California Department of Fish and Game, keeps site records of agency-listed plant and animal species in the state. It has the potential to serve as a clearinghouse and manager of data on all species throughout California but to be effective would require a budget many times its present one. This would be an invaluable service to land managers, landowners, and government agencies throughout California. The California Environmental Resources Evaluation System is a pilot effort to make natural resource information available to the public, agencies, and businesses via the Internet; however, the value of the information delivery system is limited by the quality and quantity of information available.

A promising synthesis of the Breeding Bird Survey and the California Wildlife Habitat Relationships System, entitled Avesbase, has been produced by the U.S. Forest Service, Pacific Southwest Region (Davidson and Manley 1993). This computer database and analytical program combines information about population trends and habitat distributions for Neotropical migrant birds as an aid in assessing their risk in California.

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The status of fishes in the waters of the state as reported here is subject to rapid change as a result of changes in land use and continuing accidental and intentional introductions. Some threatened species and populations are currently monitored, but statewide trends are not systematically tracked. Invertebrates are poorly monitored, except for a few taxa of special concern. Because the distribution and abundance of many invertebrates are extremely variable in time, meaningful monitoring is difficult, and our knowledge of lower forms of all taxa is extremely limited. We still have much work ahead of us to understand the effects of human-created processes upon other organisms, and conversely, to understand the significance to humans of changes in the micro- and macrobiota of California's valuable ecosystems.

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