# THE REDWOOD FOREST

## History, Ecology, and Conservation of the Coast Redwoods

*Edited by*

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Save-the-Redwoods League

**ISLAND PRESS**

Washington, D.C. • Covelo, California

Library of Congress Cataloging-in-Publication Data
The redwood forest : history, ecology, and conservation of the coast redwoods / edited by Reed F. Noss.
p. cm.
"A project of Save-the-Redwoods League."
Includes bibliographical references and index.
ISBN 1–55963–725–0 (cloth). — ISBN 1–55963–726–9 (pbk.)
1. Redwood. 2. Redwood—Ecology. 3. Forest ecology. 4. Forest conservation. I. Noss, Reed F. II. Save-the-Redwoods League.
SD397.R3R455 2000
634.9'758—dc21 99-16799
CIP

Printed on recycled, acid-free paper

Manufactured in the United States of America
10 9 8 7 6 5 4 3 2 1

Chapter 5

# Terrestrial Fauna of Redwood Forests

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The redwood forests support an unknown but large number of invertebrate species and, over all seasons, more than two hundred species of vertebrates (A. Cooperrider, unpub. comp.). Beyond this, knowledge of the redwoods fauna is surprisingly limited. Despite the enormous public attention that has been focused on redwood forests in recent years, comparatively little has been written about the ecology of their terrestrial fauna. One explanation for this deficiency is that few animal species are endemic to the redwood region and no known species is restricted to redwood stands. Although the biogeography of redwood forests and associated fauna has not been well studied, the evidence suggests that most vertebrate species opportunistically adapted to life in the redwoods relatively recently, rather than having coevolved with redwoods over a long period of geologic time. Vertebrate species lists from redwood and Douglas-fir forests in the redwood region show few differences (table 5.1), with a nearly 95 percent

*Author contributions:* Cooperrider, lead writer and organizer; Noss, writing and editing throughout; Welsh, amphibians and reptiles; Carroll and Zielinski, forest carnivores; Olson, invertebrates; Nelson, marbled murrelet; Marcot, editing throughout and contribution to table on endemics.

Table 5.1. Similarity of Terrestrial Vertebrate Fauna of Redwood and Douglas-fir Forests.

| | *Number of Native Species* | | |
|---|---|---|---|
| | *Redwood Forest* | *Douglas-fir Forest* | *Species in Common* |
| Amphibians | 18 | 18 | 16 |
| Reptiles | 16 | 18 | 15 |
| Birds | 105 | 110 | 101 |
| Mammals | 63 | 66 | 61 |
| Total | 202 | 212 | 193 |

*Note:* Data are derived from the California Wildlife Habitat Relationships (California WHR) system (Mayer and Laudenslayer 1988; Zeiner et al. 1988, 1990a,b). Nonnative species have been excluded, but no effort was made to revise or correct the WHR (i.e., several reviewers pointed out errors in the WHR, which we will assume balance each other in species numbers).

overlap in species presence; furthermore, the species that account for the 5 percent dissimilarity are not species characteristic of one type or the other. Nevertheless, the redwood forests contain some of the older and more sensitive vertebrate taxa that characterize the temperate rain forests of the Pacific Coast.

## Vertebrate Distributions

Most of this chapter focuses on vertebrates because information on invertebrates in redwood forests is extremely limited. Invertebrates are addressed, however, as the first of three "case studies" of redwoods fauna later in this chapter. Below we review the biogeographic history and current biogeography of terrestrial vertebrates in redwoods.

### *Historical Biogeography*

The amphibians and reptiles (herpetofauna) of the temperate rainforests of the Pacific Northwest, inclusive of the redwoods, appear to have derived from at least three historical sources. The oldest group probably evolved *in situ* from an Eocene or earlier origin, at least 50 million years ago; some of the progenitors of these species (e.g., the salamander genera *Aneides* and *Plethodon*) had a transcontinental distribution that was fragmented by tectonic uplift and mountain-building during the Miocene (5–20 million years ago; Welsh 1990). Lineages with this history have been referred to as the Western American Complex of the Old Northern Element (Savage 1960). Other examples include the giant salamanders, the torrent salamanders, salamanders of the genus *Ensatina*, the tailed frog, and a reptile, the western pond turtle.

A second component of the Pacific Northwest herpetofauna had a relatively

recent Asian origin, having diffused across the Bering land bridge during the Pleistocene about one million years ago (the Holarctic Element; Savage 1960). Members of this group include the red-legged frogs (two subspecies) and the western toad. Lineages of the Western American Complex of the Old Northern Element and the Holarctic Element have been described as temporally distinct components of a Pacific Northwest track (Welsh 1988).

The third group of Pacific Northwest herpetofauna is the Madrean Track (*sensu* Welsh 1988). This track derives from the south, with forms radiating northward during the Pliocene-Pleistocene from earlier origins in the Sierra Madre Occidental region of Mexico. It consists of species that diffused both north and west into present-day Arizona and California, and then south onto the Baja California peninsula (Welsh 1988). Madrean Track forms in the Pacific Northwest include the salamander genera *Batrachoseps* and *Hydromantes,* the frog genus *Pseudacris* (formerly *Hyla*), and most of the genera of snakes and lizards that occur in the redwood zone (e.g., *Sceloporus, Elgaria, Eumeces,* and *Thamnophis;* see complete list in Welsh 1988). Several snake and lizard lineages are members of the North American Desert and Plains Track (Welsh 1988) and are at the extremes of their distributions in the mesic Pacific Northwest (e.g., gopher snake, common kingsnake).

The mammals of the redwood region also have diverse origins. Some groups, including the marsupials (now extinct in the region, except for the Virginia opossum, an introduced species from eastern North America), multituberculates (extinct egg-laying mammals, probably ancestral to the monotremes), and some placental mammals, apparently evolved in North America or other portions of Laurasia from reptile-like progenitors; they were well established as a diverse assemblage across much of North America by the early Cretaceous, 135 million years ago (Eisenberg 1981). Other mammal groups immigrated from Eurasia at various times. By the late Cretaceous, 70 million years ago, North America had been invaded by several families of Asian placental and multituberculate mammals. Other early mammal groups apparently migrated directly through a Europe–North America connection about 50 million years ago, when Asia and Europe were separated (Hallam 1994); many of these archaic groups were lost in a late Eocene extinction. The largest extinction of North American mammals occurred during the Miocene, about 6 million years ago, during a period of rapid climate change.

During the Pliocene, about 5–3 million years ago, beavers (*Castor*) and bears (*Ursus*) arrived from Eurasia, probably crossing the Bering Strait. Also during the Pliocene, porcupines arrived from South America via the newly created Isthmus of Panama (Hallam 1994). Interchange between North America and Eurasia continued across the Bering land bridge during the Pleistocene. Elephants (e.g., *Mammuthus*) arrived in North America about 1.6 million years ago, and the first wave of humans (*Homo*) arrived at least 25,000 years ago

(Hallam 1994). Elk, members of the genus *Martes* (marten, fisher), and some other mammals also arrived from Eurasia and have close relatives in the Old World today. Many mammals of the Pacific states, as elsewhere in North America, went extinct during the Pleistocene, especially toward the end of the epoch (Ingles 1965). The late-Pleistocene extinctions have been attributed to overkill by humans (Martin 1984), but climatic changes certainly played a role (Webb and Barnosky 1989). Many mammals found in the redwood region today appear to be relatively recent (post-Pleistocene) arrivals to the West Coast.

The origin of redwood forest birds is even more complex and difficult to generalize about because of the small fossil record and birds' great mobility and wide-ranging migratory habits. Most of the modern families of birds in North America and Europe were there by the early Oligocene, some 35 million years ago (Martin 1983). Some of the less-mobile birds of the redwood forest, such as the blue and ruffed grouse, are closely related to Eurasian species and have no South American counterparts. Thus, their origin probably parallels that of the mammals that show a circumboreal, Northern Hemisphere distribution. Most of the bird species in the redwoods today, however, are neotropical migrants—species that migrate from North America to tropical regions of Mexico and Central and South America. Many of them, such as the nine warblers (family Parulidae), are members of groups that are widespread in South America but not found in Eurasia, although their origins within the Americas are complex (Darlington 1957; Brown and Gibson 1983).

## *Current Biogeography*

Among amphibians and reptiles, member lineages of the Pacific Northwest Track occur throughout the redwood zone. Several genera of amphibians have more than one species in the Pacific Northwest, and some (e.g., *Dicamptodon, Plethodon,* and *Aneides*) have more than one species in the redwoods. The single reptile member of this track, the western pond turtle, occurs in larger streams and rivers, as well as ponds, throughout the redwoods region and most of the Pacific Northwest (though it is in decline). Some member lineages of the Madrean Track (i.e., *Batrachoseps* and *Pseudacris regilla*) reach far northward and occur throughout the redwood forest. Many of the reptiles members of this track, and those of the North American Desert and Plains Track, are near or at their physiological limits in the cool, moist habitats that characterize these forests and are therefore patchy in occurrence and more likely to be found in ecotonal habitats, where they can bask to maintain critical physiological functions.

The birds and mammals of the redwood forest are, for the most part, much less responsive to the moisture regime of the habitat and are not restricted to moist habitats. Rather, most are widely distributed along the Pacific Coast, the

western states, or the continent. In generalizing about the Pacific coastal rain forest, Bunnell and Chan-McLeod (1997) concluded that although the area is extremely rich in vertebrate diversity, relatively few species (41 species; 11 percent of the total) are restricted to the region. Of these 41 Pacific coastal rain-forest species, 21 are found in the redwood forest, which represents the southern terminus of the region. This includes 12 of the 21 amphibians, all 3 reptiles, and 8 of 11 mammals, but none of the 6 bird species. The bird species included in Bunnell and McLeod's categorization are all coastal species (five seabirds and one shorebird) rather than forest dwellers.

## *Endemism and Near-Endemism*

No species or subspecies of vertebrate is known to be strictly endemic to the redwood forest. Several species and subspecies, however, are endemic to the redwood region and several more are near-endemic (table 5.2). The red-bellied newt is found largely in redwood forests, but also in other habitats (Stebbins 1985; Petranka 1998). Some of the species listed in table 5.2 have extremely limited distributions. For example, the Santa Cruz long-toed salamander is found in a small area of Santa Cruz County but has never been reported in redwood forest. Several families of amphibians are endemic to the temperate rain forests of the Pacific Northwest; they comprise a large part of the amphibian fauna of the redwoods. These families are the Ascaphidae, a frog family with a single species (the tailed frog), considered the most primitive extant frog on earth (Ford and Cannatella 1993); the Dicamptodontidae, the giant salamanders, which are the largest terrestrial salamanders in the world; and the Rhyacotritonidae, the very ancient and primitive torrent salamanders (Good and Wake 1992). This high endemism at the family level is unusual, normally found only at much larger geographic scales.

Six species of birds—blue grouse, Steller's jay, pygmy nuthatch, hermit thrush, hairy woodpecker, and red crossbill—have subspecies confined to the coastal coniferous forest, including the redwood region, but the species are much more widespread, occurring in montane forest as well (Small 1974). Because many ornithologists no longer recognize subspecies, and the American Ornithologists' Union no longer maintains a checklist of subspecies, these birds (if any were to qualify) are not listed in table 5.2. One mammal species and several subspecies are more or less confined to the redwood region.

Although it appears that no species or subspecies is restricted to redwood forests, many are found largely within the redwood region. The ultimate survival of several taxa is probably tied to the persistence of these forests. The temperate rain forest of the Pacific Coast, inclusive of the redwoods, contains many ancient, "long-branch" animal taxa indicative of *in situ* evolution over millennia. The fauna of late-seral (i.e., mature and old- growth) redwoods likely represents

Table 5.2. Terrestrial or Amphibious Vertebrate Species Endemic or Near-Endemic (i.e., > 75% of Total Range) to the Redwood Region.

| *Species* | *Endemism and Status* | *Range* | *Habitat* | *Source* |
|---|---|---|---|---|
| AMPHIBIANS | | | | |
| California giant salamander (*Dicamptodon ensatus*) | Endemic to redwood region | From Sonoma and Napa Counties south to Santa Cruz Co. | In and about permanent and semipermanent streams in mesic coastal forests | Good 1989, Petranka 1998 |
| Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*) | Endemic to redwood region; G5T1/S1, FE, CE, CP | Small portion of Santa Cruz and Monterey Counties, around Monterey Bay | Under debris near water; not reported in redwood forests | Smith 1978, Petranka 1998 |
| California slender salamander (*Batrachoseps attenuatus*) | Near-endemic to redwood region | Extreme southwestern Oregon south in coast ranges to slightly south of San Francisco Bay; also in west foothills of Sierra Nevada | Under logs and rocks in forests and other habitats, including grasslands, chaparral, and oak woodlands | Leonard et al. 1993, Yanov 1980, Petranka 1998 |
| Red-bellied newt (*Taricha rivularis*) | Endemic to redwood region and virtually to redwood forest | Northwestern California in Sonoma, Mendocino, and Humboldt Counties | Along clean, rocky streams with moderately fast flow; in redwood forests, but also Douglas-fir/hardwood and meadows | Stebbins 1985, Petranka 1998, H. Welsh pers. obs. |
| Del Norte salamander (*Plethodon elongatus*) | Near-endemic to redwood region; G3/S3, CSC, CP | Southwestern Oregon and northwestern California Coast Ranges | Rocky talus and outcrops within old redwood and Douglas-fir forests | Welsh 1990, Raphael 1988, Diller and Wallace 1994, Petranka 1998 |
| California (southern) clouded salamander (*Aneides vagrans*) | Near-endemic to redwood region; recently split from A. ferreus | From the South Fork of the Smith River in extreme northwestern California to just north of San Francisco Bay | Coarse woody debris and large logs in coastal forests; highly arboreal, nesting up to >40 m in redwoods | Petranka 1998, T. Jackman pers. comm. |
| Black salamander (*Aneides flavipunctatus*) | Near-endemic to redwood region | Extreme southwestern Oregon south into Santa | Decaying logs or stumps or wet talus within mature | Leonard et al. 1993, Raphael 1988, |

| | | | | |
|---|---|---|---|---|
| | | Cruz and Santa Clara Counties, California | mixed evergreen and hardwood forests | Petranka 1998 |
| **Reptiles** | | | | |
| San Francisco garter snake (*Thamnophis sirtalis infernalis*) | Endemic to redwood region; subspecies of common garter snake; G5T2/S2, FE, CE, CSC, CP | Western portion of San Francisco Peninsula from about S.F. Co. line south along crest of hills at least to Crystal Lake and along coast to Point Ano Nuevo, San Mateo Co. | Ponds, marshes, roadside ditches, streams, meadows, city lots; near water, within coastal scrub forest and redwood forest | Bounty and Rossman 1995 |
| Pacific Coast aquatic garter snake (*Thamnophis attratus attratus*) | Near-endemic to redwood region | From southwestern Oregonto Sonoma and Marin Counties, where it intergrades with T.a. hydrophilus | Primarily rivers and streams, but also other aquatic habitats | Rossman et al. 1996 |
| Pacific Coast aquatic garter snake (*Thamnophis attratus hydrophilus*) | Near-endemic to redwood region | From Big Sur coast around San Simeon north to Sonoma and Marin Counties, where it intergrades with T.a. attratus | Primarily rivers and streams,but also other aquatic habitats | Rossman et al. 1996 |
| Coast garter snake (*Thamnophis elegans terrestris*) | Near-endemic to redwood region; subspecies of western terrestrial garter snake | Coast ranges from southern Oregon to Point Conception, California | A variety of habitats, including grassland, brushland, woodland, and forest, from sea level to mountains | Stebbins 1966, Rossman et al. 1996 |
| **Mammals** | | | | |
| Fog shrew (*Sorex sonomae sonomae*) | Near-endemic to redwood region (barely); split from S. pacifica | From central Oregon Coast Range south to Marin Co. | Alder/ salmonberry, riparian alder, and skunk-cabbage marsh habitats; less often in mature and immature coniferous forest | Maser et al. 1981, Carraway 1990 |

(*continues*)

Table 5.2. (*continued*)

| *Species* | *Endemism and Status* | *Range* | *Habitat* | *Source* |
|---|---|---|---|---|
| Point Reyes mountain beaver (*Aplodontia rufa phaea*) | Endemic to redwood region; G5T2/S2, FSC, CSC | Small portion of Marin County (Point Reyes) | Coastal scrub | Steele 1989 |
| Point Arena mountain beaver (*Aplodontia rufa nigra*) | Endemic to redwood region; G5T1/S1, FE, CSC | Small area north of Point Arena, Mendocino Co. | Coastal scrub thickets on north-facing slopes; also herbaceous and wooded areas | Steele 1986, 1989 |
| Point Reyes jumping mouse (*Zapus trinotatus orarius*) | Endemic to redwood region; G5T2?Q/S2?, FSC, CSC | Marin County (Point Reyes) | Riparian, grassland, and wet meadow habitats | Zeiner et al. 1990b |
| California tree vole (*Arborimus pomo*) | Near-endemic to redwood region; G4S3, FSC, CSC | Northern to central California Coast Range | Dense coastal forests of at least Douglas-fir; poorly known | Johnson and George 1991 |
| Salt-marsh harvest mouse (*Reithrodontomys raviventris*) | Endemic to redwood region; G1G2/S1S2, FE, CE, CP | Wetlands of San Francisco Bay and its tributaries | Dense pickleweed salt marsh and marginal habitats | Zeiner et al. 1990b |
| Humboldt marten (*Martes americana humboldtensis*) | Endemic to redwood region; G5T2T3/S2S3, CSC | Coastal forests in northern California to near (or slightly beyond) Oregon border | Redwood and other conifer and mixed hardwood-conifer forests | Hall 1981 |

*Note:* No known vertebrate is strictly endemic to redwood forests, but at least one (red-bellied newt) is virtually so. Species that occur largely within the region but do not meet the near-endemic criterion include the tailed frog (*Ascaphus truei*), red-legged frog (*Rana aurora*), and Allen's hummingbird (*Selasphorus sasin*); their conservation within the region would account for a substantial portion of their overall distribution. Status information includes California Natural Diversity Data Base codes: G1 = less than 6 viable element occurrences (EOs) or less than 1000 individuals or less than 2000 acres; G2 = 6-20 EOs or 1000-2000 individuals or 2000-10,000 acres; G3 = 21-100 EOs or 3000-10,000 individuals or 10,000-50,000 acres; G4 = apparently secure, yet factors exist to cause some concern; G5 = demonstrably secure. T codes signify status of taxonomic subcategory (subspecies or variety); S codes signify status within state (CA); range of values (e.g., S2S3) and ? signify uncertainty about appropriate status. Federal and state status: FE = federally endangered, FT = federally threatened, FSC = federal special concern; CE = California endangered, CT = California threatened, CP = California protected, CSC = California special concern. This list is probably incomplete, because scientific information on the status and distribution of subspecies and races of vertebrates in the region is incomplete and under revision.

the more vulnerable end of a continuum of biological resilience in coastal temperate rain forests, with many species showing relatively narrow adaptations and tolerances.

## Faunal Description

In this section, we review the extant vertebrate fauna of the redwoods. We provide more detail for amphibians and reptiles than for mammals and birds because the amphibians and reptiles of the redwoods have been better studied as a group in this habitat. Much more detail on one group of mammals (the forest carnivores) and one species of bird (the marbled murrelet) will be provided later in the case studies.

### *Amphibians*

Amphibians display the widest range of natural history strategies of all vertebrates, including the typical biphasic aquatic larvae and terrestrial adult mode to strictly terrestrial and strictly aquatic modes. This range of strategies can be found among both the anurans (frogs and toads) and the salamanders. Except for the lungless salamanders of the family Plethodontidae, however, all of the amphibians of the redwood forest use aquatic habitats for reproduction. Consequently, the streams, wetlands, and riparian habitats of the redwoods are rich in amphibian life, potentially containing up to ten species during the breeding season (one toad, four frogs, and five salamanders). Though the adults of some species (e.g., tailed frog, foothill yellow-legged frog, and southern torrent salamander) are closely associated with riparian and aquatic habitats throughout their lives, adults of other species (e.g., Pacific tree frog, California and northern red-legged frogs, western toad, Pacific and California giant salamanders, northwestern salamander, and the rough-skinned and red-bellied newts) can be found throughout forest habitats. The adults of this latter group of more terrestrial species make annual or semiannual migrations to aquatic sites, such as ponds, marshes, or streams, during the breeding season but otherwise spend much of their lives in the upland forest. Many of these species use subterranean haunts, such as rodent burrows and root channels, for shelter during the day and forage on the forest floor at night. The Pacific tree frog is highly arboreal and can be found at any stratum of the forest from underground to the canopy.

The amphibian order Anura (frogs and toads) is represented by four families in the redwood forest: the Bufonidae, or true toads, with one species, the western toad; the Ranidae, or true frogs, with three species, the California and northern red-legged frogs and the foothill yellow-legged frog; the Hylidae, or treefrogs, with one extant species, the Pacific tree frog; and the Ascaphidae ( or Leiopelmatidae) with a single extant species, the tailed frog. All of these anurans exhibit the classic biphasic life history with aquatic larvae and terrestrial or semi-

aquatic adults. The tailed frog is associated with old forests, in low-order, fast-flowing, shaded streams with cold, clear waters and low amounts of fine sediments and abundant clean, coarse sediments (Welsh 1990, 1993). The foothill yellow-legged frog is associated with larger streams with open canopies and abundant, abovewater rocky substrates for basking. The northern and California red-legged frogs and the western toad use primarily lentic (nonflowing) waters with vegetated banks for breeding, but are less permanently associated with stream-bank and riparian habitats than the tailed frog and foothill yellow-legged frog. Details of the larval biology of these anurans and those of the aquatic salamanders described below will be discussed in chapter 6.

The amphibian order Caudata (salamanders) is represented by five families in the redwood forest: the Ambystomatidae, or mole salamanders, with a single species, the northwestern salamander; the Dicamptodontidae, or giant salamanders, with the Pacific giant salamander (north of Sonoma Co.) and the California giant salamander (south of Sonoma Co.); the Plethodontidae, or lungless salamanders, with seven species; the Rhyacotritonidae, or torrent salamanders, with a single species, the southern torrent salamander; and the Salamandridae, the true salamanders or newts, with two species, the rough-skinned newt and the red-bellied newt. Except the Plethodontidae, these salamander families all have aquatic larvae and therefore use lentic or lotic aquatic habitats for reproduction. Torrent salamanders, a species associated with headwaters in mature forests (Welsh 1990), and paedomorphic individuals (individuals that retain larval characteristics such as gills when sexually mature) of the giant salamander, are highly aquatic and rarely leave the water. The northwestern salamander and the two newt species spend much of their adult lives in uplands habitats, usually seeking shelters in burrows and under logs during the day or during dry or cold periods.

The amphibians with the greatest representation in the redwoods are the lungless salamanders (family Plethodontidae). Four genera of plethodontid salamanders are found in redwood forests: the slender salamanders (genus *Batrachoseps*), ensatina (genus *Ensatina*), the climbing salamanders (genus *Aneides*), and the woodland salamanders (genus *Plethodon*). The California slender salamander occurs north of the Pajaro River in Santa Cruz County, whereas the Pacific slender salamander occurs south of the Pajaro River to San Luis Obispo County. Welsh and Lind (1991) reported ensatina, followed by the California slender salamander, the most abundant salamander species in the mixed conifer–hardwood forests of northwestern California. The California slender salamander is the most common salamander in the redwood forests, followed closely by ensatina (fig. 5.1). Several subspecies of *Ensatina,* including the Oregon salamander *(E. e. oregonensis),* the painted salamander *(E. e. picta),* and the yellow-eyed salamander *(E. e. xanthoptica),* occur in the redwoods. Research from mixed conifer–hardwood forests of the eastern United States indicates that

plethodontid salamander biomass can equal or surpass that of all other small vertebrates combined in forested habitats (Burton and Likens 1975). Population estimates equaling or surpassing those reported for the eastern United States have been reported for plethodontid salamanders in forested habitats of the Pacific Northwest (see Welsh and Lind 1992 and references therein). Although these studies were not conducted in redwood forest, there is every reason to believe that the numbers of plethodontid salamanders (especially the slender salamander and ensatina) in redwoods may equal or surpass those in other forest types of the Pacific Northwest. The California slender salamander has been found significantly more abundant in mature and old-growth redwood forest compared with young forest (ANOVA; $F = 5.90$, $P = 0.013$; fig. 5.2).

The genus *Aneides* includes two species in the redwoods, the terrestrial black salamander and the more arboreal clouded salamander. The clouded salamander frequents large conifer logs in the forests of northwestern California and is a good climber (Welsh and Lind 1991). Recently, it has been found nesting 40 m above the ground in a large, live redwood tree, using fern mats and other microhabitats in the canopy (Welsh and Wilson 1995; S. Sillettt, pers. comm.). This is the only salamander outside of the New World tropics known to use forest canopy, and is therefore the focus of a new research effort.

The genus *Plethodon* is represented by two species in the redwoods, the Del

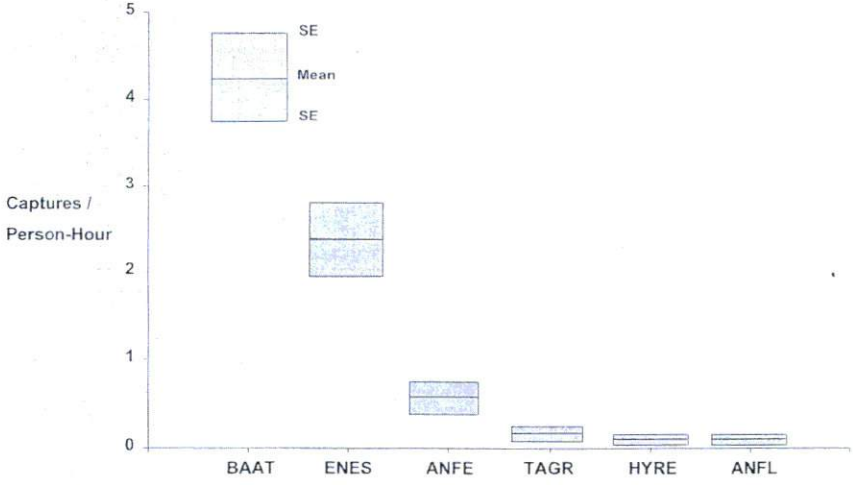


Figure 5.1. Relative abundance of the six most common amphibian species from eighteen redwood stands. Data were collected using time-constrained searches (Welsh 1987) in the springs of 1984–1986. BAAT = California slender salamander; ENES = ensatina; ANFE = clouded salamander; TAGR = rough-skinned newt; HYRE = Pacific tree frog; and ANFL = black salamander.

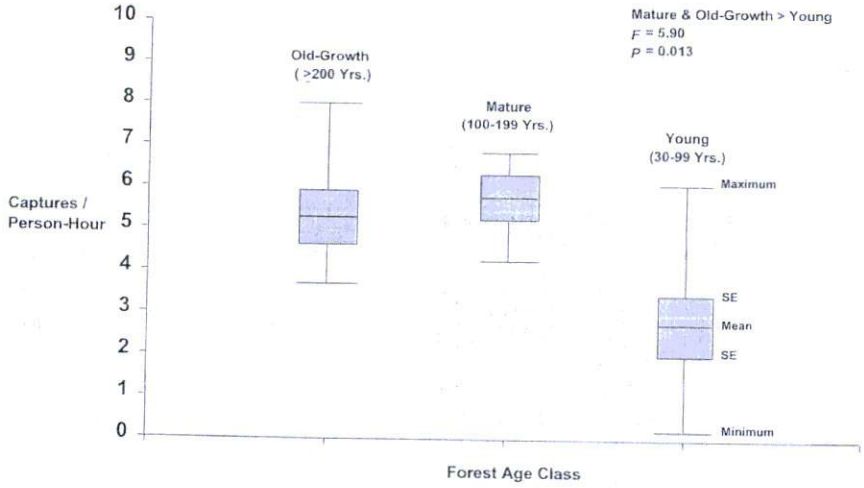


Figure 5.2. Captures of California slender salamanders (*Batrachoseps attenuatus*) by forest age class from eighteen redwood forest stands. Data were collected by time-constrained searches (Welsh 1987) in the springs of 1984–1986.

Norte salamander and Dunn's salamander. The Del Norte salamander, while occasionally using downed wood, is most often associated with rock substrates, such as talus, rock rubble, and rock outcrops (Welsh and Lind 1995). Based on data primarily from interior conifer-hardwood forests, Welsh (1990) described this species as associated with late-seral forests. Forest canopy closure was the best predictor of the presence of Del Norte salamanders, with sites supporting salamanders having a mean of 83 percent closure (Welsh and Lind 1995). On the other hand, Diller and Wallace (1994) did not find Del Norte salamanders restricted to late-seral stands of redwoods in north coastal California. The range of Dunn's salamander barely reaches south into the redwoods of extreme northwestern California. This species is associated with damp rocky substrates, usually near stream channels.

## *Reptiles*

Compared to amphibians, reptiles have lower overall diversity and lower relative abundances in the redwood forest. This pattern can be explained by physiological requirements. Amphibians require cool, moist habitats; many species avoid daylight or direct sunlight. In contrast, reptiles are often heliotherms, requiring direct sunlight or higher ambient temperatures to establish body temperatures sufficient to function on a daily basis. This being the case, the most likely places to find reptiles associated with redwood forest would be in clearings, along an edge with other habitat types, or along the margins of larger streams and rivers

where adequate sunlight penetrates into the forest or onto riparian substrates. A single species of turtle (order Chelonia)—the western pond turtle—occurs in ponds or lakes and along streams and rivers in redwood forest. This turtle is associated with openings for basking adjacent to deep-water habitats, where it hides from predators (Reese and Welsh 1998). The western pond turtle uses upland forested habitats both for nesting and hibernation (Reese and Welsh 1997).

The other reptiles of the redwood forest belong to the order Squamata, the snakes and lizards. The lizards are represented by five species: western fence lizard, sagebrush lizard, northern alligator lizard, southern alligator lizard, and western skink. Of these, only the northern alligator lizard is likely to be encountered in the deep forest, where it forages for invertebrates in the litter and under cover objects on the forest floor. The other species of lizards might be encountered in clearings or along stream banks in open habitats or along forest edge where sunlight penetrates. The snakes that can be found in the redwoods are representative of three families: the Viperidae, represented by the western rattlesnake; the Boidae, represented by the rubber boa; and the Colubridae, which includes the remaining nine species: sharp-tailed snake, California kingsnake, western racer, gopher snake, ringneck snake, northwestern garter snake, common garter snake, western terrestrial garter snake, and aquatic garter snake. The ringneck snake, sharp-tailed snake, garter snakes (except the aquatic garter snake), and rubber boa all frequent forest habitats and are usually associated with logs and other cover on the forest floor, where they forage for small vertebrates or invertebrates. The gopher snake, kingsnake, rattlesnake, and western racer occur in relatively open, terrestrial habitats. Aquatic garter snakes are associated with wetlands. All these species could be encountered along the redwood forest edge or in ecotones with open, sunny areas.

### *Birds*

Approximately 100 native bird species representing 28 families use redwood forests (A. Cooperrider, unpub. comp.). These figures includes species that use redwood forest for feeding, breeding (nesting), or cover in at least one season. Thus, it includes species such as the belted kingfisher, which are primarily associated with aquatic and riparian inclusions within the forest, but it does not include coastal or oceanic species unless, like the marbled murrelet, they make use of redwood forest for vital needs. The group with the most species (23) in redwood forests includes wood warblers, tanagers, sparrows, and blackbirds, most of them migratory and until recently lumped into the family Emberizidae.

Surprisingly, because birds are the easiest to observe of all forest vertebrates, the avifauna of the redwood forests has not been well studied. One general pattern has been noted by observers: moving away from the coast or from areas of hardwoods or mixed conifers into stands of pure redwood, the number of bird

species declines precipitously. Perhaps the depauperate avifauna of redwood forests explains the relative lack of interest among ornithologists. As pointed out by Small (1974), "Where the forests are thick, pure, and extensive, the number of bird species sharply declines. In California only six species of birds nest primarily in this forest."

The six bird species noted by Small (1974) as characteristic of redwood forest are ruffed grouse, resident locally in riparian areas and canyons; Vaux's swift, which nests in burned and hollowed conifers, usually redwoods; the migratory race of Allen's hummingbird, a summer visitor and transient, found largely in open areas near forest edges; chestnut-backed chickadee, a resident from the Oregon border south to about Morro Bay in San Luis Obispo County, but not restricted to coniferous forest; rufous hummingbird, which nest only in the coastal forests of Del Norte County; and "probably the most characteristic bird of the coastal coniferous forest," the varied thrush, which nests "deep in the dark forest glades where it is resident the year around although in winter there is some movement to the south and towards less dense stands of forest" (Small 1974). The varied thrush is a fragmentation-sensitive species associated with large patches of late-seral redwood forest (Hurt and George, in prep.).

A search of Breeding Bird Censuses published in *American Birds*, 1980–1994 (i.e., censuses have not been published thereafter) revealed only two censuses (1981–1982) in a redwood forest: an old-growth Douglas-fir–redwood forest in Mendocino County. Thirty-nine territorial individuals of 20 species were located in the 10.22-ha plot in 16 site visits in 1981, and 33 territorial individuals of 18 species were recorded in 16 visits in 1982 (Judah 1983). Curiously, Small's (1974) "most characteristic bird," the varied thrush, was not present. Rather, the most common species were western flycatcher, brown creeper, Wilson's warbler, chestnut-backed chickadee, hermit thrush, Allen's hummingbird, hermit warbler, rufous-sided (spotted) towhee, common flicker, hairy woodpecker, and winter wren. This avifauna is typical of coniferous forests and other habitats in the Pacific Northwest. Northern spotted owls were also present in Judah's (1983) surveys in both years.

Unlike other vertebrates, many bird species use the redwood forest on a seasonal, as opposed to year-round, basis. Many birds, such as the hermit warbler and Vaux's swift, nest and raise young in the redwoods, then migrate south for the winter. Others, such as Townsend's warbler, nest farther north or at higher elevations and then winter in the redwoods. Even birds such as mountain quail, blue grouse, and the varied thrush, which are permanent residents in the redwoods region, often make seasonal, elevational movements.

## *Mammals*

The redwood forests support 61 species of mammals, representing 19 families (A. Cooperrider, unpub. comp.). Four of these families—Vespertilionidae (in-

sectivorous bats; 11 species), Sciuridae (squirrels and chipmunks; 8 species), Muridae (mice and voles; 13 species), and Mustelidae (the weasel family; 6 species)—make up more than half of the species present. Almost all of these species make use of the forest for breeding, feeding, and cover. Most of these species are permanent residents, except some of the bats, which make short- to long-distance migrations, and the ungulates (elk and mule deer), which may make moderate seasonal movements and use habitats besides redwood forest. Some of the bat species, such as the Yuma myotis and fringed myotis, raise young in caves and crevices.

Among the mammals that appear most closely tied to late-seral redwoods are the bats. Until recently, bats had been virtually unstudied in redwood forests. Recent research on the use by bats of basal hollows in old-growth redwoods confirmed that these hollows are important roost sites, as judged by the quantities of bat guano in hollows. Species of bats could not be identified by guano; however, three fecal morphotypes were identified (Gellman and Zielinski 1996). Further study determined that bat use of hollows in old-growth redwoods is greatest in small, residual stands of old growth on commercial forestland, as opposed to within larger areas of unfragmented old growth (Zielinski and Gellman 1999). Eight species of bats were mist-netted in the study areas, with the Yuma myotis most abundant. This research underscores the value of retaining remnant stands of old growth in managed forests.

The role of mammals in the functioning of the redwood ecosystem is not well understood. We expect that many of the relationships among species groups and ecosystem functions are common to many Pacific Coast forests. For example, Maser (1988) describes the complex interaction among northern flying squirrels, mycorrhizal fungi, and tree growth in Douglas-fir forests, a set of relationships apparently common to redwood forests (see chap. 4 on the ecological role of fungi).

Another way in which vertebrates can affect forests is through potential alteration of succession by herbivory. Foresters have been concerned that heavy browsing by ungulates might prevent regeneration of "desirable" tree species. In some forest regions, deer and elk are known to alter the species composition of forests, at least locally, by overbrowsing seedlings and saplings of favored species of trees and shrubs (e.g., see Alverson et al. 1988). Heavy browsing, in turn, can reduce densities of other animals, shrub-nesting birds, for example (Noss and Cooperrider 1994 and references therein). We found no documentation of regeneration of redwoods or associated woody species being affected significantly by browsing of native ungulates, although these animals occasionally cause damage to individual trees. Damage to regenerating forests by dusky-footed woodrats was investigated by Giusti (1999), who found that woodrats live "within clumps of sprouting redwoods, feeding heavily on the emergent sprouts." The extent of damage and its effect on stand regeneration were not

established. Damage to trees by black bears, who strip bark to eat the sugar-rich cambium, apparently can be a greater problem, especially when bears emerge in late winter (Giusti 1990), but whether this damage has a significant effect on regeneration at a stand level remains an open question. Bears appear to do most damage to young, even-aged redwood stands, as they concentrate their feeding on stems 25–50 cm dbh (Giusti 1990).

## Species Richness Patterns

One simple, though incomplete, expression of biodiversity is the number of species present in an area: species richness (Noss and Cooperrider 1994). Among temperate coniferous forests and other major ecosystems in North America, the redwood region does not stand out as extremely high in native species richness (Ricketts et al. 1999), though it is biologically distinct in other ways (see chap. 1). Late-successional redwood forests, in particular, have been characterized as relatively depauperate in vertebrate species. Few quantitative data are available to confirm this observation, however. We pose the following generalizations about species richness patterns of terrestrial vertebrates in redwood forests as working hypotheses, which can be verified or falsified by further research.

1. Vertebrate species richness is lowest in homogeneous stands of young or mature redwood-dominated forests. Species richness of vertebrates is generally higher in heterogeneous habitats than in more homogeneous ones, a phenomenon well documented for bird communities in many types of habitat (MacArthur et al. 1962; Roth 1976) but not well studied in redwood forests. Lower vertebrate species richness in homogenous redwood stands is predicted by the knowledge that many vertebrates require habitat features and resources, such as fruit and nut-bearing trees and shrubs, that tend to be scarce in pure stands of redwoods. The scarcity of these plants, and of herbaceous flora, is at least partially explained by low light levels, which also affect some vertebrates (e.g., heliothermic reptiles) directly. Furthermore, old-growth redwood forests, which like other old-growth forests can be expected to have higher rates of treefall gap formation (Clebsch and Busing 1989), are predicted to have greater vertebrate diversity than young (40–100 years) or mature (100–200 years) forests as a result of higher structural heterogeneity and light levels (see chap. 4, box 4.1). Light levels (solar radiation) near ground level decrease in old-growth redwood forests with increasing proximity to boundaries with young redwood plantations (Russell et al. In press).
2. Species richness of vertebrates is greater where redwood-dominated stands have inclusions of riparian habitat. This prediction is based on the addition

of species that depend on riparian or aquatic habitat for at least some of their life-history needs. Higher light levels and rates of gap formation (because of vulnerability to wind and bank undercutting along streams) in riparian areas will contribute to greater heterogeneity and species richness.

3. Species richness is greater where redwood forest includes codominants such as tanoak and Douglas-fir in the canopy. As in the first two generalizations above, this prediction follows from the presence in mixed forests of resources such as acorns, which some animal species rely on.
4. Species richness is greater where late-seral (mature or old-growth) redwood forest is replaced by a mixture of seral stages, from the herb-shrub through old-growth stages. This prediction, which has considerable potential for misinterpretation, follows from the increase in horizontal habitat heterogeneity (among-habitat diversity) and edge effects when a landscape is composed of a mosaic of stands of different ages (Noss 1983). Foresters and wildlife managers have often claimed that logging and creation of edge effects is good for wildlife, but in fact, many native species are sensitive to fragmentation and increase in the amount of edge habitat (see review in Noss and Cooperrider 1994:196–203). For high species richness of native vertebrates to be sustained on a regional scale, effects of fragmentation must be moderated by maintaining patches of late-seral forest large and connected enough for persistence of species that require such forest.
5. Species dependent on specific structural components of old-growth redwood forests (e.g., snags, downed logs, complex canopies of live trees) will decline as these forests are replaced by simplified plantations; therefore, species richness or abundances are predicted to be lower in plantations compared to natural forests of any age (Hansen et al. 1991; Noss and Cooperrider 1994). Many salamanders, for example, are dependent on coarse woody debris (see above). Plantations and other young, managed forests that retain structural legacies will be expected to retain more species, at least temporarily (see chap. 8).

## Habitat Relationships

In making decisions regarding land uses or conservation priorities, questions such as the following often arise:

- What species are (or would be expected to be) present in a given area?
- How significant is one area relative to others for supporting a given species or group of species?
- How might the species composition of an area—or the abundance of a particular species of concern—change when habitat is changed?

Answering these questions would help ensure that limited resources for conservation activities, such as money for purchasing forestlands, are used most effectively, and that land management plans consider potential effects of habitat alteration on species composition. Ideally, a conservation decision-maker would have time and funding to conduct a thorough on-the-ground inventory of all areas for all species of concern. Typically, neither time nor money is available for such efforts, and some assessment must be made without a complete field inventory.

## *Habitat Relationships Models*

To deal with questions such as these, wildlife biologists have developed several methods, termed *habitat evaluation techniques* or *habitat relationships models,* for evaluating areas generically. These techniques take advantage of the observation that presence and abundance of wildlife species depend on available habitat; thus, knowledge of habitat characteristics can be used to predict presence/absence and sometimes abundance of wildlife species. These techniques have been described and explored in detail in other publications (see Cooperrider 1986a and Cooperrider et al. 1986); the discussion here focuses on specific techniques developed for or in common use in the redwood region.

Virtually all habitat evaluation methods developed to date are for vertebrates, with the most detailed models for birds and mammals. This bias reflects the interests of wildlife agencies (funded largely by hunting and fishing licenses) in vertebrates and the lack of natural history information on most species of invertebrates. A common method of predicting presence/absence of vertebrates in an area is based on the vegetation type and seral stage. For example, violet-green swallows are largely dependent on older seral stages of forest for breeding and feeding habitat, whereas cliff swallows favor early seral forests or open grasslands. Thus, armed with knowledge of the vegetation types and seral stages present in a landscape, a biologist often can predict with reasonable accuracy which species are likely to occur there.

Predictions from habitat relationships models, however, often contain substantial errors of omission and commission. For example, an assessment of the reliability of the California Wildlife Habitat Relationships (WHR) model in four seral stages of mixed evergreen forest in northwestern California found that 14 percent of the species were observed but not predicted (an error of omission), whereas 11 percent of the species predicted to occur were not observed (an error of commission). Species richness among seral stages differed significantly from model predictions for birds but not for amphibians, reptiles, and mammals (Raphael and Marcot 1986). Similarly, gap analysis models, which use simple habitat relationships models to associate vertebrate distributions with vegetation maps derived from remote sensing, always include some errors of omission and commission—11 percent and 21 percent, respectively, in the Idaho gap analysis (Scott et al. 1993). The accuracy of prediction tends to vary by taxonomic class,

with predictions for birds generally being most reliable (Scott et al. 1993; Edwards et al. 1996). Distributions of rare, endemic, and patchily distributed species are least successfully predicted by habitat relationships models (Smith and Catanzaro 1996), which underscores the need to survey these species individually through a "fine filter" approach, rather than relying on modeling (Noss and Cooperrider 1994).

A more refined prediction of species occurrence can be made using knowledge of what biologists call "special habitat features" or "special habitat elements." These include habitat features other than vegetation type and seral stage that are required by many species. Snags, downed logs, springs, talus slopes, caves, and cliffs are examples of such features. Because these features usually cannot be surveyed remotely (i.e., from satellite or airplane), their measurement requires ground surveys, which are more costly. When predictions of vertebrate species distributions are made for large areas, as in gap analysis projects, the probability is relatively high that essential microhabitats are present; for smaller areas, predictions are less robust (Csuti 1996). Combining line (e.g., streams) and point data (e.g., locations of caves or other special habitats) with maps of vegetation can result in more accurate predictions for many species associated with these features over large areas (Edwards et al. 1995).

The California WHR system uses three basic habitat parameters—vegetation type, seral stage, and presence of special habitat elements—to predict presence or absence of vertebrate species (Airola 1988; Mayer and Laudenslayer 1988). Garrison (1992) applied the California WHR system to a 2,400-ha, second-growth (80–100-year-old) redwood forest watershed, to show how trends in species richness could be predicted and explained from simple knowledge of habitat requirements of vertebrates. The WHR model was used to predict the effects of a mixture of even-age and uneven-age management applied to the study area. Predicted responses included declines of 70 percent of the amphibian species and increases of 88 percent of the reptile species, 64 percent of the bird species, and 61 percent of the mammal species. Overall vertebrate species richness was predicted to increase with logging.

Although no attempt was made to verify Garrison's (1992) predictions, we suspect that at least the general trend (increased species richness as more seral habitat is created) would prove true (see generalization no. 4 in preceding section). Nevertheless, assigning positive conservation value to an abstraction such as "species richness" is foolhardy without considering the individual species added or lost when changes are made in the distribution of seral stages on a landscape. When an older forest is converted to earlier seral stages, the species likely to be lost are those closely associated with old forest, such as the spotted owl and marbled murrelet; that is, those that are rare regionally or globally and for which intensive conservation efforts are being undertaken. On the other hand, the species added to the forest tend to be relatively common or weedy

ones, and may include exotics, such as wild pig. Therefore, all species cannot be treated as equal in conservation planning (Diamond 1976; Noss 1983; Noss and Cooperrider 1994).

Among other limitations, the California WHR does not consider the area requirements of particular species, the need of many species for contiguity or connectivity among patches of suitable habitat, or the need for spatial juxtaposition of different habitat types or habitat elements. The WHR assumes that one hectare of habitat is equivalent to 1,000 or 10,000 ha. And 100 ha are assumed to be of equivalent value in this system whether they are distributed in 10-ha patches or in one 100-ha block. This deficiency in the system has been exploited by unscrupulous companies and biologists in environmental assessments, such as timber harvest plan analyses, to mask the consequences of logging activities. One could harvest 999 out of 1,000 ha of old-growth redwood forest and show (on paper) no predicted decline in species richness or diversity. The authors and developers of the California WHR system have been forthright about this deficiency and have warned against such misuse (Airola 1988).

Another limitation of the WHR system is that many of the habitat relationships described for vertebrates of the redwood forest are nothing more than educated guesses. In searching the literature, we found few quantitative studies that would support these relationships. Despite these problems, the WHR system is widely used; therefore, it is essential that its foundations be well understood and, with future studies, validated.

### *Landscape Context*

Wildlife biologists have known for a long time that spatial arrangement of the components in the landscape are critical determinants of the capability of the habitat to support wildlife species. More than sixty years ago Aldo Leopold wrote:

> The maximum population of any given piece of land depends, therefore, not only on its environmental types or composition, but also on the *interspersion* of these types in relation to the cruising radius of the species. Composition and interspersion are thus the two principle determinants of potential abundance. (1933:128–129)

Despite this knowledge, conventional wildlife habitat relationships models ignore landscape patterns, patch sizes, and other spatial phenomena critical to the persistence—if not the immediate presence—of many species. The models are incomplete in focusing on habitat *content* but not *context* (Noss and Harris 1986). In recent years, biologists and landscape ecologists have developed sophisticated ways of describing and organizing such spatial information. And with the advent of computer-based geographic information systems (GIS), analysis of such information has become easier. We describe here three of the

most important spatial determinants of habitat suitability: patch size, juxtaposition, and connectivity. For descriptions of other spatial measurements, patch shape and porosity, for example, we refer readers to books on landscape ecology such as Forman and Godron (1986), Naveh and Lieberman (1990), Turner and Gardner (1991), Forman (1995), and Hansson et al. (1995). Chapter 7 of this book discusses application of principles of landscape ecology to conservation evaluation and landscape design.

PATCH SIZE. The size of a patch of habitat is important because a minimal area is necessary to support an individual animal or a breeding pair; a still larger area (either in one patch or several patches linked by dispersal; see below) is required to support a viable population—one with a specified probability of persisting over a given time period (Shaffer 1981; Soulé 1987). Thus, fifty 1-ha patches of old-growth redwood may not be adequate to support a single pair of a forest-interior bird species, whereas one 50-ha patch may support many breeding pairs. If animals are relegated to small patches of habitat that support only small populations, the probability of extinction may be high unless connectivity among patches is high (see below).

Fragmentation, which refers to the degree to which large blocks of habitat have been broken up into smaller, more isolated patches, is considered a leading threat to biodiversity (Wilcove et al. 1986; Noss and Cooperrider 1994; Noss and Csuti 1997). In portions of their range, redwood forests had a naturally patchy distribution; that is, they occurred in small, relatively isolated patches prior to the activities of modern humans. In other portions of the redwood region, redwood forests were relatively continuous—they constituted the landscape matrix. The spatial pattern of redwood forests today, especially in the northern section, is considerably more fragmented than the pattern before European settlement (Hurt and George, in prep.). Little research has been conducted on the effects of habitat fragmentation in the redwood region. Nevertheless, a recent study determined that the varied thrush, one of the most characteristic birds of the redwood forest, is fragmentation sensitive. Varied thrushes were present in 16 out of 17 fragments that were greater than 16 ha, but in only one of 21 fragments smaller than 16 ha (Hurt and George, in prep.). Presence of birds was also positively correlated with the size (dbh) of redwood trees in the fragments. The authors recommended maintaining redwood forest stands greater than 20 ha and older than 80 years of age to support breeding populations of varied thrushes. Similarly, a study of the red-backed vole in southwestern Oregon (Mills 1995) found this species sensitive to the area, isolation, and edge effects in forest remnants.

JUXTAPOSITION. Juxtaposition refers to the adjacency of one type of habitat to another type. For example, the adjacency or proximity of redwood habitat to

riparian areas is critical for species that require both types of habitat to meet such life history needs as feeding, nesting, or thermal cover. If the required habitat patches are too far apart, then their utility to the species may be reduced or nonexistent.

Little is known of the juxtaposition requirements of redwoods fauna. Wide-ranging generalists such as black bears are known to require a mosaic of habitats to meet their life-history needs. Bats roosting in redwood hollows deep in the forest generally forage over watercourses and other habitat edges (Zielinski and Gellman 1999). Amphibians with terrestrial adult stages (with the exception of the fully terrestrial plethodontid salamanders, *Batrachoseps, Aneides,* and *Plethodon*) require adequate juxtaposition of aquatic breeding areas and terrestrial habitats.

CONNECTIVITY. Connectivity—specifically functional connectivity—refers to the potential for successful dispersal, population interchange, or daily or seasonal movement of organisms among two or more patches of habitat (Noss and Cooperrider 1994). Because of differences among species in life histories and movement capabilities, connectivity is best described relative to a particular species or biological phenomena. Connectivity may be present in the form of corridors (strips of a given type of habitat that connect larger patches of the same or similar habitat [Beier and Noss 1998]), but that is not the only way functional connectivity may be achieved. Some animals disperse freely through a landscape, as long as suitable resting, feeding, and predator avoidance habitat features are available. For example, connectivity among spotted owl management areas was defined in terms of a forest matrix that included a minimal canopy coverage of trees of a given size class (Thomas et al. 1990). Within the home ranges of owls, however, the total amount of suitable (old-growth) habitat is more important than the connections among patches of old growth. For less vagile organisms, even narrow (i.e., to us) barriers can prevent movement.

Connectivity is a necessary consideration in conservation planning because it potentially allows for persistence of species—for example, as metapopulations or systems of populations (Harrison 1994)—in a network of habitat areas, no single one of which is large enough to support a viable population. With functional connectivity, a whole can be greater than the sum of its parts (Noss and Harris 1986). Such considerations are crucial for species, such as the forest carnivores discussed later in this chapter, with demanding area requirements. Habitat fragmentation that poses barriers to movement can have severe effects on animals that need to travel from one kind of habitat to another daily or seasonally (see comments on juxtaposition, above). Roads, which cause a variety of ecological problems, often serve as barriers for species that hesitate to cross openings or that suffer high mortality from vehicles (Noss and Cooperrider 1994; Trombulak and Frissell 2000).

## *Special Habitat Characteristics and Features*

Although relatively few vertebrates are endemic to the redwood region (table 5.2) and none strictly to the redwood forest, the redwood forest is a unique ecosystem that, nonetheless, shows commonalities with other portions of the Pacific coastal rain forest that stretches from the redwood region north to southeastern Alaska. Throughout this vast region, the life histories of most native vertebrates are closely tied to water and to the complex structure of natural forests (Bunnell and Chan-McLeod 1997). Most redwood forests are coastal and within the fog belt (see chap. 3 and 4). As with the rest of the coastal rain forest, the link between redwoods and coastal and estuarine habitat is critical to many species. For example, virtually all redwood forests have (or once had) streams with runs of anadromous salmonids. These runs supplied a pulse of food and nutrients for many terrestrial vertebrates, such as black bears, grizzly bears (now extirpated from the region), and bald eagles. The consequences of losing the fish runs—or having them greatly diminished—are poorly understood, but may include influences on forest productivity throughout the food web. Similarly, the connection between riparian areas and upland redwoods is critical; the richness and productivity of riparian forests, as well as their structural complexity and abundance of snags and downed wood under natural conditions, are crucial to the persistence of many populations (Bunnell and Chan-McLeod 1997).

The dependence of many terrestrial vertebrates on features of the natural old forest, such as snags, dead and downed woody material, and tree cavities, is well documented in other forests of the Pacific Northwest (Norse 1990; Ruggiero et al. 1991). What may be less apparent is that many terrestrial vertebrates surviving in managed (i.e., "cutover") forest stands may be there largely because of the legacies remaining from unmanaged forests. In British Columbia, for example, black bear dens could be found in second-growth forests, but primarily within structures (live trees, snags, or logs larger than 1 m in diameter) that were left over from the previous old-growth forest (Bunnell and Chan-McLeod 1997). Spotted owls may nest in second-growth redwoods only because of the structural legacies left from previous, old-growth stands (Noon and Murphy 1997). These observations leave us to wonder what will happen to native wildlife over subsequent, short rotations as the structural legacies from the natural forest gradually return to the soil.

## *Endangered and Imperiled Species*

Forty-two vertebrate species of the redwood forest are considered by state and federal agencies endangered, threatened, or otherwise of concern (tables 5.2 and 5.3). Four invertebrate species are currently listed by the federal government as endangered or threatened; twelve others are federal species of concern (former and perhaps future candidates for listing) (table 5.4). None of these species is restricted to redwood forest. Our lack of knowledge, especially about forest

Table 5.3. Imperiled Terrestrial or Amphibious Vertebrates Found Within, But Not Endemic or Near-Endemic to, the Redwood Region.

| *Species* | *Category* |
|---|---|
| AMPHIBIANS | |
| Southern torrent salamander (*Rhyacotriton variegatus*) | G4/S2S3, FSC, CSC, CP |
| Tailed frog (*Ascaphus truei*) | G3G4/S2S3, FSC, CSC, CP |
| Northern red-legged frog (*Rana aurora aurora*) | G4T2?/S2?, FSC, CSC, CP |
| California red-legged frog (*Rana aurora draytonii*) | G4T2T3/S2S3, FT, CSC, CP |
| Foothill yellow-legged frog (*Rana boylii*) | G3/S2S3, FSC, CSC, CP |
| REPTILES | |
| Western pond turtle (*Clemmys marmorata*) | G4S3, FSC, CSC, CP |
| BIRDS | |
| Aleutian Canada goose (*Branta canadensis leucopareia*) | wintering: G5T2/S2, FT |
| Tufted puffin (*Fratercula cirrhata*) | nesting: G5/S2, CSC |
| Osprey (*Pandion haliaetus*) | G5/S3, CSC |
| White-tailed kite (*Elanus leucurus*) | G5/S3, CP |
| Bald eagle (*Haliaeetus leucocephalus*) | G4/S2, FT, CE, CP |
| Northern harrier (*Circus cyaneus*) | G5/S3, CSC |
| Sharp-shinned hawk (*Accipiter striatus*) | G4/S3, CSC |
| Cooper's hawk (*Accipiter cooperi*) | G4/S3, CSC |
| Northern goshawk (*Accipiter gentilis*) | G4/S3, FSC, CSC |
| Golden eagle (*Aquila chrysaetos*) | G4/S3, CSC, CP |
| Merlin (*Falco columbarius*) | G5/S3, CSC |
| Peregrine falcon (*Falco peregrinus anatum*) | G3T2/S2, FE, CE, CP |
| Prairie falcon (*Falco mexicanus*) | G5/S3, CSC |
| Ruffed grouse (*Bonasa umbellus*) | G5/S4, CSC |
| Marbled murrelet (*Brachyramphus marmoratus*) | G3/S1, FT, CE, CSC |
| Northern spotted owl (*Strix occidentalis caurina*) | G3T2T3?S2S3, FT |
| Black swift (*Cypseloides niger*) | G4/S2, CSC |
| Purple martin (*Progne subis*) | G5/S3, CSC |
| Black-capped chickadee (*Parus atricapillus*) | G5/S3, CSC |
| Yellow warbler (*Dendroica petechia brewsteri*) | G5T2/S2, CSC |
| San Pablo song sparrow (*Melospiza melodia samuelis*) | G5T2??S2?, FSC, CSC |
| Alameda song sparrow (*Melospiza melodia pusillula*) | G5T2?/S2?, FSC, CSC |
| MAMMALS | |
| Salt-marsh wandering shrew (*Sorex vagrans halicoetes*) | G5T1/S1, FSC, CSC |
| Townsend's big-eared bat (*Corynorhinus townsendii townsendii*) | G5T3T4/S2S3, FSC, CSC |
| San Francisco dusky-footed woodrat (*Neotoma fuscipes annectens*) | G5T2T3/S2S3, FSC, CSC |
| Monterey dusky-footed woodrat (*Neotoma fuscipes luciana*) | G5T3?/S3?, FSC, CSC |
| White-footed vole (*Arborimus albipes*) | G4/S2S3, FSC, CSC |

*Note:* Codes as in Table 5.2.

Table 5.4. Imperiled Invertebrates of the Redwood Region. Species listed are ranked G1, G2, S1, or S2 by the California Natural Diversity Data Base. None of the species is known to be restricted to redwood forest (most are narrow endemics, and many are restricted to caves or other unusual environments).

| *Species* | *Status* |
|---|---|
| GASTROPODS | |
| Mimic tryonia (California brackish-water snail) (*Tryonia imitator*) | G2G3/S2S3, FSC |
| Pomo bronze shoulderband (snail) (*Helminthoglypta arrosa pomoensis*) | G2T1/S1, FSC |
| Rocky coast Pacific sideband (snail) (*Monadenia fidelis pronotis*) | G1/S1, FSC |
| ARACHNIDS | |
| Edgewood blind harvestman (*Calicina minor*) | G1/S1, FSC |
| Empire Cave pseudoscorpion (*Fissilicreagris imperialis*) | G1/S1, FSC |
| Dolloff cave spider (*Meta dolloff*) | G1/S1, FSC |
| Tiburon micro-blind harvestman (*Microcina tiburona*) | G1/S1, FSC |
| CRUSTACEANS | |
| Mackenzie's cave amphipod (*Stygobromus mackenziei*) | G1/S1, FSC |
| Tomales isopod (*Caecidotea tomalensis*) | G2/S2, FSC |
| California freshwater shrimp (*Syncaris pacifica*) | G1/S1, FE, CE |
| INSECTS | |
| Globose dune beetle (*Coelus globosus*) | G1/S1, FSC |
| Mount Hermon (barbate) June beetle (*Polyphylla barbata*) | G1/S1, FE |
| Ricksecker's water scavenger beetle (*Hydrochara rickseckeri*) | G1G2/S1S2, FSC |
| Fort Dick limnephilus caddisfly (*Limnephilus atercus*) | G1G3/S1, FSC |
| Lotis blue butterfly (*Lycaeides argyrognomon lotis*) | G5T1/S1, FE |
| Oregon silverspot butterfly (*Speyeria zerene hippolyta*) | G5T1/S1, FT |

*Note:* Codes as in Table 5.2.

invertebrates, suggests that probably many other species are very rare or imperiled. Some imperiled species, listed or not, have presumably always been rare (i.e., such is the case with many endemics), whereas others have become rare because of human activities and face a high probability of extinction if those activities continue unabated. The case studies in the following sections provide examples of imperiled species and illuminate the forces that threaten them.

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We cannot do justice, in one chapter, to the biology of the redwoods fauna. We noted earlier that this fauna has been poorly studied in comparison with many other major vegetation types. Yet what is known is fascinating. We offer, below,

three case studies that give glimpses of the native fauna of redwoods that merit concern because of the activities of humans. The case studies are of (1) invertebrates, a group much more diverse than vertebrates but about which little is known for redwoods and other forests; (2) forest carnivores, a group that includes highly imperiled forms and is receiving increased research attention; and (3) the marbled murrelet, a federally threatened species that finds optimal habitat in old-growth redwoods. Together, these case studies provide strong lessons for conservation.

## Invertebrates of the Redwoods and Other Northwest Forests

Invertebrate communities in redwood forests resemble those found throughout the temperate rain forests of the Pacific Northwest. Because information specific to redwood invertebrates is scarce, this similarity allows us to broadly characterize the redwood fauna using examples from other Pacific Northwest rain forests. Arthropods are some of the most diverse and best studied invertebrates of these habitats and will be emphasized in the following discussion.

### *An Extraordinary Diversity*

As in most other terrestrial communities (Wilson 1992), invertebrates constitute the vast majority of animal species in redwood forests. An estimated 8,000 arthropod species comprise around 85 percent of all species of vertebrates, vascular plants, and arthropods in a relatively undisturbed Oregon Cascade forest (Asquith et al. 1990; Lattin 1990). Species densities can be amazingly high for invertebrates as well, with 200 to 250 species of invertebrates per square meter in undisturbed forest soils (Moldenke 1990). Arthropod abundance also can be high—more than 200,000 individual oribatid mites have been estimated for one square meter of forest floor, representing 75 species (Moldenke 1990). Temperate rain forests of the Pacific Northwest are also global and continental foci of diversity for several taxa. For example, the diversity and abundance of mites in old-growth forests here is thought to rival or exceed their diversities in many other terrestrial ecosystems, including tropical forests (Lattin 1990; Moldenke 1990). More species of slugs (24) live in these forests than any other in North America (Frest and Johannes 1993, 1996).

### *Comparing Temperate and Tropical Rain-Forest Faunas*

The structure of arthropod communities in temperate rain forests differs from that observed in tropical rain forests in several ways. An abundance of mites, millipedes, isopods, and earthworms fills the role of major detritivores and decomposers in temperate rain forests, a function dominated by fungi and bacteria in tropical rain forests. For example, a Pacific Northwest cyanide-produc-

ing millipede (*Harpaphe haydeniana*) and sowbug (*Ligidium gracile*) are believed to be responsible for breaking down much of the litter and rotting wood into humus (Moldenke 1990; Lattin and Moldenke 1992).

Ants are exceptionally abundant in tropical forests; together with termites they constitute roughly a third of the dry-weight animal biomass, and are dominant consumers and predators (Wilson 1987). The relatively low diversity and abundance of ants in temperate rain forests is likely the result of the unfavorable cool and moist conditions of the forest floor. The scarcity of ants may contribute to the prevalence of land snails and slugs in temperate rain forests relative to tropical rain forests. Butterflies and native bees are also scarce in temperate old growth, leaving the role of pollinating understory plants to flies, moths, and beetles. Despite these differences, tropical and temperate rain forests share the vast majority of invertebrate higher taxa, and the complex old-growth forests of each have relatively similar structures and ratios of different functional guilds.

## *The Redwood Invertebrate Fauna*

Distinct invertebrate assemblages are associated with three primary habitats in Pacific Northwest old-growth forests: the forest floor and understory, the forest canopy, and riparian habitats. The forest-floor invertebrate fauna of old growth harbors a large proportion of sedentary species (wingless and flightless forms) with narrow tolerance ranges to temperature and moisture conditions (Moldenke and Lattin 1990a; Lattin and Moldenke 1992; Frest and Johannes 1993). Such characteristics are seen in numerous species of oribatid mites, harvestman, millipedes, centipedes, springtails, beetles, flies, wasps, spiders, crickets, land molluscs, and isopods. Some taxa, such as millipedes, lack a waxy cuticle, making them sensitive to desiccation stress and restricting them to moist microhabitats. On an even finer scale, some soil arthropods, such as oribatid mites, are predictably associated with different combinations of soil temperature, moisture, structure, fungal abundance, limiting nutrients, and even the litter of different tree species (McIver et al. 1990; Moldenke 1990). Because of their specialized requirements, most forest-floor species appear to be poor at dispersing among old-growth fragments, and populations and locally endemic species are prone to extinction. Many old-growth associated species of millipedes and harvestmen known only from single patches of old growth, including some redwood fragments, have not been collected again since the type localities were logged (Olson 1992).

Knowledge of canopy invertebrates is rudimentary, but the few studies conducted in this challenging research environment reveal a highly diverse and distinctive fauna (Voeghtlin 1982; Schowalter 1989; Winchester 1993, 1996, 1997; Winchester and Ring 1996a,b). Most higher taxa found on the forest floor also are observed in the canopy on foliage, bark, and branches, or living in the detritus, moss, and root mats covering large branches in undisturbed tem-

perate rain forests. These assemblages of canopy species, however, are quite distinct from forest-floor communities and those of younger forests, indicating a specialized arboreal old-growth fauna (Winchester 1996; Winchester and Ring 1996a,b). Canopy arthropod faunas are dominated by phytophagous and predator/parasitoid guilds (Schowalter and Crossley 1987; Schowalter 1989; Winchester and Ring 1996b), a pattern typical of functionally diverse and complex ecosystems (Winchester and Ring 1996b). Moreover, the amount and kinds of plant material lost to herbivory and the significant predator/parasitoid presence suggest that epizootic outbreaks are rare in late-seral forests (Winchester and Ring 1996b). Canopy invertebrates in moss mats are sufficiently numerous to support populations of clouded salamanders in redwood forests (see earlier discussion). Mating stoneflies and "pulses" of adult caddisflies observed in the canopies of old-growth Sitka spruce on Vancouver Island (Winchester 1993) also suggests a key role of canopy habitats in the life cycle of invertebrates more commonly linked to forest-floor and riparian habitats.

Although some canopy invertebrates are vagile dispersers with relatively widespread ranges, increasing evidence suggests that a sizable component of the canopy biota consists of species restricted to specialized microhabitats, such as moss mats. If such canopy species have limited geographic ranges, as observed in many forest-floor invertebrates (Olson 1992), then the loss and fragmentation of old-growth forests will lead to increasing extinction—before species are even discovered, in some cases (see Winchester and Ring 1996a). Given the diversity, specialization on old-growth environments, and limited ranges observed in many forest-floor and canopy invertebrates, it is highly likely that a wave of invertebrate extinctions already has accompanied the catastrophic loss of coastal old-growth forests.

Invertebrates associated with riparian and aquatic habitats in old-growth forests are poorly documented, but some species of stoneflies, caddisflies, and ground beetles are known to be restricted to these habitats. Some species are very localized, such as some ground beetles (e.g., *Nebria* spp.) whose only known localities are small stretches of streams (D. H. Kavanaugh, California Academy of Sciences, pers. comm.). Destruction of old-growth forests is known to severely affect streams and their biota (see Frest and Johannes 1996 and chap. 6, this volume).

The patterns of habitat specialization, low vagility, and restricted distribution displayed by a large percentage of the canopy, forest-floor, and aquatic invertebrate fauna are features often associated with forests that have enjoyed relatively stable and benign conditions for long periods of time, as have the redwoods of the Northern California Coastal Forest ecoregion (Lattin and Moldenke 1992; Ricketts et al. 1999). The ancient heritage of redwood forests is reflected in the presence of such primitive invertebrates as the silverfish, *Tricholepidion gertschi,* a living fossil that closely resembles the hypothetical ancestor of higher

insects (Powell and Hogue 1979). Other relic species include the ant *Amblyopone oregonense,* the California swollen-footed pointed-wing moth *(Paraphymatopus californicus),* which resembles the ancestor of moths and butterflies, and the colonial wood-feeding roach *(Cryptocercus punctulatus),* a link between the roaches and termites (Lattin and Moldenke 1992). Many other distinctive taxa occur throughout the rain forests of the Pacific Northwest, including the taxonomically unique (e.g., monotypic genera) long-jawed nimble millipede searcher *(Promecognathus laevissimus),* Matthew's ground beetle *(Zacotus matthewsi),* the pitch-colored bark-dwelling carabid beetle *(Psydrus piceus),* and Capizzi's blind rove beetle *(Fenderia capizzii)* (Lattin and Moldenke 1992).

Several higher taxa of invertebrates in Pacific Northwest rain forests have extraordinary disjunct ranges, with their closest relatives halfway around the world, a distribution reflecting the great age and relative stability of these rainforest ecosystems (see chap. 2). Examples include the aquatic large west American unique-headed bug *(Boreostolus americanus)* with its nearest relative in Tierra del Fuego, the flightless moss lacebug *(Acalypta saundersi)* with similar species in the Mexican Highlands, the Ozarks, and the Appalachians (Lattin and Moldenke 1992), as well as a suite of longhorn (Cerambycidae) beetle genera found only in the Pacific Northwest and East Asia (Gorton-Linsley 1963).

## *Ecological Roles of Invertebrates*

Forest invertebrates and their activities drive many key ecological processes, including control of decomposition processes and nutrient cycles, checking epizootic outbreaks, catalyzing natural disturbance and successional processes, and regulating growth and reproductive success of fungi, plants, and vertebrates (Schowalter and Crossley 1987; Schowalter 1989; Snyder 1992; Hoekstra et al. 1995; DellaSala and Olson 1996). In redwood forests, fungi and insects are implicated in the low viability (roughly 60 percent mortality) of redwood seed crops—for example, from the action of seed predators, such as the cone moth *(Commophila fuscodorsana)* and the roundheaded borer *(Phymatodes nitidus).* Loss of redwood seedlings also occurs from herbivory of the gray millipede and banana slug *(Ariolomax columbianus).* Herbivory and other forms of damage to adult trees are caused by mites and insects in diverse groups that include termites, true bugs, beetles, moths, and ants and wasps (Davidson 1970, 1971; Snyder 1992). Nevertheless, redwood trees are noted for their remarkable resistance to attack by insects (see chap. 4). This resistance is reflected in the small number of insects that feed on redwoods. Only four bark beetles and two species of miners attack redwoods, compared to 30 and 28 species, respectively, on Douglas-fir (Snyder 1992). Of the 54 insects recorded by Lauck (1964) to attack redwoods, few are believed to confine their activity to redwoods and none are capable of killing mature trees by themselves (Fritz 1957; Snyder 1992). Only the black-horned borer *(Callidium sempervirens),* another borer *(C. pallidum),*

and the large cedar borer *(Semanotus ligneus sequoiae)* have been recorded exclusively from coast redwoods (Snyder 1992). Although few invertebrates are known to feed directly on redwoods, many species are associated with the moss, fern, lichen, and other epiphyte mats that cover the branches of mature redwoods (see chap. 3).

The ecological interactions of temperate rain-forest invertebrates can be complex, with many linkages to other processes and species. For example, the ferocious folding-trap-door spider *(Antrodiaetus pugnax)* occurs at high densities in old-growth forests and is thought to regulate populations of numerous invertebrate prey species (Coyle 1971). The handsome iridescent fly *(Eulonchus tristis)* is one of the most important pollinators of understory plants (i.e., native bees avoid shade), but its reproductive success is dependent on the availability of *Antrodiaetus* as hosts for its young (Lattin and Moldenke 1992).

## *Conservation of Invertebrates*

The biota of late-seral redwood forests is sensitive to anthropogenic disturbances such as logging. The loss of large trees over extensive areas eliminates habitat for canopy invertebrates and creates desiccation stress, higher temperatures, and disturbed soil and litter habitats for forest-floor species (Olson 1992; Hoekstra et al. 1995). Selective logging of redwood forests can significantly alter guild structure, abundance, and diversity of invertebrates for long periods of time (Hoekstra et al. 1995)—predisturbance species composition may be absent even fifteen years after logging. Heavy logging of redwoods, and old-growth forests in general, causes the loss of large trees and complex microhabitats, disturbance of soil and litter habitats, loss of coarse woody debris, and substantial alteration of temperature and moisture regimes; it can also promote the invasion of alien species (Olson 1992; Frest and Johannes 1993). All of these trends seriously affect the native invertebrate biota associated with old-growth redwood forests. Flightless and mesophilic (moisture-loving) species are particularly sensitive to the loss of forest canopies and fragmentation of forests (Main 1987; Moldenke and Lattin 1990b; Olson 1992; Lattin 1993; Winchester and Ring 1996a; Winchester 1997).

The diversity and abundance of old-growth invertebrates may be irreversibly changed if logging is extensive and source populations are eliminated across the landscape (Vlug and Borden 1973; Schowalter 1990; Frest and Johannes 1993; Winchester and Ring 1996a; Winchester 1997). If many invertebrate species are restricted to local areas—and strong evidence suggests this—then the loss of more than 95 percent of the original redwood forest (U.S. Fish and Wildlife Service 1997) has almost certainly led to numerous extinctions of old-growth redwood invertebrates. A better understanding of patterns of invertebrate beta diversity (species turnover along environmental gradients), microhabitat specificity, and local endemism is urgently needed for conservation planning

(see Olson 1992; Samways 1994; Winchester 1993, 1997; Winchester and Ring 1996a).

## Forest Carnivores of the Redwoods Region

Forest carnivores (forest-dwelling mammals of the order Carnivora) merit conservation concern for their functional importance to ecosystems and for what they indicate about ecosystem condition. Carnivores affect the behavior and demography of their prey, cycle nutrients by scavenging carrion, complete or interrupt pathogen and parasite life cycles, and affect plant distribution—and likely landscape pattern—through dispersal and predation of seeds (Buskirk in press). Mammalian carnivores affect human economies and cultures positively (e.g., tourism generated by the spiritual and aesthetic value of observing them, harvest of some commercially important species) and negatively (e.g., depredations on livestock and fish at hatcheries, transmission of rabies). The population status of carnivores is a measure of ecosystem condition and integrity (Noss et al. 1996); maintaining and restoring their diversity, natural distributions, and abundances have ecological, spiritual, and economic value.

### *Historical Distributions and Abundances*

An obvious yardstick by which to evaluate the status of mammalian carnivores in the redwood region is to compare their current diversity, distribution, and abundances to what they were before intensive human activities (i.e., settlement by Europeans). Unfortunately, little is known about the wildlife of the region prior to the twentieth century. The traditional uses of furbearing mammals by Native Americans—some of which are still practiced today—and the accounts by anthropologists of the customs of tribes of the region (e.g. Scott and Kroeber 1942), provide some insight on the diversity and abundance of mammalian carnivores. Most notable are the species that were either a potential threat to human life (i.e., grizzly bears) or which had important spiritual or cultural value. Grizzly bears appear to have been common throughout the region, especially along the mouths of the major rivers. Early historical information on smaller carnivores is reflected in the ceremonial use of their skins in regalia. The Hupa (Hoopa) tribe has existed on the eastern margin of the redwood region since before recorded history; their regalia include the skins of bobcat, fox, fisher, and ringtail (B. Colegrove, pers. comm.). Some species (e.g., marten and wolverine) are conspicuous by their absence in regalia, which may signify either they did not occur in the region or were extremely rare. Early European explorers and settlers left little recorded history of the wildlife of the redwood region. The Spanish, in the late 1700s, and then the Russians and Americans in the 1800s, focused their wildlife harvesting activities just offshore, on the California sea otter, whose pelt exceeded the value of any terrestrial furbearer.

The earliest scientific account of the ecology, distribution, and status of mammalian carnivores in California is a summary by Joseph Grinnell, Joseph Dixon, and Jean Lindsdale of trapping records, interviews, and field observations during the first decades of the twentieth century (Grinnell et al. 1937). They reported eighteen species of terrestrial mammalian carnivores as suspected to have occurred in the redwood region: two ursids, two procyonids, ten mustelids, two canids, and two felids (table 5.5). They ranged in size from the short-tailed weasel (ermine), at less than 1 kg, to the 650-kg grizzly bear, and can be categorized into

Table 5.5. Mammalian Carnivores That Historically Occurred in the Redwood Region, Their Typical Habitat in the Region, Their Status in the Region in the 1920s, and Their Current Status.

| *Species* | *Habitat* | *Status in 1920s* | *Status Today* |
|---|---|---|---|
| Grizzly bear (*Ursus arctos*) | Generalist; grasslands, bays, forests, and mouths of major rivers | Extirpated but formerly common | Extirpated |
| Black bear (*Ursus americanus*) | Forests at all elevations | "Plentiful" | Regulated game species; limited season and bag limit; perhaps more abundant since extirpation of grizzly; commonly detected at track plate stations |
| Raccoon (*Procyon lotor*) | Lowlands and streamcourses in foothills and lower margins of fir forests; semi-aquatic | Moderate decline due to wetland drainage | Regulated fur-bearing game species; still common along streamcourses and near human habitation |
| Ringtail (*Bassariscus astutus*) | Open, deciduous forests on ridges and near streamcourses | 'quite plentiful, especially in northwestern California' | Protected from trapping or hunting; more common at track plate stations in interior forests than in redwoods along the coast |
| Long-tailed weasel (*Mustela frenata*) | Habitat generalist; forest/grassland edges | Not specified | Unprotected non-game species; no closed season and no limit; uncommonly detected at track plate stations |

| *Species* | *Habitat* | *Status in 1920s* | *Status Today* |
|---|---|---|---|
| Short-tailed weasel (*Mustela erminea*) | Grasslands/meadows, especially at higher elevations | Not specified limit; uncommonly detected at track plate stations | Unprotected non-game species; no closed season and no bag |
| Mink (*Mustela vison*) | Aquatic; marshes along bays and mouths of rivers and along mountain streams; found away from water more along north coast than elsewhere in California | Moderate decline due to wetland drainage | Regulated fur-bearing game species; limited season but no bag limit |
| Marten (*Martes americana*) | Mature redwood forests and on higher ridges of Douglas-fir | 'Sparse occurrence, though previously fairly numerous' | Protected; California Species of Special Concern; two *individuals* verified within the redwood range in past 50 years |
| Fisher (*Martes pennanti*) | Mature mixed coniferous and deciduous forests at all elevations but most common in mountains | Is becoming more rare, 'probably less than 300 in entire state' | Protected; California Species of Special Concern; twice petitioned to be listed under federal Endangered Species Act; commonly detected at trackplate stations in the redwood zone but less so than in interior coast ranges |
| Wolverine (*Gulo gulo*) | Unconfirmed, high-elevation forests suspected | Extinct, "formerly suspected to occur in the mountainsof the northern coast region" | Protected; California Threatened Species; sporadic unconfirmed sightings |
| Otter (*Lutra canadensis*) | Aquatic; marshes along bays and mouths of rivers and in mountain streams | "Numbers are stable and the species is expected to persist" | Protected |
| Spotted skunk (*Spilogale gracilis*) | Drier forests and upland rocky or brushy unforested areas | "Population has maintained itself rather consistently" | Unprotected non-game species; no closed season and no bag limit; commonly detected at track plate stations |
| Striped skunk (*Mephitis mephitis*) | Brushy woodlands at low elevation, regions with sod-forming vegetation, beaches | "The most abundant of the fur-bearing mammals" | Unprotected non-game species; no closed season and no bag limit |

(*continues*)

Table 5.5. (*continued*)

| *Species* | *Habitat* | *Status in 1920s* | *Status Today* |
|---|---|---|---|
| Badger (*Taxidae taxus*) | Open, unforested regions and forests interspersed with grasslands | "Numbers but little reduced from those of former times" | Regulated fur-bearing game species; limited season but no bag limit |
| Gray fox (*Urocyon cinereoargenteus*) | Brushy woodlands and forest from sea level to high-elevation forests. | "Trapping has caused relatively little change in numbers" | Regulated fur-bearing game species; limited season but no bag limit |
| Coyote (*Canis latrans*) | Brushy woodlands and forest from sea level to high-elevation forests; openings caused by timber harvest | Recent immigrant to north coast region; numbers increasing | Unprotected nongame species; no closed season and no bag limit |
| Wolf (*Canis lupus*) | Unknown | Unconfirmed in redwood region. | Protected |
| Mountain lion (*Puma concolor*) | Habitat generalist; forests, woodlands and brush at all elevations | "Breeding stock has not been greatly reduced" | Protected |
| Bobcat (*Felis rufus*) | Habitat generalist; forests and brushlands with rocky ground, river bottoms | "Wide distribution ... would be last fur animal to become extinct in California" | Regulated fur-bearing game species; limited season and bag limit; relatively commonly detected at track plate stations |

*Source*: Grinnell et al. (1937).

six groups by habitat: aquatic or semiaquatic species (otter, mink), riparian associates (raccoon, ringtail), habitat generalists (grizzly bear, black bear, coyote, mountain lion), forest generalists (gray fox, spotted skunk, bobcat, long-tailed weasel), grassland/meadow associates (striped skunk, short-tailed weasel, badger), and mature forest associates (marten, fisher, wolverine).

Only one species of mammalian carnivore, the American marten, includes a recognized subspecies that is considered endemic to the humid redwood belt. The Humboldt marten *(M. a. humboldtensis)* is distinguished from the other California subspecies, *M. a. sierrae,* by its darker color, reduced size of orange throat patch, and various cranial skeletal features (Grinnell and Dixon 1926; Grinnell et al. 1937). Genetic analysis to establish the genetic uniqueness of this subspecies is under way (Bayliss and Zielinski, in prep.).

Although the classic work by Grinnell et al. is the most extensive summary of

the ecology of mammalian carnivores of California, by the time it was undertaken, the trapping and hunting of terrestrial furbearers had already begun to decimate their populations: "Since the State was first occupied by white man, the major population trends of fur animals has been downward" (Grinnell et al. 1937:24). The grizzly was extirpated from the redwood region by the mid-1800s, the wolverine was absent and suspected to have been extirpated, and the marten and fisher were undergoing significant population declines in the early twentieth century. The decline of some species apparently occurred so soon after European colonization that it is unclear whether they ever occurred in the region. No documentation exists of the historic occurrence of wolverine or wolf in the redwood region. The wolverine was suspected to have occurred in the "mountains of the northern coast region" (Stephens 1906, cited in Grinnell et al. 1937), but this could not be verified. And of the wolf, Grinnell et al. stated, "If the northwest timber wolf ever occurred in California, which is not unlikely, it probably was restricted to the northwest coastal strip of high humidity and heavy timber." Thus, historical information provides little basis for interpreting the current apparent absence of wolverines and wolves in northwestern California.

### *Early Conservation Efforts*

By the end of the nineteenth century, the reduction in numbers of fur-bearing mammals had become so great that the "attention of thoughtful people was directed to it" (Grinnell et al. 1937). Laws were enacted in 1913 to protect the sea otter and in 1917 to set seasonal and bag limits on the take of several species of terrestrial carnivores. By the 1920s, it was clear that species with high market value—the marten, fisher, and wolverine—would require special conservation efforts (Dixon 1924), a plea that was reinforced in the 1940s (Twining and Hensley 1947). The marten was protected from trapping in 1946 in northwestern California, and the fisher season was closed statewide in the same year.

The protection of vulnerable species from commercial trapping in the mid-1900s was a pivotal conservation measure. Nevertheless, government trappers continued to trap and poison carnivores in the interest of protecting livestock. In four counties in California (including Humboldt Co.), from 1920 to 1930, government predator control agents killed an estimated 40,000 carnivores, rare forest carnivores such as fisher and marten no doubt among them.

Although targeted trapping of forest carnivores was now regulated, the second major threat to forest-dwelling mammals—timber harvest—was intensifying in the redwood region in the mid-1900s (see chap. 2). Most vulnerable are the species associated with old forests—marten and fisher. These species are typically associated with mature, mesic forests, noted for their structural complexity (uneven aged with high densities of snags and logs), large-diameter trees for resting and denning, and closed canopies (Buskirk and Ruggiero 1994; Powell

and Zielinski 1994). Clear-cutting has been the dominant silvicultural method for the harvest and regeneration of redwood (see chap. 8) and is the greatest current threat to the recovery and conservation of forest carnivores.

### *Current Status of Carnivores*

The end of the twentieth century brings renewed interest in the status of carnivores. Although the threat of trapping—at least to those species most vulnerable—has abated, most of the original redwood forest to which carnivores were adapted has been forever changed. With adequate habitat and source populations, protection from trapping usually leads to the restoration of furbearer populations (Coulter 1960; Buskirk 1993). The quality of the habitat in the redwood zone, however, has apparently declined since the fisher and marten were protected in the 1940s. The offsetting effects of protection from trapping and increasing habitat loss can be evaluated by examining the current diversity, distribution, and relative abundance of carnivores.

Since the late 1980s, carnivore surveys using standard detection methods (Zielinski and Kucera 1995) have been conducted with increasing frequency. Most surveys have been conducted in the northern redwood zone; areas south of Humboldt County have received little effort, and regions south of San Francisco Bay virtually none. The most comprehensive surveys in redwoods have been those by Klug (1996) and Beyer and Golightly (1995), but the results of other surveys conducted by timber companies, the USDA Forest Service, and environmental consulting companies have produced similar results. Considering the entire redwood region, including both redwood-dominated areas and those with substantial coverage of other tree species, the most commonly detected species are the gray fox, spotted skunk, bear, and fisher. Next most frequently detected are the raccoon, bobcat, and ringtail, with detections of weasel (*Mustela erminea* and *M. frenata* cannot be distinguished by their tracks) and striped skunk the least frequent. Each species has characteristics that place it on a continuum from relatively easy to very difficult to detect using enclosed track plate methods. Several of the most frequently detected species appear to have a low threshold for entering and re-entering track plate enclosures. Other species, such as the coyote, which appears to avoid novel items associated with humans, and the bobcat, which like many cats does not regularly consume carrion, are less effectively detected using these methods. For this reason, and due to the varying densities and home range sizes of the species, the number of detections is not a reliable index of relative abundance. For those species that regularly visit baited track plates, however, detections are a reliable measure of presence.

Survey results are somewhat different considering only redwood-dominated stands. Fishers are less common in redwood-dominated stands than in mixed redwood–Douglas-fir or Douglas-fir dominated forests that occur farther inland (Beyer and Golightly 1995; Klug 1997). Ringtails also appear less common in

the redwood-dominated stands. Black bear, gray fox, and spotted skunk are again the most commonly detected carnivores in redwood forests.

In reviewing surveys in the northern redwood zone over the past ten years, the most disturbing conclusion is the absence of the Humboldt marten. Since 1990, more than 1,000 track plate or camera stations have been deployed in more than 15,000 survey days without a single marten detection (Zielinski and Golightly 1996). This finding is especially noteworthy because martens are one of the species most readily attracted to and detected at track plate stations (Kucera et al. 1995; Zielinski et al. 1997).

Moreover, fisher researchers or commercial trappers seeking legal quarry have not trapped marten incidentally, nor has a single road-killed marten been reported to any state or federal resource agency in the redwood zone (Zielinski and Golightly 1996). Recently, marten have been detected at two locations near the eastern limit of the subspecies' original range, 20 km apart, during surveys conducted in Douglas-fir forests (Zielinski, unpubl. data.). Although these are the first martens verified within the historic range of the Humboldt subspecies, their genetic relationship to the martens that once occurred in the low-elevation redwood forests has yet to be established. Even considering these recent detections, the prognosis for the natural recovery of marten in the redwood forest is poor.

### *Consequences of Logging for Forest Carnivores*

The absence of verified records of wolverine in the redwood region and the loss of marten as a common predator in redwood ecosystems means that little local information is available on their habitat requirements. For marten, we can surmise the effects of logging based on their responses elsewhere, but the lack of data from the Pacific states makes this difficult for wolverines. Hence, most of our discussion must focus on the fisher, the only species of forest carnivore that remains in sufficient numbers to be the subject of recent research.

Almost everywhere they occur in the western United States, and like martens, fishers are associated with extensive, structurally complex, late-seral forests (Rosenberg and Raphael 1988; Buskirk and Ruggiero 1994; Powell and Zielinski 1994). Patterns of habitat association in wide-ranging carnivores, like many other species, are complex because of the interaction of processes operating at multiple scales. For example, detections of fishers in second-growth redwood stands belie a simplistic characterization of the species as an old-growth associate (Harris 1984). Though younger stands may retain habitat value at the patch scale (see discussion on WHR in the preceding section), landscape and regional-scale changes in redwood ecosystems give reason for concern about the long-term viability of coastal fisher populations—and the recovery of marten—under current timber-harvesting regimes.

Stand-level changes in redwood habitat likely to affect forest carnivores include reduction in canopy closure, tree diameter, and snag and log abundance,

as well as changes in floristic composition. High levels of overhead cover provide protection from predation, lower the energetic costs of traveling between foraging sites, and provide more favorable microclimatic conditions (Powell and Zielinski 1994; Buskirk and Ruggiero 1994; Thompson and Harestad 1994). Abundance or vulnerability of preferred prey species may be higher in areas with higher canopy closure (Buskirk and Powell 1994) or coarse woody debris. Clear-cutting, or any logging that reduces the density of large trees, affects the availability of denning and resting sites and structural components associated with prey vulnerability (Thompson 1986; Thompson and Colgan 1987; Thompson and Harestad 1994; Sturtevant and Bissonette 1997). Runoff from clear-cut sites also can severely degrade riparian areas, which not only are essential habitat for aquatic and semiaquatic carnivores but also provide critical foraging, travel, and resting habitats for marten and fisher (Powell and Zielinski 1994).

Changes in species composition associated with logging may include an increase in hardwood species (red alder and tanoak) and Douglas-fir. These floristic changes may have favored the expansion of fishers in the redwood region at the expense of martens, which are more closely associated with conifer than mixed forests. Marten have been shown elsewhere to suffer from competition with fishers, especially in regions lacking deep snow (Krohn et al. 1995). The lack of snow throughout most of the redwood zone, which if deep enough would inhibit fisher movement more than marten, may be an impediment to the recolonization of marten in regions where fishers are common.

Several structural features may enhance the resiliency of redwood forest to disturbance from logging. Regeneration by basal sprouting allows stands to recover canopy closure more quickly than in trees that regenerate from seed (see chap. 4). Historical logging methods often left behind coarse woody debris, snags, and residual "wolf" trees that provide a structural "legacy" that are favored rest sites for fishers (R. Klug, pers. comm.). Current harvesting methods are more intensive, however, and as harvested redwood stands enter short-term rotations they will increasingly lack the structural and floristic complexity they possessed before harvest (see chap. 8).

Changes in landscape patterns in the redwood region, such as the fragmentation described earlier, may limit the positive effects of stand-level resiliency. The current landscape mosaic in the redwood zone differs in several respects from the pre-settlement condition. Historically, redwood stands formed a mosaic with other forest types, such as oak woodland and closed-cone conifer forest, with fire playing a significant role (see chap. 3 and 4). The current landscape condition shows a lower abundance of older stands, smaller patch size, lower spatial and temporal variability in stand age-class distribution, and reduced natural fire frequency. These trends are likely to lead to reduced functional connectivity for species associated with older forests, as has been shown elsewhere for American marten (Hargis and Bissonette 1997).

Increased road access is often suggested as a negative collateral effect of logging primary forest. Roads provide access for trappers and are a source of vehicle-caused mortality. None of the rare forest carnivores is currently legally trapped, but they are captured incidentally in traps set for other species (Lewis and Zielinski 1996), and roadkills are not uncommon. Analyzing the effect of road density on abundance and distribution is difficult, however. For example, if productive forestlands are preferentially targeted for logging and associated road-building, a complex interaction of road density and habitat quality may be evident. Fisher detections were positively correlated with low-use road density in the eastern Klamath region, but this conclusion is difficult to interpret in light of the absence of a negative effect of high-use roads (Dark 1997). Perhaps because of the scarcity of primary forest in the redwood region, older second-growth forest with low to moderate road density probably is a critical factor as forest carnivore habitat.

### *Habitat Value of Redwoods for Forest Carnivores*

Klug's (1996) extensive surveys for fishers in the redwood zone found positive correlations between fisher detection rates and such stand-level attributes as diameter and basal area of hardwoods, canopy closure, and volume of logs. Similarly, Carroll et al. (1999), using survey data from the adjacent inland forest types, found fisher detection rates were highest at sites with large hardwoods in landscapes of dense, mixed hardwood–conifer forests.

Lower detection rates for fishers in redwood forests when compared to the redwood–Douglas-fir transition zone led Klug (1996) to conclude that redwood habitat supported smaller populations. The generality of this conclusion may be limited, however, by the predominantly early-seral character of the commercial timberlands surveyed in Klug's study. The habitat model of Carroll et al. (1999) predicts greater variability of detection rates in the redwood forest, in part because of the high contrast in average tree age and diameter between protected areas and commercial timber lands. Beyer and Golightly (1995) report generally lower than expected detection rates in redwoods; they note, however, that a survey transect in Redwood National Park recorded high detection rates. Although floristic variation, especially the abundance of large hardwoods, appears to be a major factor influencing fisher distribution, the relative habitat value of late-seral redwood stands cannot be characterized without additional surveys.

Regional-scale variation in fisher abundance confounds efforts to unravel stand-level habitat associations. Biogeographic correlations between fisher distribution and such regional factors as elevation and distance to the ocean (Klug 1996) or precipitation and geographic variables (Carroll 1997) may be as strong as those with patch or landscape-level habitat attributes. The higher detection rates in Redwood National Park as compared to Humboldt State Redwoods

Park (Beyer and Golightly 1995) and the low rate of detections on commercial timberlands in the north and south of Klug's (1996) study area may reflect these regional-scale factors.

One hypothesis links the coarse-scale distribution patterns described above to regional fisher metapopulation structure (Carroll et al. 1999). The concept of a metapopulation of populations linked by occasional dispersal may be especially applicable to fishers inhabiting the fragmented habitat of the redwood region. We use the term *metapopulation* in a broad sense here, as real-world metapopulations often do not conform to the classic "island-island" model (Harrison 1994). Instead, "Central patches are united by dispersal into a single population, slightly more isolated ones undergo extinction and recolonization, and still more isolated patches are usually vacant" (Harrison and Taylor 1997). Limited evidence concerning the structure of the regional fisher metapopulation suggests that the lower Trinity River watershed may function as a central "mainland" population. This pattern would favor occupation by fishers of redwood forest lying to the west of this area.

As with the spotted owl, fisher metapopulations may show nonlinear responses to the size and spacing of habitat clusters. If clusters of suitable habitat become too small or isolated, the imbalance between immigration and emigration can limit long-term viability (McKelvey et al. 1993; Noon and McKelvey 1996). The decline in distribution of the fisher in the western United States may be due to such regional-level dynamics (Heinemeyer and Jones 1994). Existing land management planning processes are poorly adapted to decision-making across administrative boundaries. A comprehensive plan to ensure the viability of forest carnivores and maintain well-distributed populations would need to include measures to increase levels of canopy closure on managed lands and restore connectivity through development of landscape linkages between the redwood parks and stands farther inland. The survival of the fisher and marten, like that of other wide-ranging carnivores, may ultimately depend on multiownership cooperative management on a regional scale (Mladenoff et al. 1995).

## Marbled Murrelets in Redwoods

The marbled murrelet is a seabird that nests up to 88 km inland in coastal, older-aged coniferous forests throughout most of its range from Alaska to central California. Murrelets fly at high speeds (up to 158 km/h), attend their breeding sites primarily during low light levels, and nest solitarily (Nelson and Hamer 1995a; Nelson 1997). The secretive aspects of their breeding biology have made their nests difficult to locate; the first murrelet nest was not discovered until 1974 (Big Basin State Park, California; Binford et al. 1975). Since then, more than 170 nests have been found, 18 of them in California (table 5.6).

Table 5.6. Characteristics of Marbled Murrelet Tree Nests in California.

| *Site* | *Tree species*[a] | *Diameter (dbh, cm)* | *Tree height (m)* | *Limb height (m)* | *Limb diameter at bole (cm)* | *Limb diameter from nest (cm)* | *Distance from trunk (cm)* | *Vertical cover (%)* | *Moss depth (mm)* | *Moss (%)* | *Outcome/ stage*[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Big Basin State Park 1974[c] | PSME | 167.0 | 61.0 | 45.0 | 41.0 | — | 6.8 | 100 | 0.8 | 100 | failed/chick fell out |
| Big Basin State Park 1989[d] | PSME | 210.0 | 61.2 | 43.7 | — | 47.7 | 122.0 | 100 | 1.0 | 100 | predation by CORA / egg |
| Big Basin State Park 1989[d] | PSME | 196.0 | 76.2 | 38.5 | — | 36.3 | 61.0 | 100 | 1.0 | 100 | predation by STJA / chick |
| Big Basin State Park 1991[e] | SESE | 533.0 | 79.2 | 41.1 | 61.0 | 61.0 | 0 | 100 | 0 | 0 | successful |
| Big Basin State Park 1992[e] | SESE | 533.0 | 79.2 | 53.2 | 42.0 | 42.0 | 0 | 100 | 0 | 0 | successful |
| Pacific Lumber 1992[f] | SESE | 229.0 | 86.5 | 67.0 | 21.2 | 21.0 | 0 | 100 | 0 | 0 | failed/chick died |
| Pacific Lumber 1992[f] | SESE | 254.0 | 74.3 | 67.5 | 25.0 | 20.0 | 18.0 | 100 | 0 | 0 | unknown |
| Pacific Lumber 1993[g] | PSME | 183.0 | 70.0 | 37.0 | 37.0 | 30.0 | 0 | 5 | 3.8 | 100 | inactive |
| Pacific Lumber 1993[g] | SESE | 300.0 | 83.0 | 60.0 | 37.0 | 37.0 | 5.0 | 50 | 0 | 5 | unknown |
| Jedediah Smith State Park 1993[h] | SESE | 338.0 | 79.5 | 43.6 | 21.0 | 16.0 | 90.0 | 99 | 0 | 1 | inactive |
| Prairie Creek State Park 1993[h] | TSHE | 139.0 | 66.7 | 33.3 | 29.0 | 23.0 | 20.0 | 98 | 8.1 | 100 | inactive |
| Big Basin State Park 1994[e] | SESE | 533.0 | 79.2 | 41.1 | 61.0 | 61.0 | 0 | 100 | 0 | 0 | predation/egg |
| Butano State Park 1995[i] | | | | | | | | | | | predation by CORA / egg |

(*continues*)

Table 5.6. (*continued*)

| *Site* | *Tree species*[a] | *Diameter (dbh, cm)* | *Tree height (m)* | *Limb height (m)* | *Limb diameter at bole (cm)* | *Limb diameter from nest (cm)* | *Distance from trunk (cm)* | *Vertical cover (%)* | *Moss depth (mm)* | *Moss (%)* | *Outcome/ stage*[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Big Basin State Park 1996[i] | SESE | 533.0 | 79.2 | 53.2 | 42.0 | 42.0 | 0 | 100 | 0 | 0 | predation/egg |
| Big Basin State Park 1996[i] | SESE | 174.0 | 48.8 | 31.7 | 18.0 | 18.0 | 0 | 80 | 0 | 0 | successful |
| Big Creek Lumber predation/chick 1997[k] | | | | | | | | | | | |
| Pescadero Creek County Park 1997[k] | | | | | | | | | | | predation by RSHA/egg unknown |
| Overall (mean + SE) | | 308.7 + 41.7 | 73.1 + 2.8 | 46.9 + 3.1 | 36.3 + 4.2 | 35.0 + 4.3 | 23.1 + 10.5 | 88.0 + 7.4 | 1.1 + 0.6 | 36.1 + 13.2 | |

[a] PSME = *Pseudotsuga menziesii*, SESE = *Sequoia sempervirens*, TSHE = *Tsuga heterophylla*
[b] CORA = Common Raven, STJA = Steller's Jay, RSHA = Red-shouldered Hawk
[c] Binford et al. 1975
[d] Singer et al. 1991
[e] Singer et al. 1995
[f] Kerns and Miller 1995
[g] S. Chinnici, pers. comm.
[h] T. Hamer, pers. comm.
[i] D. Suddjian, pers. comm.
[j] S. W. Singer, pers. comm.
[k] E. Burkett, pers. comm.

Murrelet nests in California, like other tree nests throughout their range (Hamer and Nelson 1995), occur in large, tall redwood, Douglas-fir and western hemlock trees (table 5.6). These nests are located above the 30 m height on large limbs with high vertical cover. In contrast to other regions, nest limbs in California generally have less moss because of drier conditions and higher daytime temperatures compared to farther north. Key components of nesting habitat in California include the percentage of old-growth canopy cover and tree species composition (>50 percent coast redwood; Miller and Ralph 1995). The amount of habitat along major drainages and at lower elevations is also useful in predicting murrelet occurrence.

Marbled murrelets in California are known to occur primarily in the coast redwood forests. Only a few observations (but no nests) have been recorded in Douglas-fir dominated forests. The distribution of redwood forests closely matches the inland extent of marine air influences and summer fog (Barbour and Major 1988; and see chap. 3 and 4). At sites farther inland, where the maritime influence is limited by rugged topography, Douglas-fir and tanoak forest types dominate. Although these forests generally have multiple tree layers, large trees, and potential nesting platforms (Jimerson et al. 1996), summer temperatures are higher, resulting in a lack of moss on tree limbs and hot, dry conditions that may be unsuitable for nesting by murrelets. The distance to the ocean is also greater, increasing energetic demands.

Murrelet nests are frequently unsuccessful; overall nest success has been only 37 percent ($n$ = 60; Nelson and Hamer 1995b; S. K. Nelson and I. A. Manley, unpub. data). Of the twelve nests with known outcomes in California, 75 percent ($n$ = 9) were unsuccessful (table 5.6). Of those that failed, seven (78 percent) failed from predation during the egg ($n$ = 5) and chick ($n$ = 2) stages. Known predators at these nests have included common ravens, Steller's jays, and red-shouldered hawks. Habitat fragmentation (smaller stand size, more edge habitat) and distance of nests from the tree trunk and stand edge (roads, clearcuts, younger forests) are factors that appear to reduce nest success (Nelson and Hamer 1995b; S. K. Nelson and I. A. Manley, unpub. data).

An estimated 60,000 or more marbled murrelets were found historically along the coast of California (Larson 1991); today, only about 6,000 birds (including breeders and nonbreeders) remain (Ralph and Miller 1995)—a 90 percent decline. Murrelet populations are projected to be declining at a rate of 4–7 percent per year (Beissinger 1995), primarily because of habitat loss and fragmentation from logging and development. This species was federally listed as threatened in Washington, Oregon, and California (U.S. Fish and Wildlife Service 1992) and state listed in California as endangered (California Fish and Game Commission 1992) in 1992.

Less than 4 percent of the original redwood forests, once totaling more than 770,000 ha, remain in California (U.S. Fish and Wildlife Service 1997).

Suitable marbled murrelet forest habitat currently occurs in three separate areas: (1) Humboldt, (2) Del Norte Counties in the north, and (3) San Mateo and Santa Cruz counties in central California; the northern and central areas are separated by a distance of about 480 km, as most of Mendocino County no longer contains nesting habitat. Most of the remaining redwood forests occur in state, county, and national parks; however, more than 36,000 ha apparently remain on private land, especially in Humboldt County. In California, critical murrelet habitat (i.e., critical for species survival) was designated primarily on federal land (64 percent; 193,150 ha). Nevertheless, 88,750 ha on state and county lands and 18,080 ha of private forests were also designated as critical because habitat protected in parks and national forests alone will not guarantee the long-term survival of the murrelet (U.S. Fish and Wildlife Service 1996). Most of the private critical habitat occurs on lands owned by the Pacific Lumber Company, which are currently the subject of a multispecies habitat conservation plan (HCP) under section 10(a) of the federal Endangered Species Act. Approved just before this book went to press, this HCP would allow some incidental take of murrelets and, many feel, does not replace the old-growth forest structure required by murrelets.

In the Marbled Murrelet Recovery Plan (U.S. Fish and Wildlife 1997), goals for recovery call for preventing the loss of any additional occupied habitat. Developing new habitat and improving the quality of existing habitat by minimizing human impacts in the parks is also recommended to ensure the long-term survival of this species. In California and elsewhere, however, many private timber companies are currently negotiating HCPs with the U.S. Fish and Wildlife Service that would allow them to log some occupied and critical habitat and cause "incidental take" of murrelets. These negotiations, under the auspices of section 10(a) of the federal Endangered Species Act, are likely to cause a continual decline in suitable murrelet habitat. The next fifty years have been identified as the most critical for murrelets, a time period in which, under the Northwest Forest Plan (U.S. Departments of Agriculture and Interior 1993), some habitat on federal lands will become suitable for nesting by murrelets. The current downward trend of available murrelet nesting habitat, however, along with pressures on their food resources from El Niño and overfishing, and adult mortality in oil spills and the gill-net fishery, place the continued survival of this seabird in jeopardy.

## Conclusions

The fauna of the redwood forest and region, though poorly known compared to many forest regions, reflects the long evolutionary history of the redwood lineage and the relative stability of this forest over millennia. Many of the animals of the region are adapted to moist, intact forest distributed over large areas and

to the structural characteristics of late-seral forest, ranging from the coarse woody debris on the forest floor to the complex canopies 100 m above the ground. Although they occurred in a mosaic with many other kinds of vegetation, old-growth redwood forests dominated the region for a long period of time before settlement by Europeans. The redwood fauna reflects this antiquity.

The drastic diminishment of old-growth redwood forests in the span of just several human generations threatens many forest species with extinction. The reduction in total area of old-growth redwoods is only part of the problem—just as threatening to many species is the continued simplification of the structure of these forests and their fragmentation into smaller, more isolated pieces. Undoubtedly, some species of invertebrates have been lost before they were ever described by science, and some vertebrates (i.e., several amphibians, Humboldt marten, fisher, northern spotted owl, and marbeled murrelet) are seriously imperiled. Although no species or subspecies is strictly endemic to the redwood forest, several are endemic to the region, and the long-term persistence of many more likely depends on conservation actions taken here.

"This is an extraordinary scientific treatment of the coastal redwood forests that should be the primary reference for all interested parties. Finally, a treatment which is done by individuals who are truly knowledgeable about the ecology of these forests! This book creates a model that hopefully will be followed for other important forest types throughout the globe."

—Jerry F. Franklin, Professor of Ecosystem Analysis, University of Washington, and editor of *Creating a Forestry for the 21st Century* (Island Press, 1997)

"This book fills a long-standing need for a synthesis of the ecology and conservation of redwood forests. It is an excellent source of scientific information on redwood trees and ecosystems written by the scientists who know them best. It will be a valuable reference for anyone seeking to understand, conserve, or manage these magnificent forests."

—Thomas Spies, Research Forest Ecologist, U.S.D.A. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon

*The Redwood Forest*, written in support of Save-the-Redwoods League's masterplan, brings together the latest insights from conservation biology along with new information from data-gathering techniques such as GIS and remote sensing. It presents the most current findings on the geologic and cultural history, natural history, ecology, management, and conservation of the flora and fauna of the redwood ecosystem.

Leading experts—including Todd Dawson, Bill Libby, John Sawyer, Steve Sillett, Dale Thornburgh, Hartwell Welsh, and many others—offer a comprehensive account of the redwoods ecosystem. *The Redwood Forest* offers a case study for ecosystem-level conservation. It contains the latest information from ground-breaking research on such topics as redwood canopy communities, the role of fog in sustaining redwood forests, and the function of redwood burls. It also presents sobering lessons from current research on the effects of forestry activities on the sensitive faunas of redwood forests and streams.

*The Redwood Forest* will be a vital resource for everyone involved with conservation of redwoods or any other forest.

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**ISLAND PRESS**

Washington, D.C. • Covelo, California

All Island Press books are printed on recycled, acid-free paper.

ISBN 1-55963-726-9

Cover design by The Visual Group.

Cover photo: Jedediah Smith Redwoods State Park.