

Cedar Log Flat  
Coquille Falls  
Portorford Cedar  
Hoover Gulch  
Ashland  
Wheeler Creek  
Lemmingsworth Gulch  
Lumpy Rock

# Klamath-Siskiyou Herpetofauna: Biogeographic Patterns and Conservation Strategies

R. Bruce Bury

Christopher A. Pearl

Forest and Rangeland  
Ecosystem Science Center  
USGS Biological Resources Division  
3200 Jefferson Way  
Corvallis, OR 97331 USA

•

Natural Areas Journal 19:341-350

**ABSTRACT:** The Klamath-Siskiyou region of southwest Oregon and northwest California (USA) has some of the most complex landscape mosaics and plant communities in western North America, reflecting its marked diversity of precipitation and topography. With 38 native species of amphibians and reptiles, the Klamath-Siskiyou region has the most species-rich herpetofauna of any similarly sized mountain range in the Pacific Northwest. Although it is a biodiversity "hot spot," there are only two endemic species, both salamanders, in the Klamath-Siskiyou region. High diversity is due to the overlap of two major biogeographic groups: the Arcto- (= northern) and Madro- (= southern) Tertiary herpetofaunas. Many of the amphibians in the Klamath-Siskiyou region are restricted to specialized habitats. Much of our knowledge about the biology of the regional fauna is based on studies elsewhere. Distributional surveys and ecological research are needed to address how the herpetofauna responds to timber harvest and other human activities that may reduce populations and increase fragmentation of suitable habitats. Conservation of the region's diverse herpetofauna should emphasize strategies directed at habitat specialists and species at the latitudinal limits of their ranges.

*Index terms:* amphibians, biogeography, conservation, Klamath-Siskiyou region, reptiles

## INTRODUCTION

The western edge of the North American continent is characterized by extensive north-south corridors of uplifted terrain, including the Coast Ranges and Cascade Mountains in the Pacific Northwest (PNW). These ranges converge in the Klamath-Siskiyou (KS) region (in which we include the Kalmiopsis, high Siskiyou, Trinity Alps, Marble Mountains, and portions of the Yolla Bolly range) of southwestern Oregon and northwestern California. Farther south, California's Central Valley again separates the ranges, and the Cascades give way to the Sierra Nevada Range. Only the highest elevations in the KS region (predominately within the Trinity Alps and Marble Mountains) were glaciated during the Pleistocene (Davis 1988), allowing animal and plant species distributions to shift north and south during periods of climatic change.

Several physical characteristics of the KS region contribute to a landscape of complicated habitat mosaics. Many rivers and streams, including the large Rogue and Klamath drainages, dissect rugged terrain, resulting in widely varied topographies (sea level to 2,200 m) and aspects. Exposed ultramafic substrates (e.g., serpentine and peridotite) and their unique floristic associates further contribute to a diverse landscape mosaic. Spatially complex fire his-

tories also typify these mountains (Agee 1991, Atzet and Martin 1991). Superimposed over the entire region are strong differences in seasonal climates (extended cool, moist winter conditions and hot, semi-arid summers) and a west-east gradient in precipitation (from about 405 cm per year near the coast to about 80 cm in the eastern rain shadow; Froehlich et al. 1982). Such physical gradients produce an array of habitat types available for reptiles and amphibians within a relatively small geographic area.

Life history traits and habitat requirements are among the most important factors governing the distribution of any taxonomic group. For example, the tailed frog is adapted to cool, rocky streams in closed-canopy forests, whereas reptiles such as the southern alligator lizard require warmer conditions often associated with exposed, rocky slopes. (Scientific names for amphibians and reptiles are given in Appendices 1 and 2, respectively.) In the KS region, these vastly different habitats can occur in close proximity and may allow more species to occur than would be expected in a more uniform environment.

The objectives of this paper are to describe the distribution patterns of the herpetofauna within the KS region, summarize the ecological roles and habitat requirements of the native amphibians and reptiles of

the KS region, and discuss considerations for conserving the diverse herpetofauna of the KS region.

## DIVERSITY AND BIOGEOGRAPHY

We estimate that 48 species of amphibians and reptiles occur in the temperate PNW, which we define as the region west of the Cascade Mountains and from San Francisco Bay northward to western Canada (Figure 1). This is a moderately rich herpetofauna with many regionally endemic amphibians (Nussbaum et al. 1983, Green and Campbell 1984, Stebbins 1985). The KS region supports at least 38 native species of amphibians and reptiles (Table 1, Appendix 1, Appendix 2), which represents the most species-rich herpetofauna among similarly sized mountain provinces in the PNW. The KS region supports the highest species richness of both salamanders and snakes within the western PNW (Table 1). Reptiles vary widely in species richness from only 4 species in the Olympic Mountains of northwestern Washington to 19 species in the KS region. In general, herpetofaunal diversity increases with southern latitude, as do the number and percentage of KS species shared between regions (Table 2). We found that 79% of the species in the KS region also occur in the Coast Range of northern California, and 63% occur in both the central Cascade Mountains and Coast Ranges of Oregon. Only 37% of KS species are shared with the Olympic Mountains of Washington, due in large part to the paucity of reptile species in the Olympic region.

The KS region represents a "hot spot" of species richness within the PNW for several reasons. Most important, the KS region is an overlap zone for two major biogeographic elements: the Madro- (southern) and Arcto- (northern) Tertiary geofaunas (Peabody and Savage 1958). The range limits of many amphibians occur in the KS region, and the overlap of northern (e.g., tailed frogs, red-backed, and Dunn's salamanders) and southern taxa (e.g., California slender salamander and black salamander) contribute to the richness of the fauna (Figure 2). Further, the mosaic and patchy nature of habitats in the KS region allows occurrence of a diverse

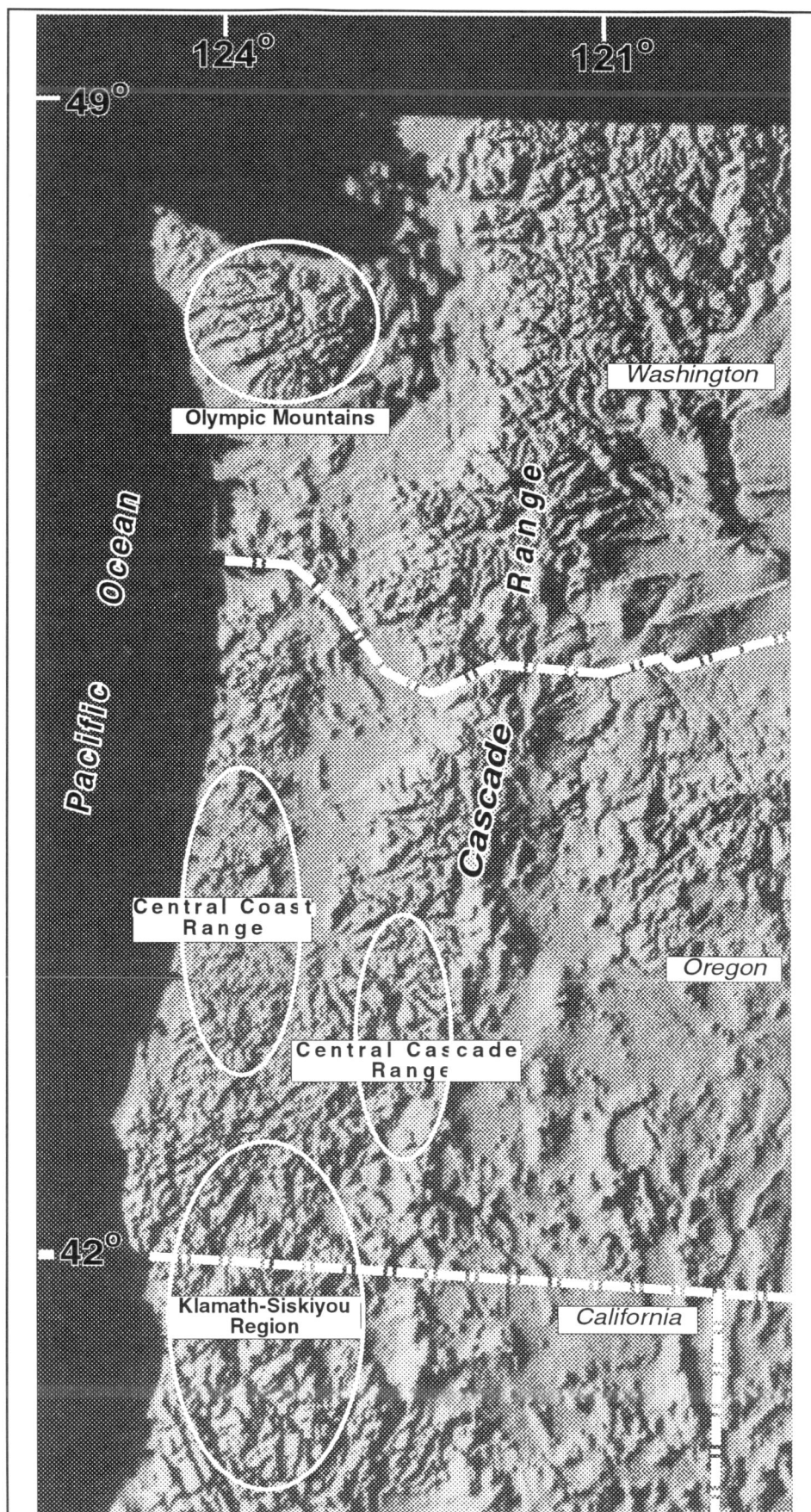


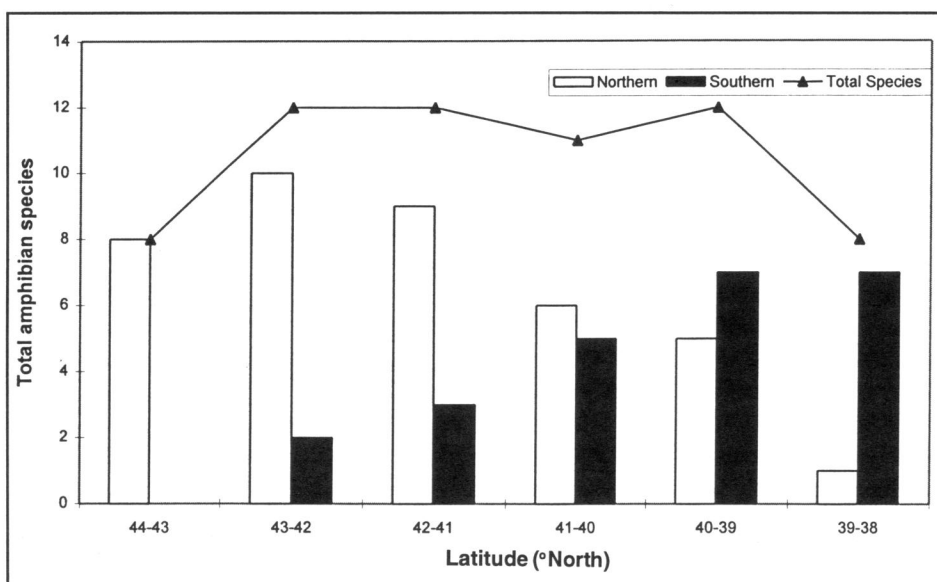
Figure 1. Location of Klamath-Siskiyou region and comparable mountain regions in the Pacific Northwest. The California Coast Range (not shown) is just south of the map limit.

**Table 1. Herpetofaunal species richness in the Pacific Northwest (number of families in parentheses). Abbreviations for mountain regions are: KS = Klamath-Siskiyou region, Oregon-California; OLYM = Olympic Mountains, northwestern Washington; OR Coast = Central Coast Range, Oregon; OR Casc = Central Cascade Range, Oregon; CA Coast = Northern California Coast Range.**

Order	Region				
	KS	OLYM	OR Coast	OR Casc	CA Coast
Anura (frogs & toads)	6 (4)	5 (4)	4 (4)	7 (4)	6 (5)
Caudata (salamanders)	13 (5)	8 (5)	9 (5)	9 (5)	11 (5)
Serpentes (snakes)	13 (4)	3 (3)	6 (2)	5 (2)	11 (3)
Sauria (lizards)	5 (3)	1 (1)	4 (3)	4 (3)	5 (3)
Testudines (turtles)	1 (1)	0	1 (1)	1 (1)	1 (1)
TOTALS	38 (17)	17 (13)	24 (15)	26 (15)	34 (17)

**Table 2. Number of species shared (percent of KS species in parentheses) between Klamath-Siskiyou herpetofauna and four other mountain regions of the Pacific Northwest. Abbreviations follow those in Table 1.**

Order	Region			
	OLYM	OR Coast	OR Casc	CA Coast
Anura (frogs & toads)	5 (83%)	4 (66%)	6 (100%)	5 (83%)
Caudata (salamanders)	5 (38%)	9 (69%)	8 (62%)	8 (62%)
Serpentes (snakes)	3 (23%)	6 (46%)	5 (38%)	11 (85%)
Sauria (lizards)	1 (20%)	4 (80%)	4 (80%)	5 (100%)
Testudines (turtles)	0 (0%)	1 (100%)	1 (100%)	1 (100%)
TOTALS	14 (37%)	24 (63%)	24 (63%)	30 (79%)



**Figure 2. Distribution of range limits for southern (= Madro-Tertiary) and northern (= Arcto-Tertiary) amphibian taxa within the Klamath-Siskiyou region (39°–43° north latitude). "Total species" includes only southern and northern species and not widespread taxa (see Appendix 1).**

herpetofauna. Reptiles tend to be most common in hotter, drier conditions (inland sites, lower elevations, and south-facing slopes), while amphibians generally are associated with mesic or wet areas (coastal or riparian sites, higher elevations, and north-facing slopes).

### Amphibians

High endemism is a feature of amphibian biogeography in western North America (Bury 1994). Most (64%) of the 22 amphibian species inhabiting forest habitats are regionally endemic to the PNW: 4 species of torrent salamanders, 2–3 species of giant salamanders, 6 species of lungless salamanders, 2 species of ranid frog, and the tailed frog. One or more species from each of these groups occur in the KS region (Appendix 1). The tailed frog is of particular interest because it represents a group of primitive anurans that occur only in widely separated ranges: tailed frogs are endemic to the PNW (as far east as western Montana), but bell toads (genus *Leiopelma*), their closest relative, occur only in New Zealand.

The high amphibian species richness in the KS region includes several different biogeographic elements: northern taxa (Arcto-Tertiary), southern taxa (Madrone-Tertiary), and widespread taxa (Appendices 1 and 2). Five of the 19 total species (26%) are geographically widespread within the region. These include species such as the roughskin newt and western toad. Three species (16%) have southern affinities, but most (58%) are associated with northern distributions. Examples include the torrent salamanders and tailed frogs, both of which represent ancient Arcto-Tertiary lineages (see Welsh 1990). Two closely related terrestrial species are endemic to the KS region: the Del Norte and Siskiyou Mountain salamanders. This number of endemic species is low but similar to other areas of comparable size in the Pacific Northwest (e.g., the Olympic Peninsula).

The KS region also has one of the most diverse salamander assemblages in western North America (Table 1, Figure 3). As many as 10 salamander species from 5 families can be found in one river basin. Recently, we discovered that up to three species of



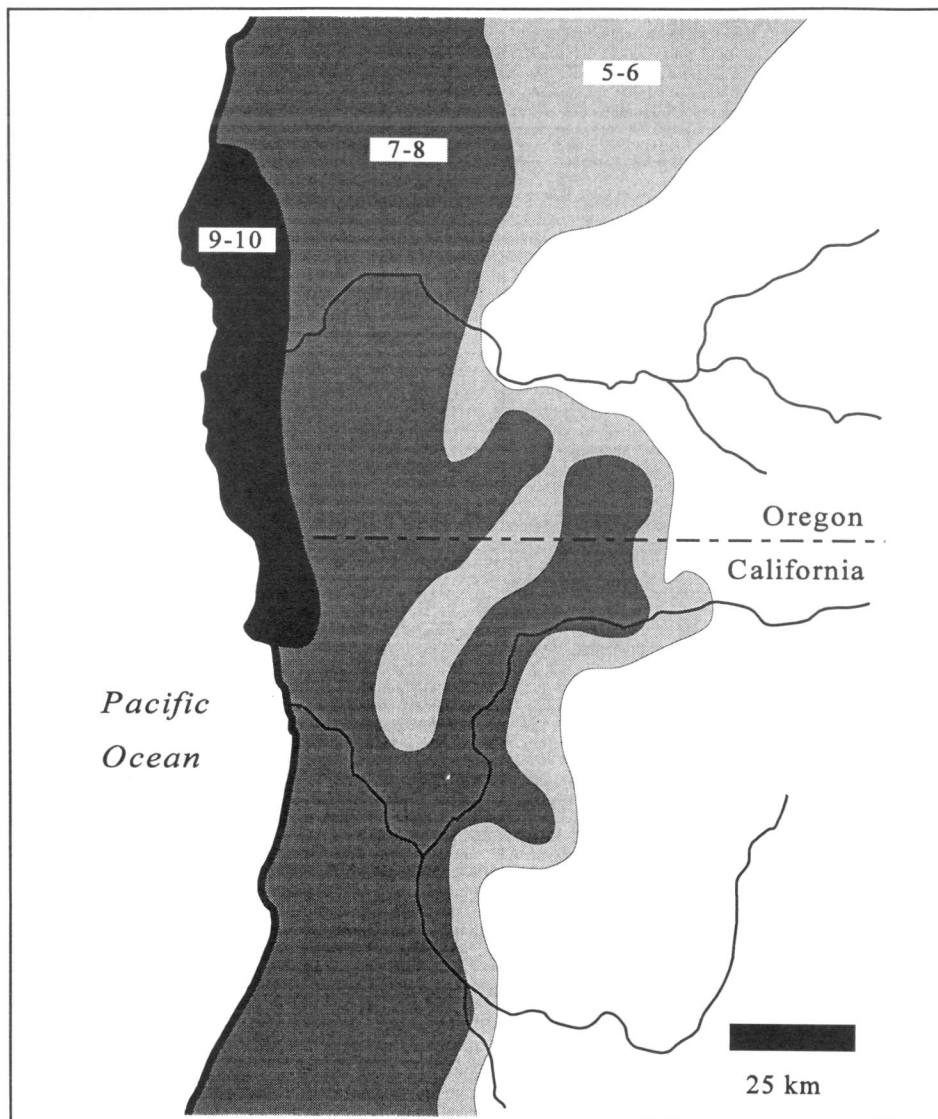


Figure 3. Centers of species richness ("hot spots") for salamanders in the Klamath-Siskiyou region of southwestern Oregon and northwestern California. Shading represents occurrence of different numbers of species: darkest shade = 9–10 species; moderate = 7–8; light = 5–6 species; no shading = < 5 species present.

lungless salamanders (genus *Plethodon*) may be encountered syntopically (overlapping in distribution) in small northern portions of the region (Figure 4). The KS region shares many characteristics with the southern Appalachian Mountains, which is the North American center of lungless salamander diversity (Highton 1995). Both of these botanically rich regions are ancient uplifts (>10 million years old) with widely varied topography and metamorphic geology that were spared the direct effects of glaciation during the Pleistocene (Whittaker 1956, 1960; Irwin 1981; Davis 1988).

### Reptiles

Nineteen species of reptiles are known to occur in the KS region, making it the most species-rich assemblage of similarly sized mountain regions of the PNW (Table 1). There is a large southern element (42%) in the reptile fauna (Appendix 2). Many of the southern species are associated with Mediterranean habitats (e.g., the common and California mountain kingsnakes, striped whipsnakes). These are reptiles that are broadly associated with the Madro-Tertiary geoflora of southern origin (Peabody and Savage 1958). Two species

(10.5%) are representative of montane or northern latitudes: the northern alligator lizard and northwestern garter snake. Other reptiles, such as the gopher snake, western fence lizard, and ring-neck snake, have widespread distribution patterns. There are no endemic reptiles in the KS region.

This relatively high richness of reptiles is due in part to the pronounced rain shadow and resulting hot, arid conditions in the eastern portions of the KS region. Many reptile species (particularly snakes) are associated with water (e.g., turtles, garter snakes) or specific terrestrial habitats (e.g., sharptail snakes in oak woodland). Xeric-associated plant assemblages such as oak woodland, pine forest, chaparral, and grassland occur in inland valleys and along the eastern flanks of the mountains. Historically, these drier areas were characterized by frequent fires that maintained their open structure (Agee 1990) and created conditions favorable to reptile use.

## ECOLOGY AND HABITATS

### Amphibians

Amphibians of the KS region are diverse in their trophic positions, life histories, and habitat use. Eleven of the 19 KS amphibian species (58%) depend on aquatic habitats for egg deposition and development of young. These species generally utilize both aquatic and terrestrial habitats during different portions of their life cycles, necessitating a dual set of suitable habitat conditions for their survival. All adult amphibians in the KS region feed on invertebrates. Most larval anurans are grazers on phytoplankton and diatoms, and can be important structuring agents in algal communities (Seale 1980, Kupferberg 1997). Larval salamanders are gape-limited predators, and may feed on zooplankton, mollusks, aquatic insects, and smaller amphibian larvae. Neotenic and terrestrial adults of the Pacific giant salamander may also eat fish, other amphibians, and an occasional small mammal. Due to their high local densities, aquatic salamander larvae can directly influence zooplankton composition (Dodson 1970) and larval anuran communities (Wilbur et al. 1983), as well as indirectly affect primary production (Morin 1995).



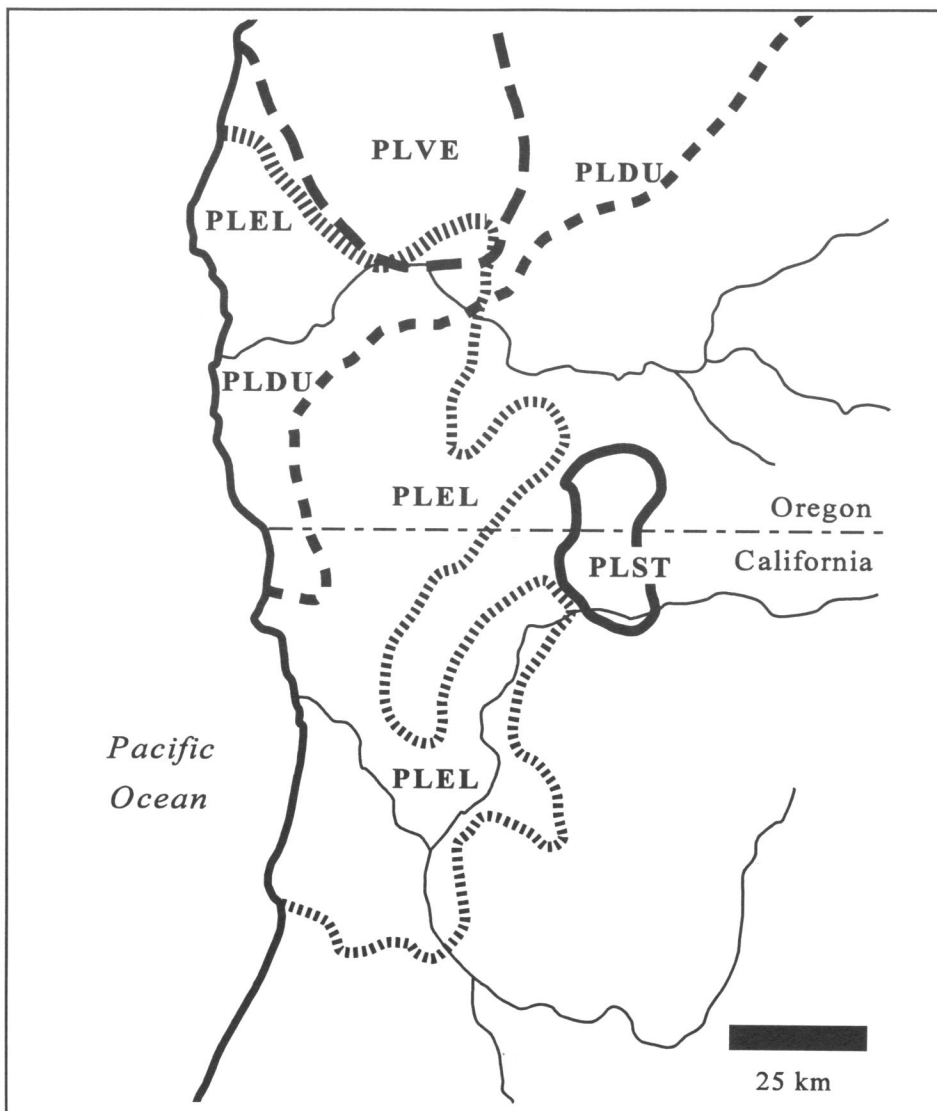


Figure 4. Distributional limits of four species of lungless salamanders (genus *Plethodon*) in the Klamath-Siskiyou region. Abbreviations: PLEL = *P. elongatus*, Del Norte salamander; PLDU = *P. dunni*, Dunn's salamander; PLST = *P. stormi*, Siskiyou Mountain salamander; and PLVE = *P. vehiculum*, red-backed salamander.

Amphibians are important components of the PNW fauna in terms of their numbers and biomass. Amphibians may be dominant predators on invertebrates of the forest floor (Bury 1994) and may be the most numerous terrestrial vertebrates in many forests. For example, Bury (1983) estimated that there were over 400 salamanders  $\text{ha}^{-1}$  in old-growth redwood forests, and Raphael (1984) reported densities of 10–180 salamanders  $\text{ha}^{-1}$  in mixed conifer-hardwood forests in northern California. Burton and Likens (1975) estimated densities of approximately 3,000 salamanders  $\text{ha}^{-1}$  in eastern deciduous forests. Such ter-

restrial salamanders can exceed 5 individuals  $\text{m}^{-2}$  in local aggregations in favored microhabitats (Jaeger 1979, Bury and Raphael 1983) and represent an important energetic pathway between microfauna and higher predators in temperate forests (Hairston 1996).

Long-toed salamanders have been observed to exceed 5 larvae  $\text{m}^{-2}$  in temporary ponds (C. Pearl, unpubl. data). Localized aggregations of larval and juvenile western toads can exceed 50 individuals  $\text{m}^{-2}$  (Nussbaum et al. 1983; B. Bury and C. Pearl, unpubl. data). Stream amphibians

can also reach high densities in seeps, creeks, and headwater stream systems. For example, larvae of the Pacific giant salamander may occur at densities of 2–5 individuals  $\text{m}^{-2}$  and are often the dominant predators in headwater streams, where they may exceed fish in numbers and biomass (Corn and Bury 1989).

The KS region derives much of its diversity from an abundance of terrestrial lungless salamanders (Family Plethodontidae). These salamanders complete reproduction and oviposition entirely on land. Since respiration occurs directly across dermal membranes and the throat, lungless salamanders generally require microenvironments with low temperature and high moisture. Talus slopes offer the moisture, temperature, and summer refuge conditions required by many of these salamanders. Some lungless salamanders, such as the clouded salamander, are closely tied to woody debris (Corn and Bury 1991). Ensatinas and red-backed salamanders prefer partially decomposed wood and are commonly found under logs and loose bark in Douglas-fir stands in the Cascades (Aubry et al. 1988).

### Reptiles

Reptiles are important predators in food webs and are prey to a variety of predators including larger reptiles, raptors, and many mammals. The regional reptile fauna is composed of species that are almost all obligate predators, and they demonstrate a range of prey specializations. Western pond turtles are mostly aquatic, and they consume invertebrates, tadpoles, vegetation, and sometimes carrion. All five species of resident lizards feed primarily on invertebrates. Snakes, the most species-rich group of the reptiles, include small, fossorial species, such as the sharp-tail snake, that feed on slugs and other invertebrates; active, agile species like the western aquatic garter snake and striped whipsnake that feed extensively on smaller amphibians and reptiles, respectively; and large constrictors, like the gopher snake, that prey primarily on small mammals. The rubber boa is the sole representative of a family of tropical species, and the western rattlesnake is the only poisonous species in the

region; both rely on small mammals for food.

Some reptile species are active in cool weather (e.g., the sharptail snake, rubber boa, and northern alligator lizard may be active in April), but most reptiles require warmer conditions for foraging and reproduction (e.g., kingsnakes tend to be most active in May/June). The western pond turtle is generally aquatic but needs basking sites in which to thermoregulate and increase its body temperature for several hours each day. There are few or no reptiles present in mature and old-growth forests of Douglas-fir or mixed conifers, primarily because of the cooler conditions under closed canopies.

Seven of the 19 KS reptile species bear live young, including the northern alligator lizard, 4 species of garter snakes, the rubber boa, and the western rattlesnake, but most species (63%) are egg layers. Reptile diversity and abundance are greatest in habitats such as cliff faces, exposed talus slopes, open woodlands or chaparral on south-facing slopes, and serpentine barrens. Talus and rocky slopes are particularly important as they may be used for egg-deposition and hibernation sites. As many as five to six reptile species have been documented sharing such overwintering habitats (Nussbaum et al. 1983, Leonard and Leonard 1998).

## CONSERVATION

The herpetofauna of the KS region is diverse taxonomically, as well as in terms of life history and habitat requirements. Thus, conservation strategies must consider a wide variety of taxa and associated habitats. Many species of PNW amphibians are associated with late-successional or old-growth forests (Raphael 1984, Bury 1994, Blaustein et al. 1995). These forests have been highly modified by human activities, with timber harvest serving as the primary agent of landscape alteration over the last half-century (Jimerson and Hoover 1991, Jules 1997). Many plethodontid species are sensitive to the effects of logging, and most are reduced in abundance in clearcut forests (Bury 1994). Coarse woody debris is a major component of old-growth

forests, and amounts remaining on forest floors have been greatly reduced by past forestry practices (Maser and Trappe 1984, Harmon et al. 1986). Occurrence of salamanders appears to be closely linked to abundance of coarse woody debris on the forest floor (Corn and Bury 1991), indicating a need to increase retention of large wood after logging.

Both the Siskiyou Mountain and Del Norte salamanders appear to be adversely affected by timber harvest on forested talus slopes that comprise their primary habitat (Welsh and Lind 1995). These salamanders are recognized as "Survey and Manage Species" under the Northwest Forest Plan (Thomas et al. 1995), and surveys for their presence are required prior to ground-disturbing activities. Also, current guidelines suggest protection of historic salamander sites and retention of buffers around occupied sites. However, research is needed to evaluate the effectiveness of buffer widths for salamander conservation.

The KS region represents the southern terminus for a number of northern amphibian and reptile species, while a few southern species reach their northern limits in the Siskiyou Mountains of southwestern Oregon. These taxa are presumably at or near their thermal and/or moisture tolerances. Additional research is needed to better understand their responses to changes in their favored microhabitats, which may be associated with short- or long-term climatic changes.

Aquatic taxa face a wide array of threats and are sensitive to local environmental change (Richter et al. 1997). Due to limited Pleistocene glaciation and the current climatic regime, large pond or lake habitats are relatively rare below the uppermost elevations in the KS region (mostly in the Trinity and Marble Mountains of northwestern California). However, the KS region does contain a variety of smaller slump ponds, seeps, and vernal pools. Four anuran species (Pacific chorus frog, western toad, northern red-legged frog, and Cascade frog) and three salamanders (roughskin newt, and long-toed and northwestern salamanders) require pond habitats for successful reproduction.

The rarity and isolation of standing waters have important implications for recolonization by amphibians and other aquatic taxa after local extinctions (see Sjogren 1991). Amphibian dispersal and successful reestablishment in widely separated pond and lake habitats, particularly across altered terrestrial habitat, may be limited in the KS region. Further, small isolated populations are generally more vulnerable to stochastic environmental or demographic stresses and are naturally more prone to local extinction (Lande 1988). The scarcity of standing water may partially explain the apparent absence of the Cascade frog in the high Siskiyou Mountain range along the Oregon-California border. This species is present at many lentic sites in the Oregon Cascades (Nussbaum et al. 1983) and occurs farther south in the formerly glaciated areas of the Trinity Alps and Marble Mountains of northern California (Jennings and Hayes 1994).

Establishment of nonnative mammal species (e.g., feral pigs [*Sus scrofa*], opossums [*Didelphis marsupialis*]) may have negative impacts on some terrestrial herpetofauna, but, to our knowledge, there have been no studies conducted in the western United States. Some experimental and distributional evidence suggests that introduced species such as bullfrogs and a suite of stocked game fish may interact negatively with native aquatic herpetofauna (Hayes and Jennings 1986, Kiesecker and Blaustein 1998). Bullfrogs, native to the eastern United States, have been widely introduced in western North America, and even in other continents, as a food source. Bullfrogs may affect amphibians and aquatic reptiles by predation, competition, or acting as disease vectors (Bury and Whelan 1984, Kupferberg 1997, Kiesecker and Blaustein 1998). Bullfrog expansion in the KS region has occurred primarily in low-elevation stock ponds and along large rivers, but mid-elevation aquatic habitats may also be colonized.

As many as 95% of lakes in the mountain areas of the western United States were historically fishless (Bahls 1992). Presently, most high-elevation lakes in the KS region have been stocked with brook trout

(*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) for sport fishing (L. Webb, pers. com.). Introduced trout are now implicated in local declines of aquatic amphibians (Bradford 1989, Fellers and Drost 1993, Tyler et al. 1998). Introduced largemouth bass (*Micropterus salmoides*) are commonly stocked in low-elevation ponds and lakes, and are effective predators on a variety of small vertebrates including amphibians (Moyle 1986). Our observations of largemouth bass in one lake at 1,200 m elevation (C. Pearl, pers. obs.) suggest that the moderate climate within the KS region can allow the persistence of this nonnative fish across a wide elevational range.

The association of pond-breeding amphibians with older forests is unclear, but all pond-breeding species use terrestrial habitats to varying extent. Red-legged frogs and western toads may spend considerable time in terrestrial areas, particularly in humid weather. Similarly, roughskin newts and mole salamanders (Ambystomatidae) migrate overland to breeding waters and reside on land for much of the year. There is little information on how habitat alterations may affect northwestern pond-breeding amphibians during the periods when they occur in terrestrial habitats, but research on mole salamanders in the eastern United States indicates that forest habitat as much as 250 m away from breeding pools may be extensively used by adults and probably is important in the persistence of the breeding population (Semlitsch 1999).

Headwater streams also are critical habitat for several species of amphibians endemic to the Pacific Northwest (e.g., tailed frog, torrent salamander). These taxa require cool temperatures and persistent waters. Timber harvest affects aquatic amphibian populations by increasing water temperature to lethal levels and through siltation of streambeds (Corn and Bury 1989). Recently, we found that stream amphibian populations in the Oregon Coast Range had not recovered 35–50 years after clearcut harvesting (B. Bury and D. Major, unpubl. data). Although adults of the tailed frog are considered to be closely associated with streams (Blaustein et al. 1995), we discovered that in forested

stands some adults may occur relatively long distances (up to 500 m) from water during the wet season (Corn and Bury 1991). Also, we observed that recently transformed frogs appear to disperse into terrestrial habitats with the onset of heavy fall rains (B. Bury and L. Jones, pers. obs.). Thus, retention of riparian zones and adjacent forests in older stages is likely critical to the survival of stream amphibian species. Further research on this topic is critically needed.

## CONCLUSIONS AND RECOMMENDATIONS

In the past, clearcut logging decreased local populations of the KS herpetofauna and further fragmented a montane landscape that naturally contained patchy habitats. Today, many sensitive species are isolated in disjunct habitat patches, and timber harvest at these sites may further deplete remaining populations. Although more ecologically based methods of timber harvest are being implemented (e.g., stand thinning, retention of riparian buffer zones), studies assessing the effect of these new practices on the herpetofauna are in their infancy.

While studies of individual species are necessary, we recommend a habitat-based approach for more effective conservation of the regional herpetofauna. Specialized habitats are important to the survival of many species of the KS herpetofauna, particularly endemic salamander species. Thus, we recommend that conservation efforts focus on three important habitats: talus slopes, headwater streams, and ponds. We can conserve a large portion of sensitive KS herpetofauna with continued research, improved management, and protection of these spatially limited habitats.

The Klamath-Siskiyou region is one of the least-explored mountain regions of western North America. Distributions and life histories of the native herpetofauna are still relatively poorly known, and much of our knowledge of these species is derived from other regions. We need greater knowledge of species' biology and habitat requirements for better management and protection of the KS herpetofauna. Finally, an understanding of the complex bio-

geography of this diverse region will benefit from better coordination among research biologists in different disciplines. For example, many of the habitats necessary for survival of sensitive amphibian and reptile species are also needed by other taxa (e.g., mollusks). Cooperative studies involving resource managers, scientists, and conservationists have begun, and further collaborative efforts should be encouraged.

## ACKNOWLEDGMENTS

Fieldwork was supported in part by the U.S. Forest Service, Pacific Northwest Research Station, and the Bureau of Land Management. We thank Don J. Major for field assistance and final preparation of the figures, Michael J. Adams for comments on the manuscript, and the Department of Geography, University of Oregon, for use of maps.

---

*Bruce Bury is a Research Zoologist in the USGS Forest and Rangeland Ecosystem Science Center in Corvallis, Oregon. He is a 27-year veteran of government service. His research interests feature ecological and conservation issues of amphibians and reptiles.*

*Christopher Pearl is a temporary Wildlife Biologist with the USGS Forest and Rangeland Ecosystem Science Center. His research interests include biology of ranid frogs in the Pacific Northwest, wetland ecology, and paleoecology of the Willamette Valley.*

## LITERATURE CITED

- Agee, J.K. 1990. The historical role of fire in Pacific Northwest forests. Pp. 25-37 in J.D. Walstad, S.R. Radosevich, and D.V. Sandberg, eds., *Natural and Prescribed Fire in Pacific Northwest Forests*. Oregon State University Press, Corvallis.
- Agee, J.K. 1991. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. *Northwest Science* 65:188-199.
- Atzet, T. and R.E. Martin. 1991. Natural disturbance regimes in the Klamath Province. Pp. 40-48 in R.R. Harris and D.E. Erman, tech. coords., and H.M. Kerner, ed., *Pro-*



- ceedings of Symposium on Biodiversity of Northwestern California. Report No. 29, University of California, Wildland Resources Center, Berkeley.
- Aubry, K.B., L.L.C. Jones, and P.A. Hall. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir forests in Washington. Pp. 32-37 in R.C. Szaro, K.E. Severson, and D.R. Patton, eds., Management of amphibians, reptiles, and small mammals in North America: Proceedings of the symposium. General Technical Report RM-166, U.S. Department of Agriculture, Forest Service, Tempe, Ariz.
- Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science 66:183-193.
- Blaustein, A.R., J.J. Beatty, D.H. Olson, and R.M. Storm. 1995. The biology of amphibians and reptiles in old-growth forests in the Pacific Northwest. General Technical Report PNW-337, U.S. Department of Agriculture, Forest Service, Portland, Ore. 98 pp.
- Bradford, D.F. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California: implication of the negative effect of fish introductions. Copeia 1989:775-778.
- Burton, T.M. and G.E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975:541-546.
- Bury, R.B. 1983. Differences in amphibian populations in logged and old growth redwood forest. Northwest Science 57:167-178.
- Bury, R.B. 1994. Vertebrates in the Pacific Northwest: species richness, endemism and dependency on old-growth forests. Pp. 392-404 in S. K. Majumdar, F.J. Brenner, J.E. Lovich, J.F. Schalles, and E.W. Miller, eds., Biological Diversity: Problems and Challenges. The Pennsylvania Academy of Sciences, Easton.
- Bury, R.B. and M.G. Raphael. 1983. Inventory methods for amphibians and reptiles. Pp. 416-419 in J.F. Bell and T. Atterbury, eds., Renewable Resource Inventories for Monitoring Changes and Trends. SAF 83-14, Oregon State University, Corvallis. 737 pp.
- Bury, R.B. and J.A. Whelan. 1984. Ecology and management of the bullfrog. Resource Publication 155, U.S. Department of Interior, Fish and Wildlife Service, Washington, D.C. 23 pp.
- Corn, P.S. and R.B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. Forest Ecology and Management 29:1-19.
- Corn, P.S. and R.B. Bury. 1991. Terrestrial amphibian communities in the Oregon Coast Range. Pp. 304-317 in L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff, tech. coords., Wildlife and vegetation of unmanaged douglas-fir forests. General Technical Report PNW-285, U.S. Department of Agriculture, Forest Service, Portland, Ore.
- Davis, P.T. 1988. Holocene glacier fluctuations in the American cordillera. Quaternary Science Reviews 7:129-157.
- Dodson, S.I. 1970. The effect of predation on the community structure of fresh-water zooplankton. Ph.D. diss., University of Washington, Seattle.
- Fellers, G.M. and C.A. Drost. 1993. Disappearance of the Cascades frog *Rana cascadae* at the southern end of its range, California, USA. Biological Conservation 65:177-181.
- Froehlich, H.A., D.H. McNabb, and F. Gaweda. 1982. Average annual precipitation 1960-1980 in Southwest Oregon. Cooperative Extension Service, Oregon State University, Corvallis. 4 pp.
- Green, D.M. and R.W. Campbell. 1984. The Amphibians of British Columbia. Handbook No. 45, British Columbia Provincial Museum, Victoria, Canada. 101 pp.
- Hairston, N.G., Sr. 1996. Predation and competition in salamander communities. Pp. 161-190 in M.L. Cody and J.A. Smallwood, eds., Long-term Studies of Vertebrate Communities. Academic Press, San Diego, Calif.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.
- Hayes, M.P. and M.R. Jennings. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology 20:490-509.
- Highton, R. 1995. Speciation in eastern North American salamanders of the genus *Plethodon*. Annual Review of Ecology and Systematics 26:579-600.
- Irwin, W.P. 1981. Tectonic accretion of the Klamath Mountains. Pp. 29-49 in W.G. Ernst, ed., The Geotectonic Development of California. Prentice-Hall, Englewood Cliffs, N.J.
- Jaeger, R.G. 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus*. Herpetologica 35:90-93.
- Jennings, M.R. and M.P. Hayes. 1994. Amphibian and reptile species of special concern in California. Final Report. California Department of Fish and Game, Inland Fisheries Division. 255 pp.
- Jimerson, T.M. and L.D. Hoover. 1991. Old-growth forest fragmentation: changes in amount, patch size, and edge as a result of logging. Pp. 168-174 in R.R. Harris and D.E. Erman, tech. coords., and H.M. Kerner, ed., Proceedings of Symposium on Biodiversity of Northwestern California. Report No. 29, University of California, Wildland Resources Center, Berkeley.
- Jules, E.S. 1997. Rapid changes in plant distribution and abundance in the Sucker Creek watershed: a case study of *Trillium ovatum*. Pp. 71-79 in J. Beigel, E.S. Jules, and B. Snitkin, eds., Proceedings of the First Conference of Siskiyou Ecology. The Siskiyou regional Education Project, Cave Junction, Ore.
- Kiesecker, J. and A.R. Blaustein. 1998. Effects of introduced bullfrogs and smallmouth bass on microhabitat use, growth, and survival of native red-legged frogs (*Rana aurora*). Conservation Biology 12:776-787.
- Kupferberg, S.J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. Ecology 78:1736-1751.
- Lande, R. 1988. Genetics and demography in biological conservation. Science 241:1455-1460.
- Leonard, W.P. and M.A. Leonard. 1998. Occurrence of the sharptail snake (*Contia tenuis*) at Trout Lake, Klickitat County, Washington. Northwestern Naturalist 79: 75-76.
- Maser, C. and J.M. Trappe. 1984. The seen and unseen world of the fallen tree. General Technical Report PNW-164, U.S. Department of Agriculture, Forest Service, Portland, Ore. 56 pp.
- Morin, P.J. 1995. Functional redundancy, non-additive interactions, and supply-side dynamics in experimental pond communities. Ecology 76:133-149.
- Moyle, P.B. 1986. Fish introductions into North America: patterns and ecological impact. Pp. 27-43 in H.A. Mooney and J.A. Drake, eds., Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.
- Nussbaum, R.A., E.D. Brodie Jr. and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow. 332 pp.
- Peabody, F.E. and J.M. Savage. 1958. Evolution of a Coast Range corridor in California and its effect on the origin and dispersal of living amphibians and reptiles. Pp. 159-186 in C.L. Hubbs, ed., Zoogeography. Publi-

cation 51, American Association for the Advancement of Science, Washington, D.C.

Raphael, M.G. 1984. Wildlife populations in relation to stand age and area in Douglas-fir forests of northwestern California. Pp. 259-274 in W.R. Meenhan, T.R. Merrell Jr. and T.A. Hanley, tech. eds., Fish and Wildlife Relationships in Old-growth Forests. American Institute of Fisheries Research Biologists, Juneau, Alaska.

Richter, B.D., D.P. Braun, M.A. Mendelson, and L.L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081-1093.

Seale, D.B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond system. Ecology 61:1531-1550.

Semlitsch, R. 1999. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113-1119.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). Biological Journal of the Linnean Society 42:135-147.

Stebbins, R.C. 1985. A Field Guide to Western Amphibians and Reptiles. 2nd Ed. Houghton Mifflin, Boston, Mass.

Thomas, J.W., M.G. Raphael, R.G. Anthony, and others. 1993. Viability assessment and management considerations for species associated with late successional and old-growth forests of the Pacific Northwest. Report by Scientific Analysis Team, U.S. Department of Agriculture, Forest Service, Portland, Ore. 530 pp.

Tyler, T., W.J. Liss, L.M. Ganio, G.L. Larson, R. Hoffman, E. Deimling, and G. Lomnick. 1998. Interaction between introduced trout and larval salamanders (*Ambystoma macrodactylum*) in high-elevation lakes. Conservation Biology 12:94-105.

Welsh, H.H., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology 4:309-319.

Welsh, H.H. Jr. and A.J. Lind. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus* (Caudata: Plethodontidae), in northwestern California. Journal of Herpetology 29:198-210.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338.

Wilbur, H.M., P.J. Morin, and R.H. Harris. 1983. Salamander predation and the structure of experimental communities: anuran responses. Ecology 64:1423-1429.

**Appendix 1. Species of native amphibians found in the Klamath-Siskiyou region in southwestern Oregon and northern California. This list was compiled from Nussbaum et al. (1983), Stebbins (1985), and the Integrated Taxonomic Information System (<http://www.itis.usda.gov/itis/>).**

FAMILY			Distribution
<i>Species (Author)</i>	Common Name		Pattern
AMBYSTOMATIDAE			
<i>Ambystoma gracile</i> (Baird)	northwestern salamander		northern
<i>Ambystoma macrodactylum</i> (Baird)	long-toed salamander		widespread
DICAMPTODONTIDAE			
<i>Dicamptodon tenebrosus</i> (Baird and Girard)	Pacific giant salamander		northern
PLETHODONTIDAE			
<i>Aneides ferreus</i> Cope	clouded salamander		northern
<i>Aneides flavipunctatus</i> (Strauch)	black salamander		southern
<i>Batrachoseps attenuatus</i> (Eschscholtz)	California slender salamander		southern
<i>Ensatina eschscholtzii</i> Gray	ensatina		widespread
<i>Plethodon dunni</i> Bishop	Dunn's salamander		northern
<i>Plethodon elongatus</i> Van Denburgh	Del Norte salamander		endemic
<i>Plethodon stormi</i> Highton and Brame	Siskiyou Mountain salamander		endemic
<i>Plethodon vehiculum</i> (Cooper)	Western red-backed salamander		northern
RHYACOTRITONIDAE			
<i>Rhyacotriton variegatus</i> Stebbins and Lowe	southern torrent salamander		northern
SALAMANDRIDAE			
<i>Taricha granulosa</i> (Skilton)	roughskin newt		widespread
BUFONIDAE			
<i>Bufo boreas</i> Baird and Girard	western toad		widespread
HYLIDAE			
<i>Hyla</i> (= <i>Pseudacris</i> ) <i>regilla</i> Baird and Girard	Pacific treefrog		widespread
LEIOPELMATIDAE			
<i>Ascaphus truei</i> Stejneger	tailed frog		northern
RANIDAE			
<i>Rana aurora</i> Baird and Girard	red-legged frog		northern
<i>Rana boylei</i> Baird	foothill yellow-legged frog		southern
<i>Rana cascadae</i> Slater	Cascade frog		northern

**Appendix 2. Species of natives reptiles found in the Klamath-Siskiyou region in southwestern Oregon and northern California. This list was compiled from Nussbaum et al. (1983), Stebbins (1985), and the Integrated Taxonomic Information System (<http://www.itis.usda.gov/itis/>).**

<b>FAMILY</b> <i>Species (Author)</i>	<b>Common Name</b>	<b>Distribution Pattern</b>
<b>ANGUIDAE</b>		
<i>Elgaria coerulea</i> Wiegmann	northern alligator lizard	northern
<i>Elgaria multicarinata</i> (Blainville)	southern alligator lizard	southern
<b>IGUANIDAE</b>		
<i>Sceloporus graciosus</i> Baird and Girard	sagebrush lizard	widespread
<i>Sceloporus occidentalis</i> Baird and Girard	western fence lizard	widespread
<b>SCINCIDAE</b>		
<i>Eumeces skiltonianus</i> (Baird and Girard)	western skink	southern
<b>BOIDAE</b>		
<i>Charina bottae</i> (Blainville)	rubber boa	widespread
<b>COLUBRIDAE</b>		
<i>Coluber constrictor</i> Linnaeus	racer	widespread
<i>Contia tenuis</i> (Baird and Girard)	sharptail snake	southern
<i>Diadophis punctatus</i> (Linnaeus)	ring-neck snake	widespread
<i>Lampropeltis getulus</i> (Linnaeus)	common kingsnake	southern
<i>Lampropeltis zonata</i> (Lockington Ex Blainville)	California Mountain kingsnake	southern
<i>Masticophis taeniatus</i> (Hallowell)	striped whipsnake	southern
<i>Pituophis catenifer</i> (Blainville)	gopher snake	widespread
<i>Thamnophis atratus</i> (Kennicott)	aquatic garter snake	southern
<i>Thamnophis elegans</i> (Baird and Girard)	terrestrial garter snake	widespread
<i>Thamnophis ordinoides</i> (Baird and Girard)	northwestern garter snake	northern
<i>Thamnophis sirtalis</i> (Linnaeus)	common garter snake	widespread
<b>VIPERIDAE</b>		
<i>Crotalus viridis</i> (Rafinesque)	western rattlesnake	widespread
<b>EMYDIDAE</b>		
<i>Clemmys marmorata</i> (Baird and Girard)	western pond turtle	southern