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Amphibian Biodiversity of the Pacific Northwest with Special Reference to Old-Growth Stands

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Introduction

The amphibian fauna of the Pacific Northwest includes several species that are found nowhere else (Nussbaum et al. 1983). Many of these are of special interest, such as the highly predatory Pacific giant salamanders (*Dicamptodon* spp.), which may be the world's largest terrestrial salamanders; the tailed frog (*Ascaphus truei*), whose males have copulatory organs; and the Cascades frog (*Rana cascadae*), whose larvae aggregate in schools composed primarily of relatives (see Nussbaum et al. 1983; Blaustein 1988). A significant proportion of the amphibians of the Pacific Northwest possesses relatively specific ecological requirements and have extremely limited distributions, which increases their risk of local extinction. Indeed, five species of Pacific Northwest amphibians are candidates for the United States (U.S.) endangered species list (Federal Register 1991): the western spotted frog (*Rana pretiosa*), red-legged frog (*R. aurora*), Cascades frog (*R. cascadae*), Larch Mountain salamander (*Plethodon larselli*), and Siskiyou Mountains salamander (*P. stormi*). Many other species, especially those associated with old-growth forests, are listed on the state threatened lists of California, Idaho, Oregon, Washington, and British Columbia.

Old-growth forests of the Pacific Northwest are among the most productive biological systems in the world (Waring and Franklin 1979) and they support a varied and unique fauna and flora. Harvesting of old-growth stands from British Columbia south to northern California has had a significant impact on plants and animals in these forest ecosystems. For example, old-growth harvesting has imperiled populations of the northern spotted owl (*Strix occidentalis caurina*) such that it is currently listed as threatened in the U.S. The

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listing of the spotted owl has had profound economic effects within the Pacific Northwest as the proponents for saving the owl contend with those that advocate continued harvesting of old-growth stands (Salwasser 1987). Loss of other species found within old-growth stands, such as the Pacific yew (*Taxus brevifolia*), may have important medical as well as economic benefits. The yew contains taxol, a substance that is important in controlling certain types of human cancers.

The loss of species within old-growth forests reflects the general loss in biodiversity that is occurring at an increased rate throughout the world (Wilson 1988; McNeeley et al. 1990). Vertebrates are threatened with increasing rates of extinction (IUCN Red List of Threatened Animals 1990; McNeeley et al. 1990). Indeed, reports of declining amphibian populations, the subject of this paper, have become especially alarming. Numerous recent reports have suggested that many amphibian species are undergoing population declines and range reductions (Barinaga 1990; Blaustein and Wake 1990; Phillips 1990; Wyman 1990; Wake 1991). These declines are especially perplexing because many species are disappearing in areas of the world that are relatively pristine and devoid of obvious habitat destruction, pollution, and introduced exotic competitors or predators.

This loss of amphibian diversity may have significant ecological consequences because amphibians are extremely important components of many ecosystems. Aquatic larvae, terrestrial juveniles, and adults may function as either top carnivores or as the major food source of many other vertebrate species and aquatic invertebrates, thus serving an important role in food webs. In some forest ecosystems, amphibians may actually comprise the major portion of the vertebrate biomass (e.g., Burton and Likens 1975a, b). Moreover, amphibians are probably the most sensitive vertebrate bioindicators of environmental change because a complex life cycle characterizes many species, thus doubling their exposure to agents of mortality in both aquatic and terrestrial environments (see Blaustein and Wake 1990; Vitt et al. 1990). The decline of some amphibian populations may be an early warning signal that, ultimately, other organisms are at risk (Blaustein and Wake 1990; Vitt et al. 1990).

In the Pacific Northwest, populations of several species of amphibian have apparently become locally extinct, and the ranges of numerous species have become drastically reduced (Blaustein and Wake 1990; McAllister and Leonard 1990, 1991; Fellers and Drost, in press; see also Blaustein and Olson 1991). Most of the declines have occurred in forest-dwelling species (Blaustein and Wake 1990; McAllister and Leonard 1990, 1991; Fellers and Drost, in press). Some



The Cascades frog, *Rana cascadae*. Photo by Grant Hokit

of these species are intimately tied to old-growth stands and inhabit areas where other animals and plants are "sensitive" or threatened. Like several species in other areas of the world, the extinctions and range reductions of amphibians in the Pacific Northwest have occurred primarily in seemingly pristine habitat devoid of overt habitat destruction or manipulation (Blaustein and Wake 1990).

Our purpose is to review briefly the species diversity of amphibians in the Pacific Northwest, to provide a synthesis of the specific habitat requirements of those species associated with old-growth forest ecosystems, and to address the effects of habitat disturbance, primarily through logging, on amphibian populations. We examine the species diversity of three main categories of amphibian habitat, each of which is characterized by the availability of water and type of aquatic system it contains. Using this classification, we identify key assemblages of amphibians that may be associated with each habitat. We therefore emphasize the possible consequences of habitat manipulation to entire groups of species associated with old-growth forest ecosystems. Last, in addition to the U.S. listed threatened species discussed above, we identify several other species that have limited distributions and/or relatively strict ecological requirements. For the purposes of this paper, we define an amphibian with a "restricted range" as one whose known geographic distribution is confined to a relatively small region or locality within the Pacific Northwest. By "habitat requirements," we refer to the range

TABLE 1. The diversity of living amphibians worldwide and in the Pacific Northwest. Numbers of species in the Pacific Northwest are indicated by () (Nussbaum et al. 1983; Duellman and Trueb 1985).

	Families	Genera	Species
Caudata (salamanders)	9 (4)	62 (8)	352 (20)
Anura (frogs & toads)	21 (5)	301 (6)	3,438 (14)
Gymnophiona (caecilians)	6 (0)	34 (0)	162 (0)
Total	36 (9)	397 (14)	3,952 (34)

(broad or narrow) of environmental conditions in which a given species is known to breed. Some of these species may be especially sensitive to the harvesting and manipulation of old-growth stands.

Overview of Amphibian Biodiversity in the Pacific Northwest

Species diversity is a measure of the number of species in an area (richness) and the relative numbers of individuals of each species. Because information on population sizes for amphibians in the Pacific Northwest is limited (e.g., Aubry and Hall 1991; Corn and Bury 1991; Gilbert and Allwine 1991; Welsh and Lind 1991), we restrict our discussion to species richness.

Of the 3,952 extant species of amphibians known worldwide, only 34 (.9%) occur in the Pacific Northwest (Table 1). However, this richness constitutes approximately 17% of all the species of amphibians found in the United States (Harding 1983) and 49% of all species found in Canada (Cook 1984; Green and Campbell 1984). Based on the total number of species occurring within a given area, the Pacific Northwest contains the second highest richness of amphibians (after the Southeast) in the U.S. (Kiestler 1971) and the highest concentration of amphibians in Canada. This pattern of species richness is principally attributed to the high amounts of annual rainfall received in the Southeast and Pacific Northwest regions (Kiestler 1971).

Biodiversity of Amphibians Associated with Aquatic Habitats

Ponds and Lakes as Predominant Breeding Sites

Most (73.5%) of the amphibians of the Pacific Northwest are forest dwellers, many of which are found within old-growth stands (Table

TABLE 2. General habitat characteristics of amphibians whose distributions are correlated with older forest ecosystems* and other habitats in the Pacific Northwest. L = larvae, P = paedomorphs, M = metamorphs, X = lungless salamanders (no aquatic larval stage).¹

	Ponds/Lakes	Streams	Terrestrial
Salamanders (Order Caudata)			
<i>Ambystoma macrodactylum</i>	L, M		M
* <i>Ambystoma gracile</i>	L, P, M	L, P, M	M
* <i>Ambystoma tigrinum</i>	L, P, M		M
* <i>Dicamptodon</i> spp.	L, P, M	L, P, M	M
* <i>Rhyacotriton olympicus</i>		L, M	
* <i>Taricha granulosa</i>	L, M	L, M	M
* <i>Aneides flavipunctatus</i>			X
* <i>Aneides ferreus</i>			X
* <i>Batrachoseps wrighti</i>			X
<i>Batrachoseps attenuatus</i>			X
* <i>Ensatina eschscholtzii</i>			X
* <i>Plethodon dunni</i>			X
* <i>Plethodon larselli</i>			X
* <i>Plethodon elongatus</i>			X
* <i>Plethodon stormi</i>			X
* <i>Plethodon vandykei</i>			X
* <i>Plethodon vehiculum</i>			X
Frogs & Toads (Order Anura)			
<i>Bufo woodhousei</i>	L, M	L, M	M
* <i>Bufo boreas</i>	L, M	M	M
* <i>Hyla</i> [= <i>Pseudacris</i>] <i>regilla</i>	L, M	L, M	M
<i>Pseudacris triseriata</i>	L, M	L, M	M
* <i>Ascaphus truei</i>		L, M	M
* <i>Rana aurora</i>	L, M	L, M	M
* <i>Rana boylei</i>		L, M	M
* <i>Rana cascadae</i>	L, M	L, M	M
* <i>Rana pretiosa</i>	L, M	L, M	M
<i>Rana catesbeiana</i>	L, M	L, M	M
<i>Rana clamitans</i>	L, M	L, M	M
<i>Rana pipiens</i>	L, M		M
<i>Rana sylvatica</i>	L, M	L, M	M
<i>Spea intermontana</i>	L, M		M

¹ Natural history information was obtained from Symp 1975; O'Hara 1981; Nussbaum et al. 1983; Cook 1984; Green and Campbell 1984; Stebbins 1985.

2). Of these, 60% are completely dependent upon bodies of water (ponds, lakes, or streams) as sites for breeding. Aquatic-breeding amphibians have complex life cycles, characterized by an aquatic egg and sexually immature larval stage, as well as semi-terrestrial or primarily terrestrial juvenile and adult stages. Six species of Pacific Northwest salamanders (*Ambystoma gracile*, *A. tigrinum*, and four species of *Dicamptodon*) that utilize such habitats may be paedo-

morphic—sexually mature while retaining characteristics of the larval form.

Of the amphibians associated with old-growth stands, three salamander species (*Ambystoma gracile*, *A. tigrinum* and *Taricha granulosa*) and five species of anurans (frogs and toads) (*Bufo boreas*, *Hyla* [= *Pseudacris*] *regilla*, *Rana aurora*, *R. cascadae*, and *R. pretiosa*) predominantly breed in ponds and lakes (Table 2). Except for *Bufo boreas*, these species may occasionally breed in streams as well (Table 2). Furthermore, with the exception of populations of paedomorphic salamanders and possibly *B. boreas*, these species are known to breed in both permanent and temporary (seasonal) bodies of water. Thus, these species generally possess relatively broad habitat requirements.

Closer scrutiny of the microhabitat preferences of some species, however, suggests that their requirements may be more stringent than initially assessed. For example, during the non-breeding season, adults of many aquatic breeders are still restricted to riparian areas and the moist periphery of the terrestrial pond-side habitat (Table 2). Second, adults of *Rana cascadae* are known to breed in both permanent and temporary ponds, as well as streams, yet they favor the shallow, sunny margins of the water for depositing eggs (oviposition) (O'Hara 1981; Nussbaum et al. 1983). Breeding, in particular, appears to be more prevalent in shallow, temporary sites, rather than permanent ponds and lakes (Syse 1975; O'Hara 1981). Temporary aquatic sites may be favored for reproduction by several species of amphibians because (1) they may have high productivity and provide an opportunity for rapid larval growth (Wilbur 1987), (2) their shallowness permits warmer water temperatures that further enhance growth (O'Hara 1981), and (3) their temporary nature inhibits use by predatory fish. Thus, old-growth stands that harbor temporary ponds and pools may be especially important for those species that have adapted to exploit such habitats.

Relationship to Old Growth and Potential Impact of Habitat Loss

In addition to the importance of old-growth ponds and lakes as breeding sites for many amphibians, these aquatic habitats may be of special significance for a number of other reasons. First, at least one anuran (*B. boreas*) and the paedomorphic forms of six salamander species are only found in permanent bodies of water (see Nussbaum et al. 1983). Second, many amphibians are known to be site specific, returning to the same area each breeding season; dispersal to other suitable breeding sites is thought to be low (e.g., see Duellman and

Trueb 1985; Sinsch 1990). Thus, destruction of aquatic breeding sites and their adjacent terrestrial habitat may cause the local extinction of an assemblage of several species of amphibians. However, because the adults of pond and lake breeders are primarily terrestrial, the loss of terrestrial habitat not immediately adjacent to breeding sites also may severely impact adult amphibians. For example, Semlitsch (1981) found that, in South Carolina, adults of the pond-breeding salamander *Ambystoma talpoideum* migrated as far as 261 m from the edge of breeding sites to establish summer home ranges. Thus, when habitat alteration is unavoidable, terrestrial "buffer zones" surrounding ponds and lakes are needed to provide undisturbed, old-growth habitat for metamorphosed amphibians.

Streams as Predominant Breeding Sites

In addition to the pond/lake-breeding amphibians that occasionally breed in streams, there are two groups of salamanders (*Dicamptodon* spp. and *Rhyacotriton olympicus*) and two species of anurans (*Ascaphus truei* and *Rana boylei*) that are associated with the stream environment (Table 2). Except for the *Dicamptodon* species complex, both the larvae and adults of the remaining species are found exclusively in, or very near, the stream environment. For *Dicamptodon*, metamorphosed juveniles and adults are inhabitants of the forest floor as well as the stream channel; larvae and pedomorphs may occur in ponds and lakes as well.

Dicamptodon, *Rhyacotriton* and *Ascaphus* commonly occur in the same range (sympatric) in smaller mountain streams, spring heads, and seepages, whereas *Rana boylei* characteristically occupies larger streams and rivers (see Nussbaum et al. 1983; Stebbins 1985). Adults of *R. boylei* are found at the edges of rocky pools formed during the low stages of rivers and streams; oviposition and subsequent larval development occur within these pools (Nussbaum et al. 1983). *Dicamptodon*, *Rhyacotriton* and *Ascaphus* differ markedly in their microhabitat use (Bury et al. 1991).

Rocky headwater streams may be subdivided into four zones (from the middle of the stream outward): pools, riffles, shallow seeps, and the banks/splash zone. Large larval and pedomorphic *Dicamptodon* may be found in the deeper pools of streams, whereas smaller individuals occupy riffles and shallow pools (Bury et al. 1991). Adults of *Ascaphus* are usually only found in cold, flowing water, occurring most commonly in riffle areas, whereas their tadpoles may be found attached to the smooth surfaces of rocks in fast-flowing water (Nussbaum et al. 1983; Bury et al. 1991). Adults of *Rhyacotriton* inhabit the splash zone of stream banks and waterfalls, and also may be

found alongside larval forms underneath rocks in riffle areas and shallow seeps (Nussbaum et al. 1983; Bury et al. 1991).

Relationship to Old Growth and Potential Impact of Habitat Loss

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Of all the anurans discussed in this paper, *Ascaphus truei* is probably the most likely to be affected by old-growth habitat loss and destruction. Tailed frogs are intimately associated with fast-flowing streams in forested areas and are commonly found within old-growth forests (Bury 1983; Bury and Corn 1988a, b; Raphael 1988; Welsh and Lind 1988; Corn and Bury 1989; Aubry and Hall 1991). Bury (1983) found *A. truei* on undisturbed old-growth sites but none in logged old-growth areas. Bury and Corn (1988a, b) considered *A. truei* to be "sensitive to timber harvest." Survival of this species depends upon protection of cool flowing streams required for breeding and larval development (see also Bury et al. 1991). Tailed frogs are likely to be affected by increased water temperatures that result after clear-cutting (Bury and Corn 1988b). Tailed frogs are most often found in streams in logged stands when uncut trees remain upstream (Corn and Bury 1989). Because tailed frogs are extremely site specific and their populations are significantly separated from other populations (Metter 1964; Metter and Pauken 1969), recolonization of some habitats after local extinction may take a relatively long time.

Corn and Bury (1989) documented high densities of *Dicamptodon* salamanders only in steep portions of logged streams, whereas individuals were found in both steep and low-lying areas of undisturbed streams. Logging appears to lower the abundance of *Dicamptodon* by increasing levels of fine sedimentation in low-lying, logged areas, and filling cracks and crevices where the animals live. Similarly, Hawkins et al. (1983), in a study of streams in Oregon and northern California, only found *Dicamptodon* in streams occurring in steep terrain characterized by coarse substrata. Hawkins et al. (1983) documented increased densities of both salamanders and fish in streams with little or no forest canopy. This increase was attributed to enhanced primary production and, thus, an expansion of populations of aquatic invertebrate prey (Hawkins et al. 1983).

The effects of disturbances on populations of *Rhyacotriton* are similar to those observed for *Ascaphus* and *Dicamptodon*: the density and biomass are significantly higher (2-7 times) in streams of uncut forests (Corn and Bury 1989). Bury and Corn (1988a, b) suggest that *Rhyacotriton* found near small headwater streams are threatened by

timber harvest. *Rhyacotriton*, like *Ascaphus*, has stringent habitat requirements (cold, flowing, permanent water in forested areas), and appears to be highly susceptible to forest practices, such as logging, that can elevate water temperatures.

Lehmkuhl and Ruggiero (1991) compiled a list of species associated with late successional Douglas-fir (*Pseudotsuga menziesii*) forests in the Pacific Northwest and, for each species, modelled the risk of local extinction from habitat loss or fragmentation. According to their criteria, populations of *Ascaphus*, *Dicamptodon* spp. and *Rhyacotriton* are all considered to be at moderately high to high risk of extinction. Thus, continued logging of old-growth forests without leaving appropriate buffers of trees adjacent to streams could result in the loss of a biologically unique assemblage of amphibians that is found only in the Pacific Northwest.

Biodiversity of Terrestrial Amphibians with Direct Development

Metamorphs (adults and juveniles) of most of the pond and stream-breeding amphibians may be found in terrestrial habitats as either transient migrants, during dispersal to other aquatic sites in the wet seasons, or as residents of underground tunnel systems during the non-breeding season. Except for occasional above-ground activity following heavy rains, they seldom are seen outside of their respective breeding seasons. Presumably, they do not significantly overlap in microhabitat use with the permanently terrestrial amphibians.

The remaining ten species (40% of the forest-dwelling amphibians) listed in Table 2 are all lungless salamanders of the family Plethodontidae (*Aneides flavipunctatus*, *A. ferreus*, *Batrachoseps wrighti*, *Ensatina eschscholtzii*, *Plethodon dunni*, *P. elongatus*, *P. larselli*, *P. stormi*, *P. vandykei*, and *P. vehiculum*). *Aneides ferreus* is arboreal to some extent, but otherwise these species are all terrestrial, with direct development. The eggs are deposited terrestrially in moist, hidden cavities. They hatch into juveniles that exhibit the characteristic adult morphology (Nussbaum et al. 1983; Duellman and Trueb 1985; Stebbins 1985). Thus, an aquatic, free-living larval stage is absent from their life cycle.

The distribution of these species on the forest floor follows a moisture gradient that extends from the banks of streams to relatively dry talus (rocky) slopes that are not directly associated with bodies of water. Some of these salamanders appear to have narrow habitat requirements (e.g., *Plethodon larselli*, *P. stormi*, *P. vandykei*, and

B. wrighti), which influence their distributions along this gradient. In describing the microhabitat affiliations of these species, we acknowledge three main types of terrestrial microhabitat: streamside (riparian) habitat, the forest floor, and talus (rocky) slopes.

Inhabitants of Riparian Areas

Typically, wet, rocky substrate alongside streams, waterfalls and road cuts is the preferred habitat of *Plethodon dunni*; thus, it is often found with *Rhyacotriton*, *Dicamptodon*, and *Ascaphus* (Nussbaum et al. 1983; Bury et al. 1991). Two other species of *Plethodon* (*P. vandykei* and *P. vehiculum*) are often associated with seepages and small streams from talus, although they also occupy the forest floor and relatively drier talus slopes (see below). Thus, where their ranges overlap, any (or all) of the three species of *Plethodon* may coexist (Nussbaum et al. 1983). A fourth plethodontid, *Aneides flavipunctatus*, prefers wet substrates and is often found near streams. Although it occupies a restricted range (the Siskiyou Mountains of southern Oregon), it may be found with *Plethodon stormi*, *P. elongatus*, *Ensatina eschscholtzii* and/or *Aneides ferreus*.

Inhabitants of the Forest Floor

Six species of Pacific Northwest plethodontid salamanders typically inhabit the forest floor of old-growth stands. In descending order of breadth of their distributional ranges, these species are: *Ensatina eschscholtzii*, *Plethodon vehiculum*, *Aneides ferreus*, *Batrachoseps wrighti*, *Plethodon elongatus* and *P. vandykei* (Nussbaum et al. 1983). Most of these species may occupy additional microhabitats. On the forest floor, individuals of all of these species are found beneath surface leaf litter, logs, and loose bark. Because of their similarities in microhabitat preferences, the three species with the broadest overlapping distributions (*E. eschscholtzii*, *P. vehiculum*, and *A. ferreus*) may commonly coexist. They also may coexist with *Batrachoseps wrighti* within its restricted range of the western slopes of the Oregon Cascades. *Plethodon vandykei* has a disjunct and limited distributional range—western Washington, Idaho, and Montana—so it can only coexist with *P. vehiculum*, *P. dunni* and *E. eschscholtzii* (Nussbaum et al. 1983). It may also be found with *Dicamptodon* spp. Thus, there are potentially several different groups of salamander species—ranging from two to five species within each—that appear to be



Ensatina eschscholtzii. Photo by Grant Hokit

permanent (i.e., non-transient) components of the floor of old-growth forests in the Pacific Northwest.

Inhabitants of Talus Slopes

Herrington (1988) reviewed the use of talus by Pacific Northwest amphibians and reptiles. He found that 14 salamander species and six anuran species utilized talus. Four species of *Plethodon* (*P. larselli*, *P. vandykei*, *P. elongatus*, and *P. stormi*) are restricted to talus habitats (Herrington 1988; but see Nussbaum et al. 1983 for use of alternative microhabitats in *P. elongatus* and *P. vandykei*). Although *P. larselli* may occasionally be found in continuously wet talus, individuals are most common in seasonally wet talus (Nussbaum et al. 1983). *Plethodon stormi* is restricted to the Siskiyou Mountains of southern Oregon. *Plethodon larselli* is only found in Oregon and Washington along the Columbia River Gorge and the southcentral Cascades of Washington (Nussbaum et al. 1983; Aubry et al. 1987). Four other species, *P. vehiculum*, *E. eschscholtzii*, *Batrachoseps wrighti* and *Aneides ferreus* commonly inhabit talus slopes (Nussbaum et al. 1983). Based on their distributions, *P. larselli* may coexist in talus with *P. vehiculum*, *A. ferreus*, *Ensatina eschscholtzii*, *B. wrighti* and *Dicamptodon* spp. where their ranges overlap in the Columbia River Gorge.

Relationship to Old Growth and Potential Impact of Habitat Loss

We have identified several groups of salamander species that occupy a variety of terrestrial microhabitats associated with old-growth forests. Not only are these areas the only habitats occupied by lungless salamanders in the Pacific Northwest, but they also harbor metamorphs of the aquatic breeding amphibians. Therefore, disturbance that results in deterioration or loss of these habitats may have profound consequences on amphibian communities in old-growth stands. Indeed, with the exception of *Ensatina eschscholtzii*, which is not considered to be at risk, and *Aneides flavipunctatus* and *Plethodon elongatus*, which were not evaluated, Lehmkuhl and Ruggiero (1991) categorized the remainder of the Pacific Northwest lungless salamanders as being species at moderately high to high risk of extinction from loss of habitat.

Discussion

Welsh and Lind (1991) outlined four forest management strategies necessary to maintain viable populations of amphibians. Two of these are directly pertinent to management of communities of terrestrial amphibians. The best potential strategy to preserve amphibian species is their suggestion to minimize direct logging effects. A heavier emphasis on cable logging in winter would minimize soil compaction caused by tractor logging, thus possibly reducing the impact of timber harvesting on hibernating amphibians (Welsh and Lind 1991). Additionally, retaining the maximum forest canopy possible would minimize desiccation of the soil and its associated talus, as well as minimize alteration of understory vegetation (Welsh and Lind 1991).

A second important strategy for maintenance of communities of terrestrial amphibians is the provisioning of suitable microhabitat (Welsh and Lind 1991). As discussed above, all of the inhabitants of the forest floor regularly utilize surface material (leaf litter, loose bark, down logs, and other down woody material) as refugia, as do transient species and species that live below the surface. Three species, in particular (*Aneides ferreus*, *Ensatina eschscholtzii* and *Batrachoseps wrighti*), are especially noted for their association with down wood (Corn and Bury 1991). One of the preferred microhabitats of *A. ferreus* is between the loose bark and the wood of large down Douglas-fir logs, whereas *E. eschscholtzii* appears to prefer well-decayed logs (Corn and Bury 1991). Thus, the removal and/or destruction of such woody material during and after timber harvest, salvage

and post-harvest manipulations may diminish the supply of suitable refugia for many terrestrial salamanders.

Conclusions

A growing body of evidence demonstrates that traditional methods of timber harvest may alter the species' composition of amphibian communities, reduce the number of species, as well as lower the abundance of individuals within populations (Welsh and Lind 1991, and references therein). In terms of biodiversity, the amphibian fauna of the Pacific Northwest is of special concern for two reasons: (1) because of increased disturbances and associated loss of amphibian habitat due to escalated rates of timber harvest and (2) because several species appear to have exhibited population declines and reductions in their range since the mid-1970s (e.g., Blaustein and Wake 1990; Fellers and Drost in press). At present, five of the 34 species (15%) from the Pacific Northwest are listed as candidates on the U.S. list of threatened species. Fifteen of the 28 (54%) native Oregon amphibian species are listed as sensitive by the Oregon Department of Fish and Wildlife. Eleven of the 24 (46%) amphibian species of Washington State are considered to be of special concern by the Washington Department of Wildlife. Four of the 14 (29%) amphibians of Idaho are listed as rare, threatened, or endangered by the Idaho Fish and Game Department. The status of amphibians in British Columbia is presently under review. Therefore, a relatively large proportion of the native amphibian fauna of the Pacific Northwest may be in critical condition.

We have identified several unique groups of amphibian species that are generally associated with very specific types of forest habitat. Thus, we argue that disturbance of these amphibian habitats imperils individual populations of single species as well as the survival and well-being of entire communities of interacting species. Coexisting species, such as many of the amphibians found in undisturbed stands of old-growth forest, have presumably interacted and coevolved with one another over evolutionary time. Thus, the loss of some amphibians may considerably affect competition and predation between species, and significantly alter community structure. Indeed, the elimination of top-level predators like *Dicamptodon* may have cascading effects throughout the rest of the community due to modification of prey populations (Lehmkuhl and Ruggiero 1991, and references therein). Such changes in community structure may be particularly prevalent in communities where salamanders comprise a major portion of the vertebrate biomass (Burton and Likens 1975a, b).

To sustain the biodiversity of amphibians associated with old-growth forests in the Pacific Northwest, attention must be focused on preservation of the habitats that they require for survival. In particular, habitats that are critical to highly sensitive species need protection, such as temporary ponds, headwater springs, streams and seeps, rocky outcrops, and talus slopes (Herrington 1988; Welsh and Lind 1991). Riparian areas, in general, may be especially valuable as sites for potential source populations and corridors for gene flow (Welsh and Lind 1991). In this way, such habitats may play a critical role in maintaining the relatively high species richness of amphibians in the Pacific Northwest.

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