Relictual Amphibians and Old-Growth Forests

HARTWELL H. WELSH, JR.

Pacific Southwest Forest and Range Experiment Station
Forest Service, U.S. Department of Agriculture
Arcata, CA 95521, U.S.A.

Abstract: *Terrestrial and aquatic herpetofauna were sampled by pitfall traps, time-constrained searches, and area-constrained searches (stream sites only) over a three-year period to examine the importance of forest age to amphibians and reptiles. Fifty-four terrestrial and 39 aquatic sites in Douglas-fir-dominated, mixed evergreen forests were located in southwestern Oregon and northwestern California Mean age of trees on sites ranged in age from 30 to 560 years. Thirty-one species of amphibians and reptiles were detected from the 93 localities. Only three species were found primarily on older forest sites: the Del Norte salamander* (Plethodon elongatus), *the Olympic salamander* (Rhyacotriton olympicus), *and the tailed frog* (Ascaphus truei). *Paleoecologic evidence indicates an historical association between these three amphibians and the extant elements of ancient primeval coniferous forests of the Pacific Northwest. The life histories and habitat requirements of these species suggest that these forms are scarce in younger forests because the microclimatic and microhabitat conditions they require generally exist only in older forests. The long-term viability of these species in northern California and southern Oregon may depend upon developing forestry practices that protect these critical microclimates and microhabitats.*

Resumen: *La herpetofauna terrestre y acuática se muestrearon mediante trampas excavadas, cacheos de tiempo restringido y búsquedas en áreas restringidas (solamente en los riachuelos) por un período de tres años para examinar la importancia de la edad de un bosque para los anfibios y los reptiles. Cincuenta y cuatro lugares terrestres y treinta y nueve lugares acuáticos en los bosques perennes mixtos dominados por (Douglas-fir), fueron localizados en el suroeste de Oregón y el noroeste de California La edad de los lugares variaba entre 30 y 560 años. Se detectaron 31 especies de anfibios y reptiles en las 93 localidades. Solamente se encontraron tres especies, principalmente en los lugares de bosques más ancianos: la salamandra del norte* (Plethodon elongatus), *la salamandra olympica* (Rhyacotyriton olympicus) y la *rana coluda* (Ascaphus truei). *La evidencia paleoecológica indica una asociacion histórica entre estos tres anfibios y [los elementos contemporarios de ancianos y pristinos bosques de coníferas del Noroeste del Pacifica Los requerimientos de la vida y el hábitat de estas especies sugieren que estas formas son más escasas en bosques jóvenes debido a que las condiciones microclimaticas y de microhkbitat que requieren existen generalmente sólo en bosques mas antiguos La viabilidad a largo plazo de estas especies en el norte de California y el sur de Oregon puede depender en el desarrollo de prkcticas forestales que protegen estos criticos microclimas y microhábitats,*

Introduction

The old-growth, Douglas-fir-dominated, coniferous-hardwood forests of the Pacific Northwest originated millions of years in the past. These forests are remnants of a more species-rich Tertiary forest with a previously continuous circumpolar, subarctic distribution. The species comprising these ancient forests (both living and extinct) have been termed the Arcto-Tertiary Geoflora by paleobotonists (Axelrod 1976; Daubenmire 1978). These forests are presently the focus of a conflict over natural resources between those who support continued commercial harvesting for wood products and those who support protecting the remaining old growth to conserve watershed quality, fisheries populations, wildlife habitat, and recreational space (see Thomas et al. 1988 for an overview). Critical to this issue are two

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questions: how much old-growth forest should be retained, and by what criteria ought this be determined? The basis for such criteria, however, have been established de facto by federal law. The Endangered Species Act of 1973 (16th U.S. Congress) establishes that viable populations of all native plants and animals will be maintained. The National Forest Management Act of 1976 (16th U.S. Congress) requires that regulations be established that address the concept of maintenance of biological diversity on federal forest lands (see MacCleery 1982). These laws mandate that resource use take into account the potential and actual impact of that use on all resident plants and animals. Criteria for area and unit spacing for old-growth forest preservation could therefore be based on the requirements for viability of those species of plants and animals that require old-growth forests. This approach to establishing criteria must address two issues: (1) Which species require old-growth forest habitat? (2) How much of this habitat is needed and what spatial configurations are required to allow gene flow and thus assure the viability of those species?

An intensive research program has been under way since 1981, under the auspices of the U.S.D.A. Forest Service, to determine which vertebrate species require old-growth forest habitats (Meslow et al. 1981; Raphael 1984; Ruggiero & Cary 1984; Ruggiero et al., in press). The Forest Service's Pacific Southwest Forest and Range Experiment Station (PSW) collected data on forest age and habitat associations of all vertebrates (except fish) in forests of southwestern Oregon and northwestern California from 1984 to 1986. The primary objective of these studies was to examine the importance of forest age to wildlife.

During the course of this research 3 of 31 species of reptiles and amphibians that were sampled were found primarily in mature and old-growth habitats: the Olympic salamander, the Del Norte salamander, and the tailed frog. This paper reports on these three old-growth-associated forms; on the relationship between presence and abundance of these amphibians and forest age, and on aspects of their natural history that may influence this relationship. I suggest that these species are evolutionarily conservative elements of an ancient relictual forest ecosystem. I stress here that other species of herpetofauna in the Pacific Northwest exhibit characteristics suggestive of relict forms, but I lacked sufficient data to include them in my discussion.

Study Area

These studies were conducted in Douglas-fir (*Pseudotsuga menziesii*) -- dominated mixed coniferous-hardwood forests of northwestern California and southwestern Oregon. The forests ranged in age from 30 to 560 years and in elevation from 500 to 5,000 feet. Equal numbers of forest sites were selected in three general locations within the region (Fig. 1). Sites in each of the three areas were selected from young, mature, and old forests based on stand characteristics (Franklin et al. 1986). Fifty-four terrestrial study sites, ranging from 21 to 150 ha, and 39 second- or third-order streams were sampled for amphibians (Fig. 1).

Methods

Herpetofauna Sampling

Three methods were used to sample the species composition and relative abundance of the herpetofauna: pitfall traps (PF), time-constrained searches (TCS), and area-constrained aquatic searches (AQS). These methods are described briefly below and in more detail in

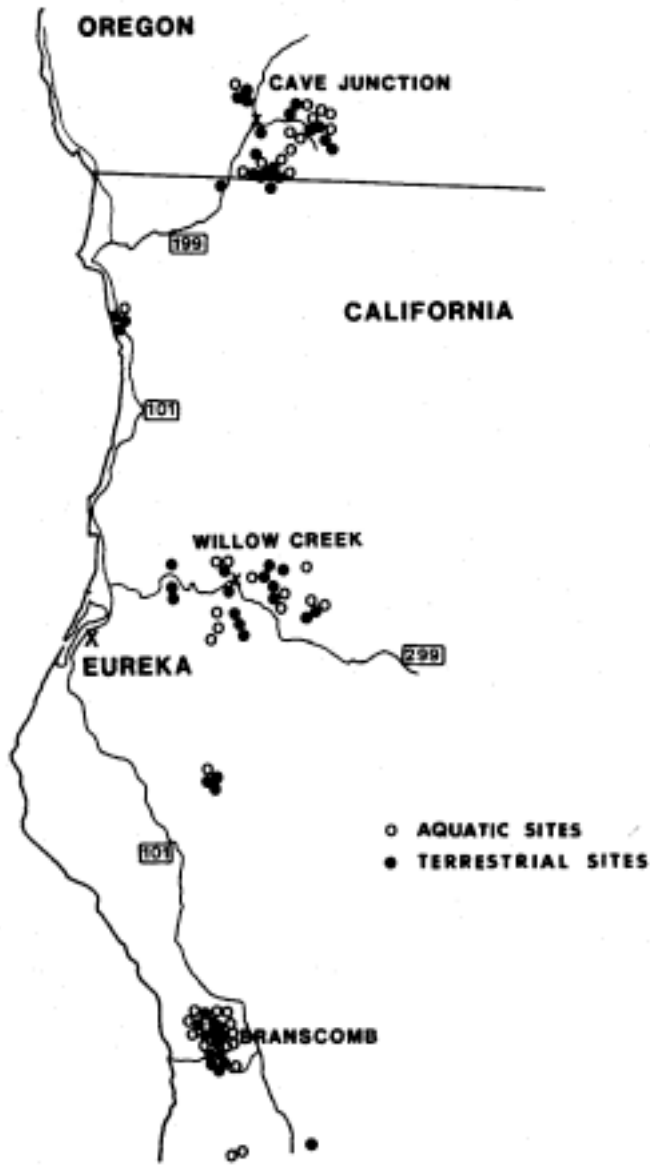

Figure 1. Study sites in northwestern California and southwestern Oregon.

Welsh (1987), Corn and Bury (1989), and Corn and Bury (in press).

Forty-nine sites contained PF trap grids with 36 traps spaced at 15 m intervals in a 6 X 6 arrangement. Traps were made of two # 10 tins taped together and buried with the lip at ground level and concealed by a cover of bark or cedar shake propped slightly above ground level. Traps were open at 49 sites in October and November of 1984 and October of 1985, for 50 and 30 nights, respectively.

The TCS method consisted of timing the search efforts of 2-3 persons as they moved through the forest sites at random examining all microhabitats encountered, including raking through litter with a potato rack, turning rocks and small logs, breaking open larger decaying logs, probing vegetation, etc. The clock was stopped when animals were encountered, and data were gathered. Four hours of TCS were conducted at each of the 54 sites between April and June of 1984 and again in 1985. Preliminary analyses of TCS data in 1984 indicated that this method was not adequately sampling the relatively uncommon and unevenly distributed microhabitat of the Olympic salamander. Consequently, potential sampling sites were preselected within the stands (Fig. 1) on the basis of presence of appropriate microhabitat (Anderson 1968; Nussbaum et al. 1983; Stebbins 1985). A separate half-hour TCS of each potential site was then conducted in 1985 to sample for the Olympic salamander.

Some workers have indicated problems with the TCS method (e.g., Corn & Bury, in press), notably the tendency of some searchers to concentrate on the types of microhabitat that yield the most animals. In forested habitat this might result in a bias toward sampling one species and decay class of rotting log. To avoid this problem, we emphasized the importance of unbiased random sampling over numbers of captures and trained all searchers to move frequently and to sample all microhabitats equally. Another critical factor to consider when using TCS is the influence of climate on the surface activities of herpetofauna. We performed TCS at all sites concomitant with the end of the rainy season when daily mean temperatures were rising and surface moisture was high in northwestern California.

The AQS method consisted of systematic searches of measured stream reaches in 39 second- or third-order streams (Strahler 1952) on or near the terrestrial sites. Three 5 m reaches 1-3 m wide were selected along each stream by walking 50 m upstream from the nearest trail or road access for the first reach and 50 m from the top of the previous reach for subsequent reaches. Each reach was measured and mapped, then all substrates were methodically searched, moving all rocks where possible, working upstream with catch nets placed downstream to capture dislodged animals. AQS were conducted in July and August of 1984 and 1985.

Determining Forest Age

Tree ages were determined by increment coring and where possible, by counting rings on stumps in adjacent logged areas (old-growth terrestrial sites). Forest age was estimated by averaging tree ages from a minimum of three trees at each site (Table 1). Dominant or codominant size classes (based on tree counts within 0.2-ha circular plots) of Douglas-fir trees were selected for aging and trees were cored at breast height. Tree age data were collected by Bingham and Sawyer (in press). On the basis of tree coring and ring counts, sites were grouped into three age classes: young forest, less than 100 years; mature forest, 100 to 200 years; and old-growth forest, more than 200 years. Four sites that met all the criteria for old-growth (numbers of large trees, snags, and logs: Franklin et al. 1986) but were less than 200 years old were also included in the old-growth category. Eight sites in the young category were previously logged sites and three sites were the result of natural fires.

Statistical Methods

I tested the null hypothesis (H_o) that no association existed between the presence or abundance of frogs or salamanders and forest age. Forest age was treated as both a continuous and a discrete variable. Simple linear

Table 1. Mean tree ages and diameters of cored Douglas-fir trees from study sites in mixed evergreen forests of northwestern California and southwestern Oregon. Sites sampled for the Olympic and Del Norte salamanders were subsets of 54 terrestrial forest sites within known geographic and elevational limits and with springs or seeps for Olympic salamanders.

	Forest age class								
	Young			*Mature*			*Old-growth*		
Species	*n*[a]	*age*[b]	*dbh*[c]	*n*	*age*	*dbh*	*n*	*age*	*dbh*
Olympic salamander	9	51.4 ± 20.0	35.2 ± 11.6	8	136.8 ± 54.4	86.0 ± 20.5	13	251.5 ± 53.3	118.3 ± 20.7
Del Norte salamander	6	35.0 ± 11.5	35.1 ± 7.0	5	105.1 ± 7.8	81.7 ± 28.7	10	265.3 ± 77.7	120.2 ± 24.1
Tailed frog	9	60.0 ± 17.7	43.0 ± 14.1	9	147.1 ± 30.4	82.2 ± 15.4	21	344.1 ± 86.4	123.8 ± 20.4

[a] *Number of sites.*
[b] *In years mean ± one standard deviation.*
[c] *Diameter at breast height, in cm, mean ± one standard deviation.*

regression was used to relate abundance of each species to site age. The abundance data were coded by adding 0.5 to each value and then square root-transformed to equalize variances (Sokal & Rohlf 1981, p. 421). I also compared the frequency of detection (present or absent) of each species on the different forest age class sites (young, mature, or old-growth). An overall chi-square "goodness-of-fit test" was performed to test for differences between forest age classes. If results were significant, this test was followed by a variation of the Tukey test for multiple comparison of proportions (Zar 1984, pp. 400-401). An alpha level of $P \leq 0.05$ was used to determine significance.

The data used for each species were from the sampling method that yielded the largest sample size, except for the Del Norte salamander, where both TCS and PF were equally effective, yielding almost equal total captures (Table 2). Here I chose to use the TCS data for regression analysis because it had lower variance; however, proportion tests were performed using presence records from both methods. For the Olympic salamander and the Del Norte salamander a subset of the original 54 sites was used (Table 2); only those sites within the known geographic and elevational ranges of these species were included, with the additional requirement of the presence of springs, seeps, or first-order streams (Strahler 1952) for the Olympic salamander. For the regression analysis of Del Norte salamander captures, one old-growth site with extremely high capture values was omitted.

Results and Discussion

From 1984 to 1986 we recorded 6,419 observations of 31 species from the 54 terrestrial and 39 aquatic sites (Fig. 1). Twelve of these species were captured in numbers sufficient to allow analyses of presence or abundance in relation to forest age, moisture class, and other habitat variables (Welsh & Lind 1988, in press). Nineteen species were too uncommon for meaningful analyses across the forest chronosequence; sixteen of these were reptiles comprising only 2.3 percent of the total sampling effort. Of those species for which sample sizes were adequate to assess distributions relative to forest age, five were found in significantly higher numbers on older sites (Welsh & Lind 1988, in press). However, three species, the Olympic salamander, the Del Norte salamander, and the tailed frog, occurred predominantly on older forest sites and were uncommon or absent on the young sites (Fig. 2).

The Olympic Salamander

The Olympic salamander occurs in isolated populations in coniferous forests at elevations below 1,200 m, throughout much of the Pacific Northwest (Stebbins 1985; Nussbaum et al. 1983). In these forests they are restricted to springs, headwater seeps, and small streams. They are rarely found in open water in even the smallest creek, preferring the cover of moss, rocks, and organic debris in shallow, cold, percolating water (Anderson 1968; Nussbaum & Tait 1977; Stebbins 1985). They require a minimum of 4.5 years to reach sexual maturity; 3.5 years in the larval form and 1 to 1.5 years after metamorphosis (Nussbaum & Tait 1977).

In this study Olympic salamanders were found in a significantly greater proportion of old growth and mature stands compared to young stands, though no differences were found between mature and old growth (Fig. 2a) (young versus mature: $q = 4.71$, $P < 0.005$; young versus old growth: $q = 7.69$, $P < 0.001$; mature versus old- growth: $q = 2.37$, $P > 0.20$). Regression of captures of Olympic salamanders on forest age was sig-

Table 2. Captures of Olympic salamanders, Del Norte salamanders, and tailed frogs from Douglas-fir-dominated, mixed evergreen forests of northwestern California and southwestern Oregon in 1984 and 1985 by time-constrained searches (TCS), pitfall trapping (PF), and area-constrained searches (AQS).

	Sampling method									
	TCS			*PF*			*AQS*			
Species	*Number of captures*	*Number of sites*	$\bar{x}$	*Number of captures*	*Number of sites*	$\bar{x}$	*Number of captures*	*Number of sites*	$\bar{x}$	*Total captures*
Olympic[a] salamander	43	30	1.43 (±2.38)	1	26	0.04 (±0.20)	1	34	0.03 (±0.17)	45
Del Norte[b] salamander	193	21	9.19 (± 18.20)	213	21	10.14 (±36.37)	0	0	--	406
Tailed frog	3	54	0.06 (±0.23)	9	49	0.18 (±0.60)	487	39	12.49 (± 18.34)	499

[a] *Thirty terrestrial and 34 aquatic sites fell within the known geographic and elevational range of the Olympic salamander, terrestrial sites were sampled once by TCS in 1985 and aquatic sites were sampled once by AQS in 1984 or 1985. Twenty-six of the terrestrial sites had pitfall traps; these traps were open in the falls of 1984 and 1985.*

[b] *Twenty-one terrestrial sites fell within the known geographic and elevational range of the Del Norte salamander, each was sampled by TCS and PF in 1984 and 1985.*

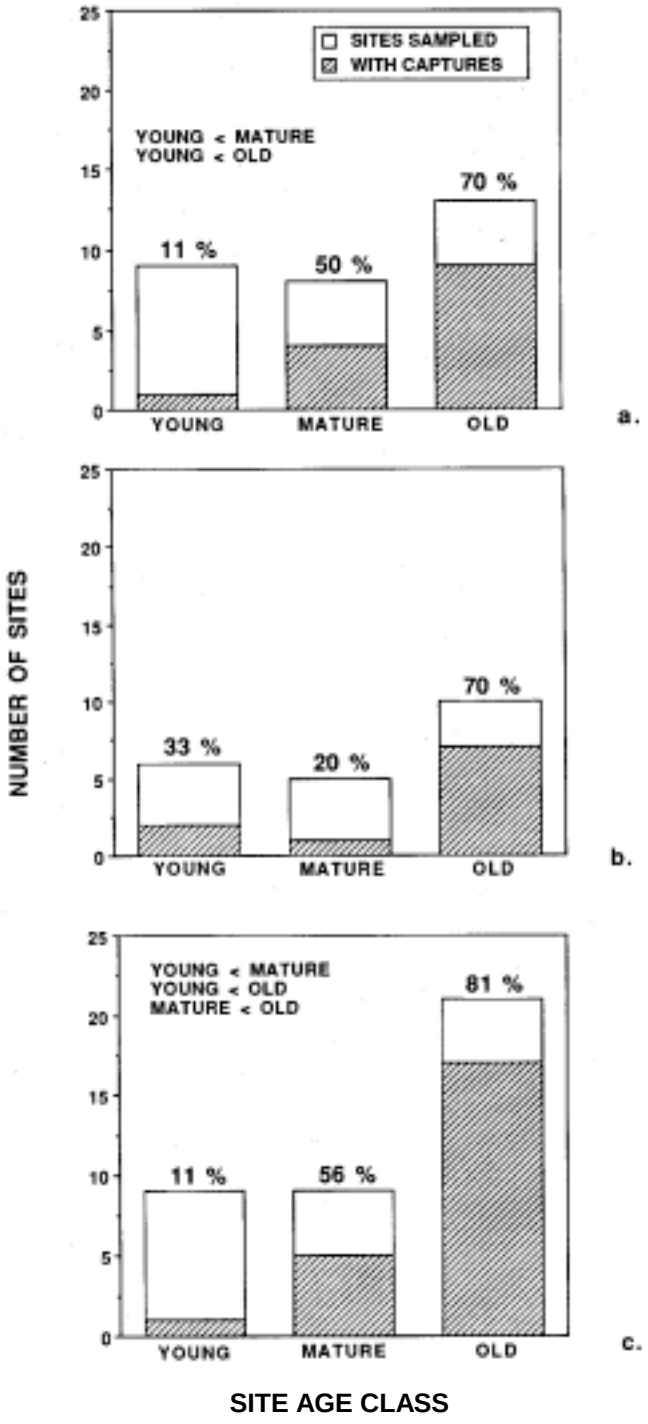

Figure 2. Proportion of mixed evergreen forest sites in northwestern California and southwestern Oregon by forest age class with captures of (a) Olympic salamanders, (b) Del Norte salamanders, and (c) tailed frogs Significant results of proportion tests are presented for each species

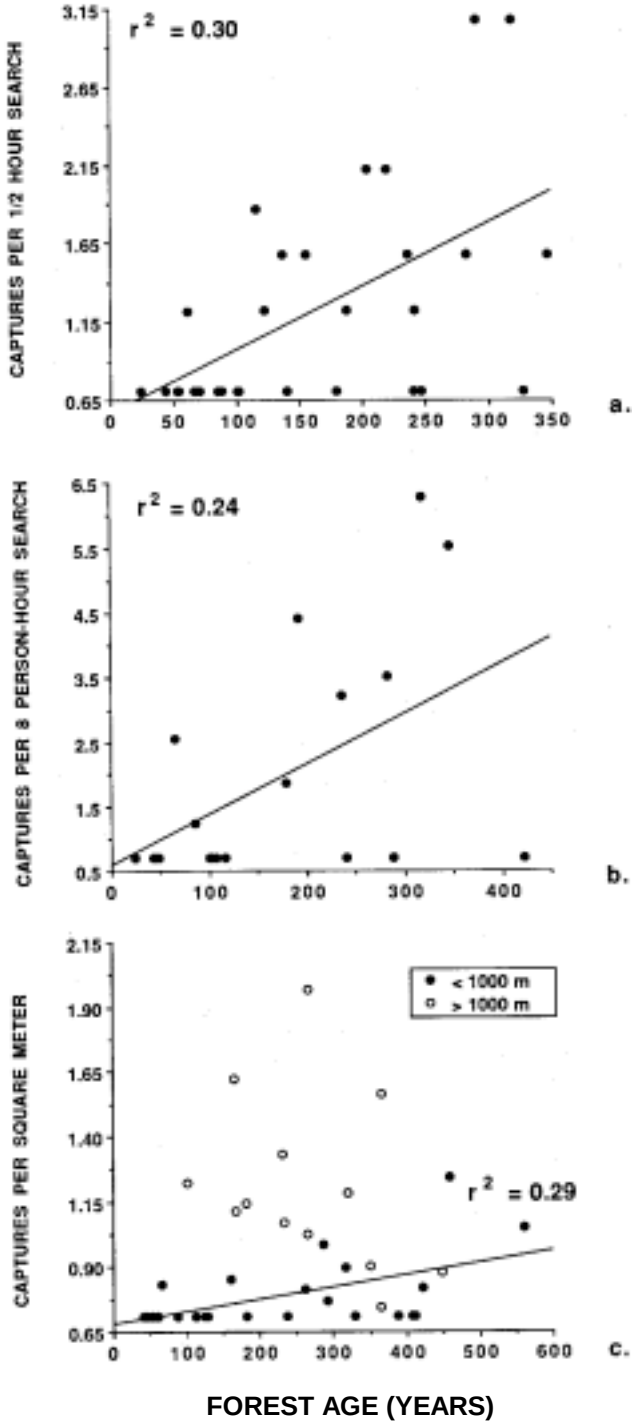

Figure 3. Captures of (a) Olympic salamanders, (b) Del Norte salamanders, and (c) tailed frogs relative to forest age on mixed evergreen forest sites in northwestern California and southwestern Oregon. For the tailed frog the regression and r^2 value are for low elevation (<1,000 m) sites only. (All abundance data were coded by adding 0.5 to each capture value and then square root-transformed)

nificant. Almost 30 percent of the variation in numbers of Olympic salamanders was accounted for by variation in forest age ($F = 13.29$, $P = 0.001$) (Fig. 3*a*).

The association with mature to old-growth forest in northwestern California is consistent with habitat associations described for other parts of its range (Nussbaum et al. 1983; Stebbins 1985). However, D. A. Good (personal communication) suggested that the Olympic salamander may have broader tolerances in the northern parts of its range, indicating that old-growth forests support the greatest concentrations of *R. olympicus* but are not the only places it is found.

The Olympic salamander has one of the narrowest tolerance ranges for temperature of any salamander (thermal maximum of 27.8-29.0° C) (Brattstrom 1963) and is also the most sensitive terrestrial salamander to loss of body water (Ray 1958). Both its narrow temperature requirements and susceptibility to water loss probably limit its use of upland habitats and its ability to disperse overland.

Recent investigations of geographic variation in allozymes in the Olympic salamander (Good et al. 1987) indicate that it is highly fragmented throughout its range, occurring in isolated populations with little or no gene flow among geographic units. Good et al. (1987) also demonstrated that the Olympic salamander possesses within its range the highest levels of fixed differences in proteins between populations ever recorded for a vertebrate taxon of similar rank. Levels of allozymic difference indicate at least three distinct geographic forms that are unique at the level of species. Proposed taxonomic revisions are currently in progress (D. A. Good, personal communication).

The Del Norte Salamander

The Del Norte salamander (*Plethodon elongatus*) is found in scattered populations in rocky areas in extreme northwestern California and southwestern Oregon (Stebbins 1985).

During this study, 91 percent of 406 Del Norte salamanders were found on old-growth forest sites. The remaining salamanders were from two mature sites, or from two young sites both adjacent to older forest.

There were no significant differences in the frequency of detection of the Del Norte salamander between any of the three age classes (Tukey test) (Fig. 2b). However, regression analysis indicated that the relative abundance of Del Norte salamanders was significantly associated with site age. Twenty-four percent of the variation in numbers of Del Norte salamanders was accounted for by forest age ($F = 7.04$; $p = 0.016$) (Fig. 3b).

Raphael's (1988) results were similar to those of the present study; he found significant differences in the relative abundance of Del Norte salamanders between forest age classes, with the highest numbers on mature and old-growth forest sites. Raphael also reported finding the Del Norte salamander on several harvested sites with early successional stages of Douglas-fir in eastern Humboldt and western Trinity counties, California. These harvested localities were generally on north-facing slopes adjacent to older forest areas.

Although the terrestrial reproductive habits of the Del Norte salamander (Nussbaum et al. 1983) have freed it from dependence on aquatic ecosystems for survival, its narrow range of moisture and temperature tolerances make it highly susceptible to perturbations in the environment that would expose it to desiccation (Brattstrom 1963; Ray 1958).

Similarly, Herrington and Larsen (1985) report that a closely related member of the genus *Plethodon*, the Larch Mountain salamander (*P. larselli*) from southern Washington, occurs in areas dominated by mature forests, and "currently available evidence strongly suggests that *P. larselli* is unable to exist for more than short periods on exposed slopes" (p. 177).

The Tailed

The tailed frog occurs in isolated populations in and along streams in the coniferous forest habitats throughout the Pacific Northwest (Nussbaum et al. 1983; Stebbins 1985). Its natural history has been investigated by Gaige (1920), Metter (1964, 1967), and Daugherty and Sheldon (1982*a, b*). This frog is highly specialized for life in cold, clear, fast-flowing mountain streams. It has evolved a strategy of internal fertilization, rare among frogs, that enables the adults to breed in fast-flowing water. Larvae are found primarily on rocky substrates in fast-flowing water. Larvae metamorphose at two to three years of age (Metter 1967). The adult frogs may take as long as seven years to reach sexual maturity; life expectancy is thought to be greater than 14 years (Daugherty & Sheldon 1982*a*).

Nussbaum et al. (1983) reported that the tailed frog disappeared from streams when areas were logged. They speculated that this was due to higher water temperatures and increased siltation. Other workers have reported that this species appears to be sensitive to watershed disturbances (Noble & Putnam 1931; Metter 1964, 1968; Bury 1968, 1983; Bury & Corn 1988). I found tailed frogs in only one stream in a managed young forest. This site was downstream from an extensive area of old-growth forest and my sampling yielded only a few larvae and no adults. Although no clearcut areas were sampled, data from other workers (Bury & Corn 1988) indicated that tailed frogs were absent from such sites. Tailed frogs are, however, common in streams in naturally regenerated young forests in Oregon and Washington (Bury et al., in press). Hawkins et al. (1988), investigating distributions of larval tailed

frogs on Mount St. Helens after the 1980 eruption, found the greatest densities in streams with a mix of forested and open reaches. They indicated that low densities of tadpoles "appeared to be most clearly related to heavy embeddedness within streams and complete loss of watershed forest among streams" (p. 250). Both of these conditions can result from clearcut,logging near streams (Murphy et al. 1981).

In this study significant differences occurred in the frequency of detection of this species between each of the three paired age class comparisons (Fig. 2*c*) (young versus mature: $q = 5.46$, $p < 0.001$; young versus old-growth: $q = 10.3$, $p < 0.001$; mature versus old-growth: $q = 3.87$, $P < 0.025$). The regression of densities of frogs on forest age pooled across sites was not significant (Fig. 3*c*). However, most of the aquatic sites in southwestern Oregon were quite different from those in California (Fig. 1), occurring at higher elevations and in forests dominated by true fir (*Abies*). My data indicate that tailed frogs from these higher sites occurred in streams with more open canopy and younger forest. Sawyer et al. (1977) indicated that the Douglas fir-dominated, mixed evergreen forest type of the Klamath Region of northwestern California and southwestern Oregon occurs below 1,000 meters. When I omitted these higher elevation true fir sites and considered only 26 low-elevation (< 1,000 m) sites, the regression was significant, with 28.5 percent of the variation in frog densities accounted for by forest age ($F = 10.98$, $P = 0.003$) (Fig. 3*c*).

Temperature plays a critical role in all life stages of the tailed frog, and evidence suggests it is a key environmental factor determining its distribution. Brattstrom's (1963) data indicate that the tailed frog has one of the lowest and narrowest ranges of tolerance for temperature of all the world's frogs. Brown (1975) reported that 18.5° C is the upper limit for egg development. deVlaming and Bury (1970) observed that one- to two-year-old tadpoles preferred 5-8° C and two- to three-year-old tadpoles preferred 12-16° C water. Claussen (1973) showed that the lethal thermal maxima for adults was 23-24° C. I found stream temperature to be an excellent predictor of tailed frog abundance, accounting for 37.3 percent ($F = 23.56$, $P = 0.00002$) of the variation observed, with higher numbers of tailed frogs occurring in streams with lower temperatures (Fig. 4). The highest stream temperature I observed with *Ascaphus* was 14.3° C.

Forest Age and Microhabitat Requirements

If mature and old-growth forests are so important to these amphibians, why are the patterns of abundance not more strongly associated with forest age (Fig. 3*a-c*)? Forest age per se appears to be an indirect measure of the factors limiting the distribution of these amphibians, whereas aspects of microhabitat or microclimate

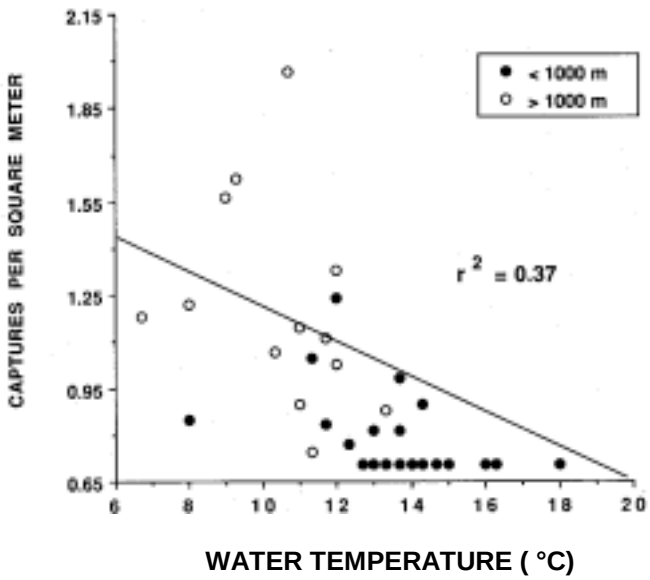

Figure 4 Captures of tailed frogs relative to water temperature in 39 streams in mixed evergreen forests of northwestern California and southwestern Oregon. The regression line and r^2 represent all sites both high and low elevation. Temperature values for each stream were derived by averaging three instantaneous measurements taken at midday during the summer stream sampling. (Abundance data were coded by adding 0.5 to each capture value and then square root-transformed)

that can vary in parallel with variation in forest age are probably the true limiting factors. Structural features of old-growth forests, indirectly a function of age (time), are also influenced by slope, aspect, elevation, latitude, longitude, climate, fire ecology, and disturbance history. Particular macro- and microhabitat elements within the forest ecosystem are critical to wildlife species resident in old-growth forests. However, the importance of these elements may vary considerably for different members of the wildlife community. The old-growth-associated amphibians discussed here all exhibit extremely high microhabitat specificity, occurring only in specific moist terrestrial to aquatic situations with low temperatures (Metter 1964; Nussbaum & Tait 1977; Daugherty & Sheldon 1982a~ Nussbaum et al. 1983; Stebbins 1985; Welsh, unpublished data).

Evolving Forests

In the Eocene (50 million years before present [m.y.b.p.]),a mesophytic mixed coniferous-deciduous hardwood forest, the Arcto-Tertiary Geoflora (Axelrod 1948), occurred continuously across North America at mid-northern latitudes. Evergreen conifers such as *Abies, Libocedrus, Picea, Pinus, Pseudotsuga;* and *Tsuga* occurred with deciduous genera such as *Acer, Aesculus, Carpinus, Caryg Fagus, Fraxinus, Ginkgo,*

Juglans, and *Ulmus* (Daubenmire 1978). Tectonic uplift during the Miocene (5 to 20 m.y.b.p.), along with other gradual changes in temperature and rainfall patterns, fragmented the range of the Arcto-Tertiary Geoflora. By the mid-Pliocene (3 m.y.b.p.) this once-extensive Geoflora had undergone major changes in both distribution and composition, losing many of the hardwood elements and retreating from increasingly arid regions east of the Rocky Mountains and the Sierra Nevada-Cascade cordillera (Axelrod 1948, 1977). Most of the dominant trees and shrubs now characterizing the redwood, Sierra Nevada, Rocky Mountain, and Pacific Northwest conifer forests occurred as similar (or identical) forms that coexisted in the widespread Miocene Arcto-Tertiary Geoflora (Axelrod 1948, 1977).

Evolving Herpetofaunas

Peabody and Savage (1958) first suggested that the evolution of the Cenozoic herpetofaunas could be broadly correlated with the evolution of the Tertiary geofloras based on the literature of paleoecology. Savage (1960:188) cited examples of correspondence between occurrences of plant and herpetofaunal forms from Paleocene and Eocene fossils whose contemporaries still coexist. He described an evolutionary correspondence between the Arcto-Tertiary Geoflora and an ancestral herpetofauna he identified as the Old Northern Element. According to Savage's scenario, this Old Northern Element fragmented and segregated - much as did the Miocene Arcto-Tertiary Geoflora - into several historical subunits, two in eastern North America, one in western North America, and one in Mexico. Examples of contemporary western forms that Savage considered to have evolved as a part of this Old Northern Element (1960:Table 2) included the talled frog genus *Ascaphus* and the salamander genus *Dicamptodon* The dicamptodontid genus *Rhyacotriton* and the plethodontid genus *Plethodon* (western species) also occur in distributions that correspond to his western complex of the Old Northern Element (1960: Fig. 1; see maps, Stebbins 1985).

Members of this fauna may be among the most conservative living derivatives of an ancient North American Mesozoic terrestrial vertebrate fauna that evolved in conjunction with the Arcto-Tertiary Geoflora; many appear to have changed little since the Mesozoic. The oldest known frog fossils, from the Jurassic (200 m.y.b.p.) of Patagonia, are of the family Ascaphidae (Estes & Reig 1973). Thus, based on the time and sequence of major continent-forming tectonic events, it can be argued that the progenitors of the tailed frog were present on the proto-North American continent by the Jurassic (Savage 1973). Fossil plethodontid vertebrae are known from the lower Miocene of Montana (Tihen & Wake 1981). Peabody (1954) reported fossil salamander trackways from the Paleocene of Montana that he considered to be from an ambystomid or dicamptodontid salamander. In both instances, the remains were associated with Arcto-Tertiary Geofloral fossils (Savage 1973). Allozyme evidence indicates that the divergence time of eastern and western plethodontid salamanders corresponds to the separation of the eastern and western Arcto-Tertiary forests (Maxon et al. 1979).

It is apparent that species such as the tailed frog, the Olympic salamander, and the Del Norte salamander are evolutionarily conservative elements of an ancient relictual forest ecosystem because of their long-term association with Tertiary forests and their absence from areas beyond contemporary remnants of these forests. Metter and Pauken (1969) present evidence for reduced gene flow between populations of the tailed frog concomitant with post-Pleistocene drying and warming trends that have reduced the range of these forests in the Pacific Northwest. The long-term, close association and exact distributional correspondence with these ancient forest types imply that these amphibians have coevolved with habitats existing only within these forests. Furthermore, the data reported here indicate that the Olympic salamander, the tailed frog, and the Del Norte salamander are absent or occur in reduced numbers in the early successional stages of these forests. This suggests that these amphibians may be dependent upon environmental conditions found only within these forests in their mature state (Franklin & Spies 1984).

Managing to Sustain All Resources

Temperature and moisture are probably the physical parameters that account for the association between the occurrence of the Del Norte salamander and old-growth coniferous forests. Records from sites in earlier successsional stages (Fig. 3b, Raphael 1988) suggest that the Del Norte salamander does not require old-growth forests per se, but probably requires the conditions of temperature and moisture that generally only exist in older forests. Because of its ability to disperse overland and the apparent suitability of some early successional forests with canopy closure to provide an equitable microhabitat, the species is probably not highly susceptible to extinction. In view of its very limited distribution and its fragmentation into small populations within its range, however, it would be prudent to assure that sufficient forested areas with the appropriate microhabitats remain between drainages to allow for gene flow and repopulation of Del Norte salamanders into harvested areas.

Given the documented requirements of the Olympic salamander and the tailed frog for a narrow range of low water temperatures, and the interrelationship between

physical and biological phenomena, one would expect a trend toward decreased numbers of frogs and salamanders on harvested sites. Differences in slope, aspect, elevation, and forest cover can have a profound effect on the amount of ambient radiation absorbed, thus influencing the ground and water temperatures at a given site (e.g., Brown & Krygier 1970). However, older, taller, and more structurally complex forests have greater daily and seasonal microclimatic stability and relatively lower overall mean substrate and air temperatures than do younger forests (Harris 1984). The narrow niche requirements, isolated population distributions, and long generation time of these species, in combination with the rapid disappearance of the requisite old-growth coniferous forests and lack of protection for headwater habitats in current forestry regulations, make local populations of these ancient and unique amphibians highly susceptible to extirpation. Furthermore, the combined effects of local extirpations, increased population fragmentation and the accompanying habitat loss, and increased restriction of gene flow and genetic drift make these species vulnerable to extinction throughout their entire range in the long term (Soulé 1980; Leigh 1981; Wilcox & Murphy 1985).

Small sedentary species with restricted distributions, specialized niches, and narrow climatic tolerances are particularly sensitive to extirpation. Loss of their requisite habitat is synonymous with the demise of the species. Timber harvesting is not necessarily incompatible with the survival of wildlife species (e.g., Johns 1985); with careful consideration of the basic requirements of sensitive species such as those discussed here, it should be possible to design and execute timber harvest plans that would not adversely affect these amphibians and their microhabitats. Buffer strips and the elimination of harvesting adjacent to all aquatic habitats would remove a small portion of the total harvestable area in a given watershed and provide the necessary protection for these species (Bury & Corn 1988; Bury 1988). At least some protected area in a drainage would sustain small populations and thus provide a source for the repopulation of harvested areas as vegetative regeneration once again provided suitable habitats (Wilcox 1980).

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