

MULTISCALE HABITAT RELATIONSHIPS OF STREAM AMPHIBIANS IN THE KLAMATH-SISKIYOU REGION OF CALIFORNIA AND OREGON

HARTWELL H. WELSH, JR.,¹ USDA Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, USA
AMY J. LIND,² USDA Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, USA

Abstract: Regional amphibian distribution patterns can vary greatly depending on species and the spatial scale of inquiry (e.g., landscape to microenvironment). These differences appear to be related both to habitat selection among species as well as availability of suitable habitats across scales. We sampled amphibians in 39 second- and third-order streams in the conifer-hardwood forests of northwestern California and southwestern Oregon, USA (the Klamath-Siskiyou Region) during 1984 and 1985. We concurrently measured spatial, structural, compositional, and climatic attributes of the forest and stream environment—attributes representing landscape, macroenvironment, and microenvironment scales—to determine key habitat relationships. We captured 7 species, 97% of which were larval and paedomorphic Pacific giant salamanders (*Dicamptodon tenebrosus*) and larval and adult tailed frogs (*Ascaphus truei*). Streams in late seral forests supported both the highest diversity of amphibians and the highest densities of *A. truei*. Overall, *A. truei* distribution was patchy in occurrence, while *D. tenebrosus* distribution was widespread throughout the region at all scales. The incidence of *A. truei* was assessable at the landscape, macroenvironment, and microenvironment scales; however, variation in density was most predictable at the microenvironment scale. Changes in density of *D. tenebrosus* were detected only at the microenvironment scale. Tree size class and plant species composition variables distinguishing younger from older, more structurally complex forests, and forest microclimates and in-stream attributes best determined the presence and density for both life stages of *A. truei*. However, only in-stream conditions were good predictors of *D. tenebrosus* density. *A. truei* occupied a narrower range of habitat conditions than *D. tenebrosus*, exhibiting an ecological dependence on lotic and riparian environments found more reliably in late seral forests.

JOURNAL OF WILDLIFE MANAGEMENT 66(3):581–602

Key words: *Ascaphus truei*, California, *Dicamptodon tenebrosus*, Klamath-Siskiyou Region, multiscale habitat analyses, Oregon, Pacific giant salamander, stream amphibians, tailed frog.

Stream-dwelling amphibians of the U.S. Pacific Northwest exist in particularly dynamic environments (Resh et al. 1988), where they exhibit a wide range of adaptations (Nussbaum et al. 1983, Leonard et al. 1993, Corkran and Thoms 1996) to cope with a variety of frequency- and scale-dependent ecological processes and disturbance regimes (Perry and Amaranthus 1997, Naiman et al. 2000). We examined the amphibian assemblage of second- to third-order streams of southwestern Oregon and northwestern California, USA (hereafter, the Klamath-Siskiyou or KS Region). Studying this assemblage allowed us to explore variation in amphibian adaptation within streams across a highly diverse and dynamic forest ecosystem. Such studies can augment our knowledge of both ecological and evolutionary processes and provide key information on how landscapes can best be managed to maintain sensitive native fauna such as amphibians (e.g., Semlitsch 2000).

Forest riparian and aquatic habitats in the Pacific Northwest, while naturally dynamic and resilient, have been profoundly altered by recent land-use practices in adjacent uplands (e.g., even-aged management, clearcutting; Reeves et al. 1995, Jones and Grant 1996, Perry and Amaranthus 1997). Amphibian biomass can be extremely high—often exceeding that of fishes—in streams of the Pacific Northwest (Murphy and Hall 1981, Hawkins et al. 1983, Bury et al. 1991), which underscores the importance of understanding the influences of various natural and anthropogenic disturbance regimes on these species. Welsh (1990) hypothesized that the greater occurrence and higher abundances of tailed frogs (*Ascaphus truei*) and southern torrent salamanders (*Rhyacotriton variegatus*) in streams in old-growth compared with young forests in the KS Region were the result of their pronounced sensitivity to the effects of forest management. Bury and Pearl (1999) reported that stream amphibian populations in the Oregon Coast Range had not recovered 35–50 years after clearcut harvesting. However, other evidence of the negative effects of forest management on native stream amphibians is equivocal (e.g., compare Murphy and Hall [1981]

¹ E-mail: hwelsh@fs.fed.us

² Present address: USDA Forest Service, Sierra Nevada Research Center, 2121 Second Street, Suite A-101, Davis, CA 95616, USA.

or Diller and Wallace [1999] with Corn and Bury [1989]), and may reflect differences in species tolerances and/or differences in environmental conditions among ecogeographic provinces within the Pacific Northwest.

During the early 1980s, the U.S. Forest Service initiated an extensive research program to examine patterns of wildlife species distribution and abundance in the Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest (the Old-Growth Forest Wildlife Habitat Research and Development Program). This program was unprecedented in its geographic scope and coordination, covering portions of 3 states (Washington, Oregon, California) and bringing together researchers and managers from dozens of national forests, federal research units, and major universities (Ruggiero 1991). As a part of this program, we investigated the species composition and ecological relationships of stream amphibian assemblages in 39 second- to third-order streams in mixed conifer-hardwood forests of the KS Region. Detailed knowledge of these relationships is of great value for forest management to preserve amphibian diversity. Our research hypothesis was that variation in stream amphibian presence and abundance can be related to species-specific and scale-dependent variation along specific environmental gradients. Specifically, we expected to find patterns in species composition and abundance relative to landscape variables such as elevation, latitude, aspect, forest seral stage and related structural attributes of the forest environment, and physical and hydrologic attributes of the stream environment. This approach was intended to increase our understanding of ecological relationships at both coarse and fine spatial scales for species that may select and use habitats differently (e.g., specialists and generalists; Futuyma and Moreno 1988, Van Tienderen 1991). Given the nature of the overall study design (Carey and Spies 1991), our work was intended to be exploratory, descriptive, and hypothesis-generating rather than hypothesis-testing. Our study design fits that described by Waters and Erman (1990:18) as a "controlled experience study," which differs from a strictly observational study in the degree to which variation in the primary variables of interest are controlled or accounted for. In this instance, forest sites were systematically selected to represent both the range of geographic variation across the mixed Douglas-fir-hardwood forests of the KS Region and the seral continuum from young to

old-growth forest. We collected data and elucidate patterns across spatial scales from regional distributional relationships to individual animal microhabitat associations. We present the first quantitative comparative analysis of habitat selection by adult and larval *A. truei*.

STUDY AREA

The 70 large study stands in the KS Region used for the Old-Growth Forest Wildlife Habitat Research and Development Program were selected by botanists to represent the range of Douglas-fir-mixed hardwood vegetation types and their seral stages (Bingham and Sawyer 1991). The terrestrial wildlife sampling sites were a subset of 54 stands that were additionally constrained by logistical factors such as road access. These 54 stands were sampled for most vertebrate taxa, including the terrestrial herpetofauna (for specifics, see Welsh and Lind 1991). For the study of aquatic herpetofauna described in this paper, we located 39 second- or third-order perennial streams that were either within or adjacent to the available terrestrial wildlife sampling sites. We then determined a random starting point for placement of our sampling units within streams (see Methods). The streams were separated into 3 age classes based on the estimated stand age of adjacent upland forest (young = 30–99 years, mature = 100–200 years, and old-growth or late seral = >200 years). We selected 9 streams each in young and mature forest and 21 streams in late-seral forest. Actual forest ages (range 41–560 yr) were determined by taking the mean of 3 tree cores in the dominant size class of conifers (Douglas-fir) alongside each stream. We selected streams across a wide geographic area to represent the range of variation in small lotic systems in the KS Region (Fig. 1; see Welsh and Lind [1991:Table 9] for township and range coordinates).

METHODS

Animal and Environment Sampling

Corn and Bury (1989) found that a single 10-m long sample reach per stream was sufficient to detect the stream amphibian species of southwest Oregon. However, Welsh (1987) considered this approach insufficient to detect variability within streams in northern California and proposed instead using 3 5-m long reaches (see also Bury and Corn 1991). We sampled 3 5-m-long reaches in each of the 39 streams during July and August of 1984 and 1985. We placed the first reach by

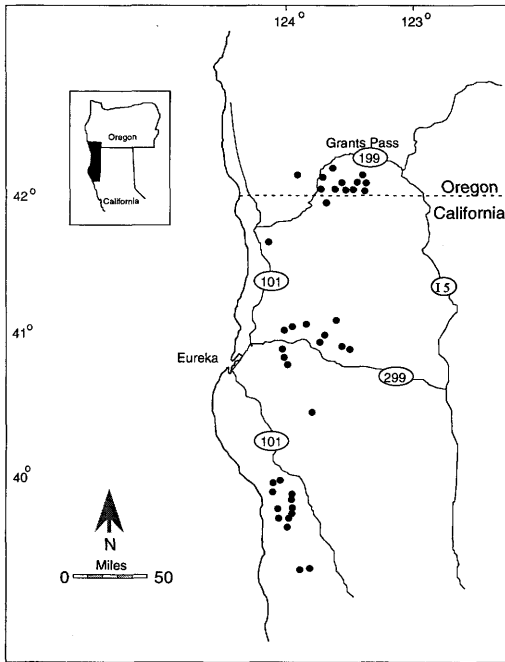


Fig. 1. Locations of 39 streams in southwestern Oregon and northwestern California, USA (the Klamath-Siskiyou Region), sampled during summers 1984 and 1985.

selecting a random starting point upstream of the nearest trail or road access and paced an additional 50 m upstream. The second and third sample reaches were located by pacing 105–110 m, and 160–165 m, respectively, from the original starting point, which provided a minimum of 50 m between reaches. We occasionally shifted reach placement slightly to avoid major obstructions such as large logs that prohibited sampling. Each reach was mapped to scale on graph paper for computation of relative amounts of available microenvironments (pool, riffle, etc.) and substrates (by size class), and to precisely map animal capture sites. Reaches for a given stream were mapped and sampled in a single day. We initially measured 58 landscape, macroenvironment-, and microenvironment-scale attributes associated with each reach and stream.

We sampled amphibians by searching all streambed substrates within each reach working systematically upstream, with hardware-cloth catch nets placed downstream, and from bank to bank to capture escaping animals (Welsh 1987). We used plexiglass viewing windows to see under water, and sifted or removed all mobile substrates within the reach. For each capture, we recorded

the sex, stage (*A. truei*: larva, metamorph, adult; *D. tenebrosus*: larva or paedomorph), snout-vent length (SVL), aquatic microhabitat (pool, riffle, seep, etc.), animal position (e.g., in, under, on), and associated rock particle size class (Platts et al. 1983). During 1984, the position of the animal determined whether the associated rock particle size class was cover or substrate (e.g., position = “under” indicated cover, position = “on” indicated substrate), and during 1985, substrate and cover were recorded as 2 separate variables.

We used the maps of each reach to calculate areas and derive percent estimates (percent substrate and cover) and amount by aquatic microenvironment category for each linear meter of stream. The following variables were estimated: aquatic microenvironment (pool, riffle, waterfall, seep); substrate; and cover (fines, detritus, gravel, pebble, cobble, boulder, bedrock). We did not assess variation in the size of subsurface substrates of our streams; thus, availability of substrate and cover were based on visual estimates of the surface layer.

Statistical Analyses

To evaluate our research hypothesis, we analyzed relationships between amphibian species and forest and stream environments using 3 statistical hypotheses to test for (1) differences in diversity, (2) patterns of presence or absence (incidence), and (3) relationships between environmental gradients and animal densities. We examined patterns of species diversity by individual stream (3 reaches combined) using the Shannon Diversity Index (SDI), a metric incorporating both richness and evenness (Magurran 1988). To test the statistical null hypothesis of “no variation in diversity relative to forest seral stage,” we regressed SDI values for the 39 streams against forest age. To test the same hypothesis for the 2 most common species, *A. truei* (life stages combined) and *D. tenebrosus* (larvae and paedomorphs combined), we used ANOVA followed by Tukey HSD tests to compare densities (captures/m²) among 3 forest age classes.

Only 2 species, *A. truei* and *D. tenebrosus*, were captured in sufficient numbers for a detailed analysis of habitat relationships. To test the statistical null hypothesis of “no relationship between *A. truei* and various environmental attributes,” we used 2 complementary multivariate methods that address the separate questions of what variables are associated with presence and absence (incidence) at a site, and what variables are associated with variation in density at occupied sites. Larval

and adult life stages were analyzed separately. We used stepwise 2-group discriminant analysis (DA; SAS Institute 1990) to detect patterns of association between *A. truei* presence and combinations of environmental variables (i.e., to find which variables added additional discriminatory power). We used all-possible-subsets regression analysis (APS; SAS Institute 1990) to examine differences in densities among occupied sites (i.e., where captures > 0), relative to the same independent variables. All-possible-subsets regression analysis allowed us to objectively select from our sets of related independent variables (Table 1) those that best tracked with changes in animal numbers, and were thus the best candidates for data-based habitat model building, and for generating meaningful new explanatory hypotheses. In the case of *D. tenebrosus*, which was present in all but 1 stream and all but 8 reaches, we used only APS and examined correlates to variation in densities (larvae and paedomorphs combined).

We conducted preliminary descriptive analyses to assess the normality of the distributions of all variables and eliminate redundant variables. Deviations were corrected by appropriate transformations (square root, arcsine, or natural log; Sokal and Rohlf 1981). We assumed that univariate normality implied multivariate normality but did not test multivariate normality directly. Variables with high numbers of zero values (>50%) were dropped or combined with other variables where appropriately additive (e.g., large and very large conifers). We used correlation analysis to eliminate highly intercorrelated pairs of variables (those with $r \geq 0.7$), retaining the 1 with the highest correlation with amphibian presence or density. This process resulted in 45 independent variables for multivariate analyses (Table 1). We arranged the 45 independent variables hierarchically, representing 3 spatial scales—landscape, macroenvironment or stand, and microenvironment (see Wiens 1989)—and then into ecological components (see Welsh and Lind 1995) representing logical classes of structural, compositional, or climatic attributes of the forest or stream environment (Table 1). Landscape variables were those characterizing broad expanses of the landscape surrounding each of the 39 streams (i.e., attributes at the scale of the drainage basin such as latitude and mean annual rainfall). Macroenvironment variables were those that described forest stand-level attributes adjacent to the streams and measured at each reach (e.g., densities of trees by type and size class). Microenviron-

ment variables were those that described conditions within each 5-m reach (e.g., proportion pool, riffle, run, aquatic substrates, and water velocity; Table 1), and fine-scale attributes associated with amphibian capture points within the reaches (see individual-based microhabitat associations analyses below).

We analyzed landscape-scale relationships at the stream level ($n = 39$) and relationships at the macroenvironment and microenvironment scales at the reach level ($n = 117$; compare with Townsend and Crowl 1991). For each species or life stage, we conducted separate analyses by ecological component to detect informative variables in each category (Table 1). We then combined these sets of variables in a second-stage analysis to derive composite habitat models by species or life stage, at both the landscape and combined macro- and microenvironment scales.

For stepwise model building in the DA, a variable was entered if the P -value for the partial F statistic was ≤ 0.10 . This moderate α -level reduces the chance of Type II errors and is more appropriate for detecting ecological trends (Toft 1991). For final model acceptance and subsequent testing, we set $\alpha \leq 0.05$. A linear discriminant function was then derived from those variables selected. We used Bartlett's modification of the likelihood ratio to test the homogeneity of variance-covariance matrices (SAS Institute 1990). We then tested the ability of our models to accurately predict whether a given site supported animals (i.e., the classification success) with a jackknife procedure (SAS Institute 1990). Cohen's kappa statistic (Titus et al. 1984) was computed for each of these tests to indicate classification success compared with chance. Here, we assumed our random representative site selection yielded a proportion of sites with or without the dependent variable that reflected true proportions. Therefore, we adjusted the prior probabilities of group membership accordingly (priors proportional; SAS Institute 1990).

For the APS, we report and discuss variables or models with the best adjusted R^2 (smallest mean square error) for each ecological component (Table 1), whether statistically significant ($P \leq 0.05$) or not, except in those instances where the best R^2 was near zero or negative. For those models where the adjusted R^2 continued to increase but the number of variables exceeded the sample size to variable ratio recommended by Johnson (1981), we used the lowest Mallows' C_p statistic (Neter et al. 1989) to determine the appropriate

Table 1. Hierarchical arrangement of ecological components represented by 45 measurements of the forest and stream environment taken in conjunction with amphibian sampling (see text). Separate discriminant (DA) and regression (APS) analyses were run for each ecological component with the resulting variables combined for composite habitat model building.

Scale	Ecological component	Variable
Landscape (stream level)	Geographic relationships	Latitude (degrees)
		Elevation (m)
		Stream slope (%)
		Aspect (degrees) ^a
		Rainfall (cm/year) ^b
Macroenvironment (reach level)	Climate	Solar index ^c
		Air temperature (°C)
		Small conifers_c
		Small hardwoods_c
		Medium conifers_c
	Forest structure ^d	Medium hardwoods_c
		Large and very large conifers_c
		Canopy closure (%) ^e
		Forest age (yr) ^f
		Understory conifers
	Shrubs and understory trees (%) ^g	Understory hardwoods
		Understory shrubs
		Herbs
	Ground-level vegetation (%) ^g	Grass
		Ferns
		Moss
		Other
		Pool ^g
Microenvironment (reach level)	Aquatic microenvironments (%)	Riffle ^g
		Waterfall ^h
		Seep ^h
		Gravel (2–32 mm)
		Pebble (32–64 mm)
	Aquatic substrates (%) ⁱ	Cobble (64–256 mm)
		Boulder (256+ mm)
		Boulder
	Overhanging cover (%) ^h	Log
		Bank
		Vegetation
		Bedrock
		Total
	Aquatic conditions	Water temperature (°C)
		Water velocity (m/sec)
		Mean depth (cm)
		Mean width (m)
		Mean bank slope (%)
	Species ^k	Stream canopy closure (%) ^j
		No. <i>D. tenebrosus</i>
		No. <i>A. truei</i> larvae
		No. <i>A. truei</i> adults

^a Aspect was measured in degrees and converted to 1 of 9 directions for analysis. In this scheme, 5 is equivalent to both due east and due west, numbers <5 are increasingly more northerly, and numbers >5 are increasingly more southerly.

^b Rainfall data were taken from National Oceanic and Atmospheric Administration weather stations. Streams were matched with the closest and most topographically similar station available; annual averages of the longest period available within the past 30 years were used (minimum = 4 yr, maximum = 30 yr).

^c Solar index is an estimate of annual incident solar radiation based on latitude, slope, and aspect (Frank and Lee 1966).

^d c = count variable (numbers per hectare); small trees = 1–9 cm diameter at breast height (dbh) and medium trees = 9–49 cm dbh were counted in a 1/20th-ha circle, large trees = 50–99 cm dbh and very large trees = >100 cm dbh were counted in a 1/5th-ha circle.

^e Visual estimate in 1/5th-ha circle.

^f Forest age is based on 1 tree core from the dominant size class of conifers adjacent to each stream reach.

^g Visual estimate of the percent of the sampling area: 1/20th-ha circle for vegetation, 5-m stream reach for aquatic microenvironments.

^h Measured and mapped area.

ⁱ Particle diameters are from Platts et al. (1983); visual estimate of percent of 5-m stream reach.

^j The average of 5 readings taken using a spherical densiometer for each 5-m stream reach.

^k Common sympatric species and/or life stages were included reciprocally as independent variables.

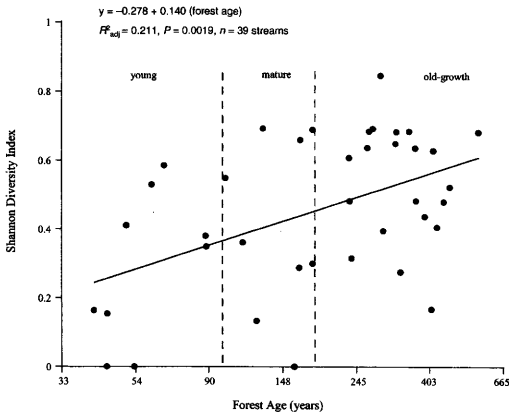


Fig. 2. Amphibian diversity (Shannon Diversity Index) of the stream amphibian assemblage relative to forest age in the Douglas-fir-hardwood forests of the Klamath-Siskiyou Region. Data and regression equation reflect natural log transformation of forest age; X-axis was back-transformed to show actual forest age.

model to report. This approach prevented the incorporation of additional variables that did not add substantially to explanatory power. For the composite habitat models, we started with the set of variables from the best ecological component models, regardless of significance; however, for model acceptance, we set $\alpha \leq 0.05$.

Last, we examined the finest-scale environmental relationships of individual *A. truei* and *D. tenebrosus* using 2 approaches: tests of association (chi-square contingency) and use-versus-availability analyses (e.g., Johnson 1980; paired *t*-tests). These analyses are hereafter referred to as individual-focused microhabitat associations and use-versus-availability analyses, respectively, and they test the statistical null hypothesis of "no differences in animal use of microenvironments." Significance levels for these analyses were set at $\alpha \leq 0.05$, and they were adjusted for multiple tests in each category using a Bonferroni adjustment (Stevens 1986).

For tests of association, we were interested in whether a given species or life stage was associated with particular aquatic microenvironment types (e.g., pool, riffle, run, etc.), substrates, or cover types relative to other species or life stages. Here, the individual animal was the unit of analysis and the aquatic microenvironment type, substrate, or cover with which it was immediately associated at capture were the descriptors. This analysis did not involve assessment of availability as did the use-versus-availability analysis

described below. Rather, it was meant to compare the use of different habitat components among the species and their size classes or life stages. We conducted chi-square (χ^2) contingency table analyses using all captures of 3 life stages of *A. truei* and 3 size classes of *D. tenebrosus*. Some substrate and cover categories were combined where appropriate to eliminate small sample sizes per cell (i.e., the composite categories comprised fines-detritus, gravel-pebble, cobble-boulder, and bedrock). Expected values were calculated using row and column totals of the contingency table (Sokal and Rohlf 1981). For each contingency table, the 3 cells with the highest χ^2 are reported regardless of significance.

For the use-versus-availability analyses, our objective was to determine whether life stages of *A. truei* or size classes of *D. tenebrosus* demonstrated habitat preferences (i.e., used a particular microhabitat type more or less frequently than its availability). Use was defined as the percent of captures of a given life stage or size class found in each aquatic microenvironment, substrate, or cover category and was calculated for each reach. Availability was derived from both measured and estimated values for each microhabitat, substrate, or cover category based on the detailed reach maps described above. We used paired *t*-tests to compare frequency of use relative to amount available in each microenvironment category by life stage or size class. The pairing here was done to link the used and available habitat information for each reach. The 5-m reach was the unit of analysis, and only those reaches where a given life stage or size class occurred were used in a particular test.

For both analyses, we placed *A. truei* into 3 life stages: larvae were those individuals from hatching through the development of 2 rear legs and front leg buds ($n = 308$); metamorphs had all 4 legs and were in the process of absorbing their tails ($n = 42$); and adults were fully developed frogs ($n = 113$). *A. truei* primarily is a nocturnal forager on streambed periphyton (larvae) or riparian invertebrates (adults) so our analyses here are characterizing streambed diurnal retreat habitat use or preference. Twenty-four captures were omitted because data on life stage were missing. We placed *D. tenebrosus* into 3 size classes: small = <45 mm SVL ($n = 414$), medium = 46–70 mm SVL ($n = 291$), and large = >70 mm SVL ($n = 83$). We omitted 82 records from these analyses because SVL was not available (i.e., escapes). The size classes, which ostensibly represent year classes (young of

Table 2. Two-group (presence-absence) stepwise discriminant analyses of environmental parameters associated with *Ascaphus truei*^a. Variables were grouped for separate analyses by ecological component (Table 1) with best models shown here. Variables are listed in the order in which they entered each model. Models with heterogeneous variance-covariance matrices are indicated by * on the first variable in the model.

Scale	Ecological component	Larvae ^a					Adult ^a			
		Sites with		Sites without			Sites with		Sites without	
		$\bar{x}$	SD	$\bar{x}$	SD		$\bar{x}$	SD	$\bar{x}$	SD
Landscape (streams)	Geographic relationships									
	*Elevation (m)	1014.4	362.8	479.2	177.1	*Elevation (m)	1091.7	372.3	541.8	214.1
	Aspect (degrees)	5.9	1.7	5.4	1.5	Aspect (degrees)	6.0	1.9	5.5	1.4
	Climate									
	Air temperature (°C)	17.7	3.4	21.7	2.7	Air temperature (°C)	17.8	4.3	20.8	3.2
Macroenvironment (reaches)	Forest structure									
	Forest age (yr)	303.4	164.0	180.6	146.7	*Large and very large conifers (stems/ha)	55.0	25.2	34.4	25.6
	Medium hardwoods (stems/ha)	123.6	161.6	217.9	151.4	Small hardwoods (stems/ha)	145.2	285.8	387.7	449.1
	Small conifers (stems/ha)	108.8	147.7	127.4	142.2	Medium hardwoods (stems/ha)	69.4	95.8	229.6	162.1
	Small hardwoods (stems/ha)	223.8	305.0	372.5	477.9					
	Shrub and understory trees (% cover)									
	*Understory hardwoods	14.7	16.2	19.0	12.2	*Understory hardwoods	10.5	16.2	20.3	11.9
	Ground-level vegetation (% cover)									
	Herbs	22.8	19.9	14.6	15.6	Herbs	27.6	19.7	13.5	15.1
Microenvironment	Aquatic microenvironments (% of reach)									
	Riffle	62.1	17.2	49.3	18.9	Riffle	64.9	16.0	49.9	18.8
	Waterfall	2.1	2.2	1.5	2.6					
	Aquatic substrates (% of reach)					No model				
	Cobble	29.9	11.9	26.1	12.3					
	Overhanging cover	No model				No model				
	Aquatic conditions									
	Water temperature (°C)	11.4	2.1	14.0	2.0	Water temperature (°C)	10.9	2.3	13.7	1.9
	Mean depth (cm)	14.7	6.0	13.7	4.3	Water velocity (m/sec)	29.5	14.6	17.1	10.5
	Water velocity (m/sec)	26.4	14.4	16.2	9.7	No. <i>D. tenebrosus</i>	1.2	1.1	0.8	0.6

^a Thirty-nine streams and 117 reaches were sampled; larvae occurred in 21 streams and 50 reaches, and adults occurred in 16 streams and 38 reaches.

the current year, second year, third year, and older), were based on Parker (1991), who studied *D. tenebrosus* in 1 of our sample streams. We also omitted observations if data were missing for a given microenvironment variable, which resulted in different sample sizes for our analyses of aquatic microenvironments, cover, and substrate.

RESULTS

Amphibian Diversity

We captured 1,400 individuals of 7 species in 39 streams. Amphibian diversity (SDI) was greater in streams traversing stands with greater forest age; 21% of the variance was explained by this single

variable (Fig. 2). Five of the 7 species occurred in relatively low numbers (0.1–1.5% of total observations). We found 2 California slender salamanders (*Batrachoseps attenuatus*), 6 black salamanders (*Aneides flavipunctatus*), 11 southern torrent salamanders (*Rhyacotriton variegatus*), 23 adult foothill yellow-legged frogs (*Rana boylei*), and 3 rough-skinned newts (*Taricha granulosa*). The 2 remaining species constituted 96.9% of all captures. Tailed frogs (*Ascaphus truei*; larvae and adults, $n = 487$) were present in 21 of 39 streams. We found *A. truei* larvae in 21 streams and 50 of 117 reaches, and adult frogs in 16 streams and 38 of 117 reaches. Pacific giant salamanders (*Dicamptodon tenebrosus*; larvae and pedomorphs,

Table 3. Classification (jackknife procedure) results for 2-group (presence-absence) discriminant analyses of environmental parameters associated with *Ascaphus truei*. Variables were grouped by ecological component (Table 1) with best models shown here. Except where indicated (*) all classification results were significant at $P = 0.05$ or less based on Cohen's kappa statistic (Titus et al. 1984).

Model	n	Larvae classification ^a					Adults classification ^a				
		Present/	Present/	Absent/	Absent/	%	Present/	Present/	Absent/	Absent/	%
		present	absent	absent	present	Correct	present	absent	absent	present	Correct
Geographic relationships	39	16	5	17	1	84.6	13	3	21	2	87.2
Climate	39	15	6	13	5	71.8	8	8	18	5	66.7
Landscape composite	Same as geographic relationships model						Same as geographic relationships model				
Forest structure	117	29	21	54	13	70.9	23	15	69	10	78.6
Shrub and understory trees	117	20	30	59	8	67.5	22	16	76	3	83.8
Ground-level vegetation	117	17	33	54	13	60.7*	11	27	70	9	69.3
Aquatic microenvironments	117	27	23	49	18	64.9	13	25	72	7	72.6
Aquatic substrates	117	11	39	56	11	57.3*	No model				
Overhanging cover	No model						No model				
Aquatic conditions	84	20	14	43	7	75.0	13	9	59	3	85.7
Macro-microhabitat composite model	84	22	12	44	6	78.6	17	5	59	3	90.5

^a Present/present = present, predicted as present; present/absent = present, predicted as absent; absent/absent = absent, predicted as absent; absent/present = absent, predicted as present.

$n = 870$) were present in all but a single stream, and in 109 of 117 reaches.

Relationships of *Ascaphus truei* with the Forest and Stream Environment

A. truei were found more often in streams in late seral forest (81%) compared with streams in mature (56%) or young forests (11%; previously reported in Welsh [1990]). *A. truei* densities (life stages combined) were significantly different among forest age classes (ANOVA: $df = 2, 36$; $F = 3.27$; $P = 0.0495$). Pairwise tests showed that *A.*

truei were more abundant in streams in late seral ($0.58 \pm 0.81/m^2$) versus young forests ($0.02 \pm 0.06/m^2$; mean ± 1 standard deviation).

Landscape Scale Relationships of Ascaphus truei.—The best geographic relationships model for indicating *A. truei* incidence (DA model) consisted of the variables “elevation” (higher for streams supporting *A. truei*) and “aspect” (more southerly for streams with *A. truei*; DA: larvae $df = 2, 36$; $F = 3.27$; $P = 0.0001$; adult $df = 2, 36$; $F = 19.57$; $P = 0.0001$; Tables 2 and 3). The best climate DA model indicated that “air temperature” was lower along streams with *A. truei* (DA: larvae $df = 2, 36$; $F = 13.27$; $P = 0.0009$; adult $df = 2, 36$; $F = 6.20$; $P = 0.0174$; Tables 2 and 3). Air temperatures alongside streams co-varied negatively with elevation ($r = -0.482$, $P = 0.0019$), which we suspect explains why temperature failed to contribute significantly to the landscape-scale composite DA model (Fig. 3A; larvae $df = 2, 36$; $F = 3.27$; $P = 0.0001$). These landscape-scale DA models were, predictably, identical for indicating the incidence of the 2 life stages of the tailed frog (Fig. 3A and 3B; adult $df = 2, 36$; $F = 19.57$; $P = 0.0001$; Table 3). We did find differences between life stages in our analyses of density (APS models) at the landscape scale. *A. truei* larvae were more abundant in higher elevation streams, and their numbers varied negatively with increasing solar index values and air temperatures (Table 4). Numbers of adult *A. truei*, however, varied positively with higher rainfall and negatively with

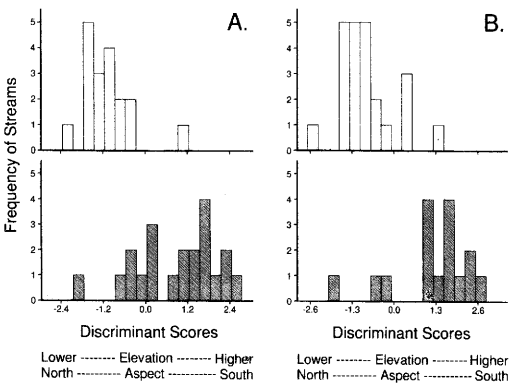


Fig. 3. Variation in the incidence (presence = filled bars; absence = open bars) of tailed frogs in streams of the Klamath-Siskiyou Region relative to the best landscape scale composite habitat model as determined by 2-group discriminant analyses. (A) Larvae. (B) Adults. Both models had heterogeneous variance-covariance matrices.

Table 4. All-possible-subsets regressions relating ecological components (Table 1) to numbers of *Ascaphus truei* and *Dicamptodon tenebrosus*, using sites with captures only. The best models (based on highest adjusted R^2) are shown. Separate analyses were conducted on each ecological component; variables entering each model were used to derive a final composite model. Variables are presented in order of relative importance in each model. Standardized coefficients are given in parentheses following the covariates (sign indicates relationship with amphibian species or life stage numbers).

Scale	Ecological component	Larval <i>A. truei</i>					Adult <i>A. truei</i>					<i>D. tenebrosus</i>				
		R^2 (adj.)	F	P	SE	Covariate	R^2 (adj.)	F	P	SE	Covariate	R^2 (adj.)	F	P	SE	Covariate
Landscape (stream)	Geographic relationships	0.274	8.55	0.0087	0.28	Elevation (0.557)	0.187	4.45	0.053	0.21	Aspect (−0.491)	0.095	2.95	0.0655	0.29	Latitude (−0.280) Stream slope (0.266)
	Climate	0.327	5.87	0.0109	0.27	Solar index (−0.516) Air temp. (−0.403)	0.203	2.91	0.091	0.21	Solar index (−0.399) Rainfall (0.381)					None
	Composite model	0.359	4.73	0.0141	0.26	Solar index (−0.344) Air temp. (−0.329) Elevation (0.305)	0.344	4.93	0.025	0.19	Aspect (−0.534) Rainfall (0.438)					None
Macrohabitat (reach)	Forest structure	0.162	3.36	0.0172	0.35	Medium conifers (−0.355) Medium hard-woods (−0.265) Small hard-woods (−0.206) Forest age (−0.152)	0.291	4.79	0.0037	0.20	Small hard-woods (−0.514) Small conifers (−0.344) Medium hard-woods (−0.181) Lg.-very lg. conifers (0.149)	0.021	3.28	0.0721	0.33	Medium conifers (0.172)
	Shrub and under-story trees	0.007	1.36	0.2489	0.38	Understory shrubs (−0.166)	0.057	3.26	0.079	0.23	Understory hard-woods (−0.288)	0.031	4.45	0.0372	0.33	Understory hard-woods (−0.199)
	Ground-level vegetation	0.132	8.44	0.0055	0.35	Herbs (0.387)	0.171	8.61	0.006	0.22	Herbs (0.439)	0.048	6.43	0.0127	0.33	Grass cover (−0.238)
	Aquatic microhabitat	0.077	5.11	0.0284	0.36	Riffle (0.310)	0.208	10.72	0.002	0.21	Pool (0.479)	0.011	6.77	0.0106	0.33	Pool (0.244)
Microhabitat (reach)	Aquatic substrates	0.040	3.05	0.0870	0.37	Boulder (−0.245)	0.496	19.22	0.0001	0.17	Bedrock (0.679) Boulder (0.168)	0.103	7.22	0.0011	0.32	Bedrock (0.280) Pebble (0.267)
	Overhanging cover	None					0.143	3.06	0.0411	0.22	Vegetation cover (−0.259) Bank cover (−0.228) Log cover (0.227)	0.011	1.41	0.2434	0.33	Boulder overhang (−0.179) Veg. overhang (−0.280) Total overhang (0.248)
	Aquatic conditions	0.336	6.57	0.0015	0.30	No. <i>Ascaphus</i> adults (0.488) Water velocity (0.398) Avg. bank slope (0.303)	0.456	8.76	0.0001	0.18	No. <i>Dicamptodon</i> (0.497) No. <i>Ascaphus</i> larvae (0.351) Mean stream depth (−0.283) Avg. bank slope (−0.164)	0.301	10.30	0.0001	0.28	No. <i>Ascaphus</i> adults (0.448) No. <i>Ascaphus</i> larvae (−0.327) Avg. stream width (−0.287) Overstream canopy (0.164) Avg. bank slope (0.108)

(continued on next page)

Table 4. continued.

Scale	Ecological component	Larval <i>A. truei</i>					Adult <i>A. truei</i>					<i>D. tenebrosus</i>				
		R^2 (adj.)	F	P	SE	Covariate	R^2 (adj.)	F	P	SE	Covariate	R^2 (adj.)	F	P	SE	Covariate
Micro-macrohabitat composite model		0.488	6.24	0.0003	0.27	No. <i>Ascaphus</i> adults (0.448)	0.688	21.36	0.0001	0.13	Ground-level herb (0.407)	0.396	8.872	0.001	0.26	No. <i>Ascaphus</i> adults (0.457)
						Total overhang (−0.399)					Bedrock (0.381)					Avg. stream width (−0.246)
						Water velocity (0.265)					No. <i>Dicamptodon</i> (0.315)					No. <i>Ascaphus</i> larvae (−0.232)
						Avg. bank slope (0.238)					Veg. overhang (−0.292)					Grass cover (−0.208)
						Understory shrubs (−0.198)										Pebble (0.198)
						Boulder (−0.197)										Pool (0.188)
																Overstream canopy (0.139)
																Avg. bank slope (0.111)
																Boulder overhang (−0.099)

increasingly southern aspect. Consequently, the landscape-scale composite APS habitat models for the 2 life stages had no variables in common (Table 4). The best landscape-scale composite habitat model for larval density combined variables from the geographic relationships and climate models, and explained 36% of their variation (Table 4). In the best landscape-scale composite habitat model for adult *A. truei* density, the variable “solar” was replaced by the highly correlated variable “aspect,” with the resulting model accounting for 34% of variation in adult numbers (Table 4).

Macroenvironment Scale Relationships of Ascaphus truei.—At this spatial scale, the negative relationships with the incidence of both life stages of *A. truei* and small and medium-size trees, and the positive relationship with either forest age or large and very large conifers (both indicative of late-seral conditions, and significantly correlated [$r = 0.411$, $P = 0.0001$]) indicated a significant relationship between *Ascaphus* incidence and older forests (DA: larvae $df = 4$, 112; $F = 10.06$; $P = 0.0001$; adult $df = 3$, 113; $F = 15.93$; $P = 0.0001$; Tables 2 and 3). The lower percent cover of understory hardwoods (DA: larvae $df = 1$, 115; $F = 6.66$; $P = 0.0001$; adult $df = 1$, 115; $F = 31.43$; $P = 0.0001$; Tables 2 and 3) and a higher herb component (DA: larvae $df = 1$, 115; $F = 6.66$; $P = 0.0001$; adult $df = 1$, 115; $F = 31.43$; $P = 0.0001$; Tables 2 and 3) at sites with *Ascaphus* present also were consistent with conditions found in moister late-seral forests (Bingham and Sawyer 1991). The macrohabitat-scale models of *Ascaphus* density (APS) differed in minor details from the incidence (DA) models (compare Tables 2 and 4; macroenvironment scale), but the APS models indicated that the 2 life stages were more abundant in late-seral forests (Table 4).

Microenvironment Scale Relationships of Ascaphus truei.—We detected the greatest differences in habitat associations between the life stages of *Ascaphus* at the microenvironment scale. Riffle habitat constituted a greater proportion of stream reaches at sites with both life stages present compared with reaches without *A. truei*, but reaches with larval incidence also were characterized by a greater proportion of waterfall habitat (DA: larvae $df = 2$, 114; $F = 9.13$; $P = 0.0002$; adult $df = 1$, 115; $F = 18.01$; $P = 0.0001$; Tables 2 and 3). Densities of larval, but not adult, *A. truei* also were positively associated with the amount of riffle (Table 4). Reaches with larval incidence also contained greater amounts of cobble-sized substrates

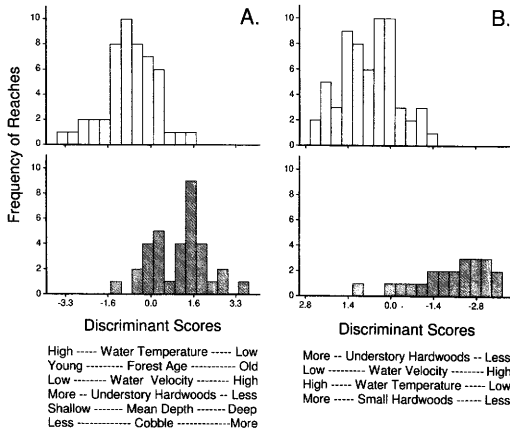


Fig. 4. Variation in the incidence (presence = filled bars; absence = open bars) of tailed frogs in stream reaches of the Klamath-Siskiyou Region relative to best macro-microenvironment scale composite habitat model as determined by 2-group discriminant analyses. (A) Larvae. (B) Adults. Both models had heterogeneous variance-covariance matrices.

(DA: $df = 1, 115$; $F = 2.82$; $P = 0.096$; Tables 2 and 3), while substrate variables were not good indicators of adult presence (Tables 2 and 3). Overhanging cover was a poor indicator of the incidence of either life stage (Table 2), but the density of larval *A. truei* was negatively associated with the total amount of overhanging cover (Table 4). While the presence of both life stages was related to lower water temperatures and higher water velocities, those reaches with larvae present also had greater water depth (DA: larvae $df = 3, 80$; $F = 14.2$; $P = 0.0001$; Tables 2 and 3), whereas the incidence of adult frogs was associated with the presence of *D. tenebrosus* (DA: adult $df = 3, 80$; $F = 14.18$; $P < 0.0001$; Tables 2 and 3). Larval densities (APS) varied positively with water velocity, average bank slope, and the number of adult frogs; this model alone explained almost 34% of the variation in numbers of larvae (Table 4). Adult frog densities at this scale varied positively with percent pools, percent bedrock, and log cover, and negatively with percent boulder, vegetation cover, and bank cover (Table 4). Adult *A. truei* density was also positively related to *D. tenebrosus* and larval *A. truei* density. Adult *A. truei* density was negatively related to stream depth and bank slope. The aquatic conditions model explained over 45% of the variation in adult frog density (Table 4).

Macro-microenvironment Scale Composite Habitat Models for *Ascapus truei*.—The composite

macro-microhabitat model for incidence of larval *A. truei* contained 2 macroenvironment variables depicting late seral forest and 4 microenvironment variables describing cold, fast-flowing water on cobble (DA: $df = 6, 77$; $F = 11.13$; $P < 0.0001$; Fig. 4A). The composite habitat model for sites with adult *A. truei* incidence also consisted of 2 macroenvironment variables indicative of older, moister mixed forest, but had only 2 microenvironment variables, describing cold, fast-flowing stream habitats (DA: $df = 4, 112$; $F = 28.80$; $P < 0.0001$; Fig. 4B). Water temperature and water velocity occurred in the composite habitat models of both life stages (Fig. 4A,B). Overall, our DA models at the macro- and microenvironment scales predicted absence more accurately than presence (Table 3). In all of these models, errors of omission (predicting absence when in fact *A. truei* was present) were more prevalent than commission errors (predicting presence when in fact *A. truei* were absent). This is especially evident in the adult frog models (Table 3).

The best composite habitat model for *A. truei* larval density (APS) at the combined macroenvironment and microenvironment scales explained 48.8% of their variation (Table 4). This model consisted of 3 negative relationships: overhanging cover, understory shrubs, and percent boulder; and 3 positive relationships: numbers of adult frogs (the best indicator of larval density), water velocity, and average bank slope (Table 4). The best composite APS habitat model for adult frogs explained 68.8% of their variation (Table 4). This model consisted of 3 positive relationships: ground-level herb cover (the best indicator of adult density), percent bedrock, and numbers of *D. tenebrosus* larvae; and 1 negative relationship: percent overhanging vegetation cover (Table 4).

Relationships of *Dicamptodon tenebrosus* with Forest and Stream Environments

Dicamptodon tenebrosus showed no relationship to forest age (ANOVA: $df = 2, 36$; $F = 1.17$; $P = 0.3233$), with densities of $0.76 (\pm 0.53)/m^2$ in young, $0.60 (\pm 0.57)/m^2$ in mature, and $0.93 (\pm 0.68)/m^2$ in old-growth forests.

Multiscale Analysis of Density of *Dicamptodon tenebrosus*.—At the landscape scale, we found no significant indicators (single variables or models) for differences in *D. tenebrosus* density (Table 4). The best composite habitat model at this scale consisted of the geographic relationships vari-

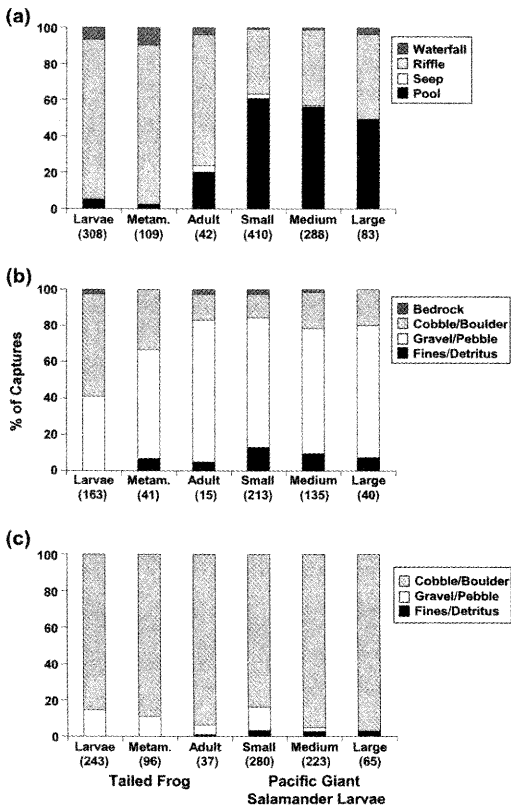


Fig. 5. Microhabitat associations of 3 age classes of tailed frogs (larva, metamorph, adult) and 3 size classes of Pacific giant salamanders for (a) stream habitat, (b) substrate, and (c) cover. Missing data resulted in different sample sizes (in parentheses) for analyses of aquatic microenvironments, cover, and substrate.

ables, latitude and slope, which was not a significant model (Table 4). At the macroenvironment scale, *D. tenebrosus* densities varied negatively with cover of understory hardwoods and grass, and positively, but nonsignificantly, with density of medium conifers (Table 4). Both understory hardwoods and grass cover are indicative of ground disturbance or natural openings, suggesting a possible avoidance of such areas by *D. tenebrosus*. The macroenvironment scale models had relatively low adjusted R^2 (Table 4), suggesting weak biotic relationships.

At the microenvironment scale, *D. tenebrosus* was more abundant in reaches with greater percentages of pool habitat and in areas with bedrock and pebble substrates (Table 4). The variables for cover failed to generate a statistically significant model (Table 4). The aquatic conditions component yielded the best model for *D. tenebrosus*, indi-

cating a positive relationship with density of adult *A. truei*, over-stream canopy, and average bank slope, and a negative relationship between density of larval *A. truei*, and average stream width. This model explained 30.1% of the variation in giant salamander density (Table 4).

The best macro-microenvironment scale composite APS habitat model for *D. tenebrosus*, consisting of 1 macroenvironment variable and 8 microenvironment variables, explained 39.6% of the variation in density of giant salamanders in our reaches (Table 4). This model indicated that reaches with relatively narrow, shady channels, with medium-coarse substrate, slow water, and pools, at less disturbed forest sites, contained the highest larval salamander densities.

Individual-focused Microhabitat Associations and Use versus Availability

These finer resolution analyses demonstrated that *A. truei* larvae and adults and *D. tenebrosus* larvae were associated with different microenvironmental conditions within streams. Both species, and life stage within species, were significantly associated with particular aquatic microenvironment types, substrates, and covers, and body size appeared to be an important factor in determining cover use (Fig. 5). For aquatic microenvironment types, small salamanders occurred more than expected in pools and *A. truei* larvae occurred less than expected in pools, and more than expected in riffles, relative to the other species or life stages ($\chi^2 = 342.5$, $P < 0.0001$; see Fig. 5 for effect sizes). For substrates, small salamanders occurred less than expected on cobble-boulder and *A. truei* larvae occurred more than expected on cobble-boulder, and less than expected on fines-detritus, relative to other species or life stages ($\chi^2 = 113.2$, $P < 0.0001$; see Fig. 5 for effect sizes). Medium and large salamanders occurred less than expected under gravel-pebble and *A. truei* larvae occurred more than expected under this substrate type relative to other species or life stages ($\chi^2 = 43.5$, $P < 0.0001$; see Fig. 5 for effect sizes).

Examining habitat use relative to availability for each species or life stage revealed patterns that were consistent with the χ^2 analysis of microenvironmental associations, but that also provided evidence of active microsite selection by these amphibians (Johnson 1980). Among aquatic microenvironments, *A. truei* larvae and metamorphs used riffles to a greater degree than they were available, and pools to a lesser degree than

Table 5. Microhabitat use relative to environmental parameter availability for 2 species and 3 life stages of stream amphibians (*Ascaphus truei* and *Dicamptodon tenebrosus*) in northwestern California and southwestern Oregon, USA. Data are from area-constrained sampling of 5 linear meters of stream in 1984 and 1985. Sample size (*n*) is the number of reaches each species–life stage occurred in for which there were complete data. Statistical significance (paired *t*-tests) is shown as: used greater than available (>), used less than available (<), or not significant (—). Significance levels are adjusted for multiple tests in each group (microenvironment $\alpha = 0.0125$, substrate $\alpha = 0.0071$, cover $\alpha = 0.0083$). Effect size for significant tests are represented as the absolute value of the mean difference between use and availability percent values; associated standard deviations are presented.

Species–size class	Aquatic microenvironment ^a					Substrate ^b							Cover ^c							
	<i>n</i>	Pool	Riff	Watl	Seep	<i>n</i>	Fine	Detr	Grav	Pebb	Cobb	Bold	Bedrk	<i>n</i>	Fine	Detr	Grav	Pebb	Cobb	Bold
<i>A. truei</i> larvae	43	<	>	—	<	35	—	—	—	>	—	<	—	40	—	—	<	—	>	<
Mean difference		27.4	26.1		2.6					20.9		16.5					17.8		32.2	13.2
SD		22.8	25.9		5.9					38.9		24.7					14.5		32.2	23.8
<i>A. truei</i> metamorphs	23	<	>	—	—	11	—	—	—	—	—	—	—	21	—	—	<	—	>	—
Mean difference		29.6	19.7														14.3		36.5	
SD		18.2	32.9														13.7		44.1	
<i>A. truei</i> adults	37	—	—	—	—	23	—	—	—	—	<	—	—	35	—	—	<	<	>	—
Mean difference											18.0						18.0	10.2	30.2	
SD											20.0						16.0	18.9	39.9	
<i>D. tenebrosus</i> <45 mm SVL ^d	90	>	<	—	—	71	—	>	>	—	<	<	—	87	—	—	<	—	>	—
Mean difference		16.4	15.5					7.7	30.6		13.1	28.3					16.0		20.0	
SD		32.1	31.7					23.4	37.6		31.3	20.3					13.7		37.5	
<i>D. tenebrosus</i> 45–70 mm SVL	85	>	<	<	<	57	—	—	>	—	—	<	—	81	—	—	<	<	—	>
Mean difference		17.7	14.2	1.2	1.9				24.0			26.0					17.0	14.4		25.6
SD		32.8	33.2	3.4	5.0				45.4			24.6					14.3	15.6		38.6
<i>D. tenebrosus</i> >70 mm SVL	46	—	—	—	<	26	—	—	>	—	<	<	<	37	—	—	<	<	<	>
Mean difference					3.8				35.1		18.0	21.6	5.3				17.4	14.8	17.0	51.7
SD					7.7				48.3		30.9	32.4	9.1				12.9	10.5	32.2	41.5

^a Abbreviations: Riff = riffle; Watl = waterfall.
^b Abbreviations: Fine = fines; Detr = detritus; Grav = gravel (2–32 mm); Pebb = pebble (32–64 mm); Cobb = cobble (64–256 mm); Bold = boulder (256+ mm); Bedrk = bedrock.
^c Abbreviations: Fine = fines; Detr = detritus; Grav = gravel (2–32 mm); Pebb = pebble (32–64 mm); Cobb = cobble (64–256 mm); Bold = boulder (256+ mm).
^d SVL = snout-vent length.

they were available. Small and medium-sized salamanders demonstrated the opposite pattern (Table 5). In general, smaller life stages or size classes were found on smaller substrates to a greater degree, and on larger substrates to a lesser degree, than they were available (Table 5). Cover use appeared to be related to size as well, with all life stages of *A. truei* using cobble cover to a greater degree than available, and using gravel and pebble cover to a lesser degree than available. Medium and large Pacific giant salamanders used boulders for cover to a greater degree than available (Table 5).

DISCUSSION

Although we detected as many as 7 species in our streams (see Bury and Pearl 1999 for a list of possible species), we found the amphibian assemblage of second- and third-order streams of the mixed conifer–hardwood forests of the KS

Region to be dominated by 2 species, *Dicamptodon tenebrosus* and *Ascaphus truei*. The other 5 species detected were far less common, and appeared to be peripheral members of the second- to third-order stream assemblage. Higher abundances of several of these species do occur along different portions of the stream continuum such as in headwaters (i.e., *Rhyacotriton variegatus* [Welsh and Lind 1996]), or further downstream where both channel gradient and over-stream canopy decrease, creating more open areas with slack water habitats (i.e., *Rana boylei*, *Taricha granulosa*; Nussbaum et al. 1983, Jennings and Hayes 1988). Other species, while part of the upland plethodontid salamander assemblage of this region (Welsh and Lind 1991), were represented along stream margins by the juvenile life stage only. Patterns of species diversity in temperate vertebrate assemblages often show 1 or 2 common species with high numbers of individuals and additional

Tailed Frog Density Relative to Forest Age and Water Temperature

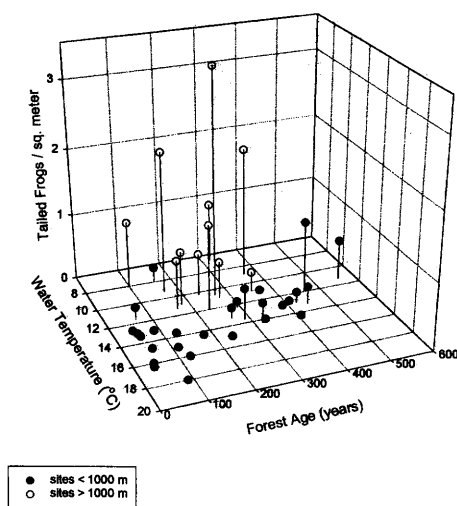


Fig. 6. Stream temperature, forest age, tailed frog abundance (both life stages combined), and elevation (< or > 1,000 m). These data were first reported in 2 separate figures in Welsh (1990).

species present in lower abundances (Brown 1995).

The 2 abundant species in our study, *D. tenebrosus* and *A. truei*, dominate the stream amphibian assemblage throughout the U.S. Pacific Northwest (e.g., Hawkins et al. 1983, Corn and Bury 1989, Bury et al. 1991, Welsh and Lind 1991, Bury and Pearl 1999). With the exception of some differences at the northern and southern extremes, these 2 species share essentially the same geographic ranges and similar biogeographic histories (Savage 1960). However, we found pronounced differences in the incidence, density, and ecological associations of *A. truei* and *D. tenebrosus* at different spatial scales within the KS Region. *D. tenebrosus* occurred in nearly all streams, whereas *A. truei* were present in only 54% of streams sampled. Also, while our ability to detect differences in the incidence and density of *A. truei* at the landscape and macroenvironment scales was highly successful, our ability to detect differences in the density of *D. tenebrosus* at these coarser scales was limited. Thus, while their overall ranges may have been influenced in evolutionary time by similar geoclimatic processes, within their similar ranges, and in ecological time, these 2 species have responded quite differently (compare to Blondel 1987).

While our approach to understanding the multiscale habitat relationships of *A. truei* and *D. tenebrosus* was primarily descriptive, our analyses demonstrated that distinct distribution patterns were present and detectable and that a substantial amount of variation in incidence and density (34–69%) could be explained by habitat variables, though our predictions of absence were more accurate than our predictions of presence (Table 3). This result is noteworthy since theory suggests, and previous research has demonstrated, that habitat is only 1 of many factors (e.g., resource availability, historical biogeography, interactions with other species, demographic stochasticities) that can influence species incidence and abundance (Van Horne 1983, 1986; Toft 1985; O'Neil and Carey 1986; Morrison 2001). In addition, our in-stream exploratory work, as well as concurrent efforts in adjacent terrestrial environments (Welsh and Lind 1991), laid the groundwork for several more detailed studies of late-seral forest-associated species, studies that have further tested hypotheses about incidence and abundance relative to forest succession and its associated attributes (Welsh 1993; Welsh and Lind 1995, 1996). Much of the discussion that follows should be considered as a set of new working hypotheses, the pursuit of which could further refine our knowledge of the habitat relationships of these 2 species.

Landscape and Macroenvironment Relationships

At both the landscape and macroenvironment scales, the habitat associations of adult and larval *A. truei* were nearly identical. Where the coarse-scale habitat models differed by life stage, the variables that replaced one another were highly correlated, and often, depending on the attributes in question, appeared to be surrogates representing different ways to measure essentially the same environmental parameter (e.g., aspect and solar index). The key difference between landscape scale models for the 2 life stages of *A. truei* was the addition of rainfall (cm/yr) for the mostly terrestrial adult frogs. Higher annual rainfall, a good indicator of moister sites, also is a good predictor of forest that can better support adult *A. truei*, which require high environmental moisture to frequent terrestrial microenvironments (Claussen 1973a,b). Given that *A. truei* larvae are strictly aquatic, the negative association with air temperature probably reflects the close correspondence between air and stream temperature (Mitchell 1999).

Several recent studies have purported to demonstrate a relationship between *A. truei* incidence or abundance and harder (more consolidated) parent geology (Diller and Wallace 1999, Wilkins and Peterson 2000). One possibility is that the strong positive relationship we found between *A. truei* incidence and density and elevation is the geographic expression of the prevalence of harder parent geology with altitude in the KS Region. However, we have found *A. truei* to be common in streams in unconsolidated geologies at both high and low elevation sites in the KS Region (this study; see also Adams and Bury 2002). We do not doubt that parent geology can have an influence, particularly at the microenvironment scale where unconsolidated materials can act to fill streambed interstices (Welsh and Ollivier 1998), but we believe this is a scale-dependent phenomenon linked to the landscape-level disturbance regime interacting with the parent geology, having nothing to do with elevation per se (see discussion of geology below). These factors probably could be sorted out with a meta-analysis of data sets from across the range of *A. truei* that included some measure of in-stream and upslope disturbance regimes along with information on parent geology and local stream substrate conditions. There is a much more compelling explanation for increases in *A. truei* with elevation at the landscape scale in the KS Region (and elsewhere; see Hawkins et al. 1994). This explanation lies in the pronounced physiological limitations of this unique frog species. Experiments with adult *A. truei* indicated that their tolerance to desiccation was lower than 17 other North American frog species tested (Claussen 1973a,b). Brown (1975, 1989) found this species to have the narrowest tolerance range (5–18.5 °C), and the lowest upper limit temperature for development (18.5 °C) of any frog in North America. Our study was conducted at the southern end of the range of *A. truei* (Metter 1968, Stebbins 1985). In this region, the incidence of *A. truei* is patchy (Bury 1968). This patchy distribution probably results from the limited capacity of this cold-adapted, moisture-dependent frog to tolerate the dry, warm conditions found throughout this portion of its range.

We found no variables at the landscape scale that were useful for predicting differences in the density of *D. tenebrosus*. It is possible that the density of *D. tenebrosus* does not vary across the region for those variables we measured at the landscape scale, or that our sample size of 39

streams was insufficient to detect differences. Welsh (1993) analyzed data from 156 sites, and from a greater proportion of the range of this salamander in California, and reported both a higher incidence and higher relative abundance of salamanders both nearer the Pacific Coast and northward. He interpreted this pattern as resulting from the direction of the prevailing cooler, moister, maritime-modified climate (Froehlich et al. 1982), which creates and sustains the region's temperate rainforests and provides optimum conditions for *D. tenebrosus* in the northwest portions of the state.

At the macroenvironment scale, the ecological relationships for both life stages of *A. truei* indicated by our analyses described a structurally diverse, older forest environment (see Forest Succession below). Macroenvironment-scale models for *D. tenebrosus* were slightly more informative than those at the landscape scale but still relatively poor compared with *A. truei*, suggesting relatively weak biological relationships. The negative relationships between salamander numbers and density of understory hardwoods and grass cover suggest that a relatively closed overstory and lack of disturbance (where young hardwoods and grass are precluded) may be attributes of the upland environment adjacent to streams supporting higher densities of *D. tenebrosus*. We suggest that differences in the strengths of these ecological relationships observed for *A. truei* and *D. tenebrosus* may be the result of evolved differences in fundamental niche breadth that manifest as different degrees of specialization by these 2 species (e.g., Futuyma and Moreno 1988, Van Tienderen 1991).

Microenvironment Relationships

Our analyses of *A. truei* habitat relationships at the finest scale revealed the importance of specific aquatic microenvironments, substrates, and stream conditions particular to each life stage. The positive associations between adult frogs and pools, and larvae with cobble and waterfalls, is an expression of morphological and physiological adaptations unique to each life stage. *A. truei* tadpoles, with rock-gripping, sucker-disk mouths, and associated feeding and breathing structures, are highly adapted to life in the fast-moving water (Gradwell 1971, Altig and Brodie 1972). Turbulence created by high water velocities over coarse substrates provides protection from predators such as *D. tenebrosus* (Metter 1963). Tadpoles attach readily to rock surfaces in strong currents,

where potential predators have to fight currents and contend with the visual impairment of "white water" which serves to hide the larvae (Welsh 1993:80). The positive relationship between the densities of the 2 life stages of *A. truei* suggests that they can be synoptic, at least during the summer when we sampled, and when forest microclimatic conditions beyond the streambed are most adverse in the KS region. The positive relationship between densities of adult *A. truei* and *D. tenebrosus* may be a result of similar affinities for pools and bedrock, or it may reflect a more direct interaction such as predation.

The individual-focused microenvironment analyses provided more detailed insights into habitat relationships than those that emerged from our multivariate analyses or from previously published work. For example, the documented selection of riffle habitats with cobble-boulder substrates by *A. truei* larvae confirms a relationship previously assumed based on laboratory studies (Altig and Brodie 1972) and correlative field data (Hawkins et al. 1988, Bury et al. 1991). Correlative evidence from earlier work on adult *A. truei* showed that they were found mostly under cobbles and boulders in slower water than tadpoles (Metter 1964, Nussbaum et al. 1983, Bury et al. 1991). We demonstrated that adult *A. truei* select pool habitats and cobble-sized rock cover more frequently than do other life stages, possibly as summer refuge from desiccating temperatures in terrestrial environments.

Analysis at the microenvironment scale yielded the best model for *D. tenebrosus*, with 2 of the strongest variables showing a positive relationship with adult, and a negative relationship with larval, *A. truei*. Both life stages of *A. truei* figured prominently in the aquatic conditions model for *D. tenebrosus*. The analysis by Welsh (1993) of the habitat of the giant salamander also indicated that the relationship between the 2 species was strongly reciprocal. Larval *A. truei* likely avoid microsites occupied by *D. tenebrosus* (Metter 1963) and tadpoles will alter normal feeding behavior in response to their presence (Feminella and Hawkins 1994).

The association of giant salamander larvae with narrow, shaded stream reaches dominated by pools and coarse substrates (see also Parker 1991) may be related to their foraging strategy. *D. tenebrosus* larvae are predominantly sit-and-wait predators (Parker 1994), and these conditions provide both cover and an abundance of ambush foraging sites.

Multiscale Forest Succession and Geology

Our finding of higher stream amphibian diversity (SDI) in late seral forest is a new result for the KS Region (compare with deMaynadier and Hunter 1999, Skelly et al. 1999). This result is not a surprise given the previously demonstrated higher incidence of several amphibians in old-growth forests in northern California (Welsh and Lind 1988, 1991, 1996; Welsh 1990). We found significant relationships between particular environmental attributes linked to late-seral stages and the incidence and density of *A. truei* (but see Diller and Wallace 1999). Higher densities of *A. truei* in streams traversing old-growth forest stands were first reported by Corn and Bury (1989) and Welsh (1990) based on univariate analyses. The multivariate results reported here confirm this earlier work and give it important context by revealing those seral stage-related attributes of the forest environment important to *A. truei*. Our multivariate models suggest that for predicting *A. truei* presence, stream temperature is more important than aspects of forest structure; however, conditions of forest structure and microclimate are closely linked (Chen et al. 1993, 1999). Regardless, the relationship with older forests likely is the expression of the physiological limits of *A. truei* at the macroenvironment scale (Welsh 1990). Our data show a close relationship between *A. truei* density, stream temperature, and forest age, as well as a clear link between stream temperature and elevation (Fig. 6; also see Hawkins et al. 1994). Both air and stream temperatures increase with reductions in forest canopy (Holtby 1988, Chen et al. 1993, Brososke et al. 1997). Consequently, the physiological response to increased water temperatures and desiccation that best explains the relationship between increasing *A. truei* density and greater elevation also accounts well for the close relationship between this frog and late-seral forest environments. Hawkins et al. (1988) reported that differences in densities of *A. truei* tadpoles among streams on Mount St. Helens from 1983 to 1987 were most clearly associated with the extent of forest cover remaining in a blast-influenced basin. In completely or partially forested basins, maximum stream temperatures were <18 °C and tadpole densities were relatively high, whereas basins with forests leveled by the 1980 eruption had temperatures near 20 °C and supported few tadpoles (Hawkins et al. 1988). After 1988, densities of tadpoles became greater in nonforested streams, a phenomenon the authors associated

with a lowering of mean maximum temperatures and a flushing of fine sediments (volcanic ejecta) from these high-gradient streams (Hawkins et al. 1997). We believe that at higher elevations such as Mount St. Helens, where water temperatures are ameliorated by altitude, forest cover is less of an issue (Fig. 6). Sensitivity of *A. truei* to light (Altig and Brodie 1972, Hailman 1982) is another possible mechanism that may influence their close relationship with forest succession at lower elevations.

Our finding that the incidence and density of adult and larval *A. truei* were positively associated with herb cover is probably related to the fact that more mesothermal-adapted herbs predominate on the forest floor in older forests as a direct result of the stable, cool, moist conditions (Spies 1991, Spies and Franklin 1991, Frost 1997). These herbs not only indicate the requisite microclimatic conditions needed by adult *A. truei*, they also provide cover and probably increase invertebrate fauna for foraging frogs (see also Daugherty and Sheldon 1982*a,b*). Better site conditions for adults adjacent to streams would also translate to more larvae in nearby streams.

The lack of a relationship between tailed frog density and seral stage reported by Diller and Wallace (1999) is best explained by the proximity of their sites to the marine-influenced coast of northern California where microclimatic extremes are ameliorated. This ameliorating effect, which can preclude the need for extensive forest canopy over the stream without adversely affecting stream temperatures, occurs over a relatively small portion of the range of the tailed frog in northern California (H. H. Welsh, unpublished data). Many of the habitat relationships reported for *A. truei* by Diller and Wallace (1999) are attributable to the unique history and characteristics of the coastal industrial forest landscape they studied, and are not typical of most of the species' range (i.e., the interior portions of the California coast ranges, and the Cascade, and Rocky mountains of Idaho, Montana, Oregon, Washington, and British Columbia).

Recent research has indicated that the type of parent geology can influence the distribution and abundance of headwater stream amphibians, particularly the tailed frog, with younger, unconsolidated parent material not as likely to support these amphibians as more consolidated types (Diller and Wallace 1999, Dupuis and Steventon 1999, Wilkins and Peterson 2000). We did not directly characterize and quantify the parent

material type at the time of our study; however, our streams occurred across a wide range of geologic types in the KS Region, from young, unconsolidated Franciscan formations on the coast to older, hard, consolidated serpentine types in the interior and at higher elevations (Wagner and Saucedo 1987). This leads us to believe that parent geology was not a biasing factor in our results. We believe that Diller and Wallace's (1999) and Wilkins and Peterson's (2000) interpretations of a primary (as opposed to secondary) effect related to geologic type is a result of their sampling only on industrial forest landscapes where only a portion of the potential forest seral continuum is represented. Had these workers examined geology along the entire seral continuum, they would have found that tailed frog larvae can and do occur on young, unconsolidated geology within late-seral forests (e.g., Welsh and Ollivier 1998, Adams and Bury 2002). In fact, Dupuis and Steventon (1999) reported that the competency of the parent geology had significant effects, but they found that these effects were greatly exacerbated by timber harvesting. Timber harvesting near streams can have a profound effect on the nature and availability of substrate interstices (Waters 1995), which are important microhabitat for tailed frogs (Welsh and Ollivier 1998). Depending on the competency of the bedrock materials, stream conditions can change dramatically following nearby tree removal (Waters 1995). Diller and Wallace (1999) and Wilkins and Peterson (2000) mistakenly interpreted changes in conditions resulting from the interaction of less competent geologic types and landscape-level disturbance, with a proclivity on the part of tailed frogs for the more consolidated geology. A similar misinterpretation occurred in an analysis of the habitat associations of the headwaters salamander (*Rhyacotriton variegatus*; Diller and Wallace 1996) where the interactions between the historical disturbance regime and the parent geology also were not considered (see Welsh et al. 2000). Understanding the nature of these processes is essential when it comes to formulating effective forest practice rules to protect sensitive headwaters amphibians and their stream habitats (Welsh 2000).

MANAGEMENT IMPLICATIONS

Viewing the forest ecosystem across broad landscapes as a dynamic mosaic of stands of different ages or seral stages affected by multiple interacting, scale-dependent, biological and geomorpho-

logical processes, can provide valuable insights into the derivation of biological patterns, and facilitate interpretations of both ecological and evolutionary processes (May 1994, Reeves et al. 1995, Perry and Amaranthus 1997). Such a perspective can provide a more holistic view within which to design forest management strategies that will preserve native biodiversity. Patch dynamics of the surrounding landscape directly affect the stream network within by influencing hydrologic patterns, microclimates, sediment loads, and energy inputs, and thus affect the incidence and abundance of the associated riparian and stream biota (Schlosser 1991, Zwick 1992, Malanson 1993, Gregory 1997, Jules et al. 1999, Naiman et al. 2000). In addition, incidence (presence or absence) and abundance may vary, both within the geographic range of a species at different spatial and temporal scales (e.g., Hecnar and M'Closkey 1997) and among species with similar geographic ranges due to variations in niche breadth (Wiens 1989, Lawton et al. 1994, Brown 1995). Such pattern differences can be a function of the interrelationships of evolutionary history, patch dynamics, disturbance, and temporal and spatial resolution (Levin 1992, Holt 1993, May 1994), all interacting with evolved differences in life histories (e.g., Southwood 1988).

Habitat preferences are based on evolved behavior and thus relate directly to the probability of persistence (Holt 1987, Ruggiero et al. 1988, Holt and Gaines 1992). In the case of *A. truei*, although present in some streams in younger forests (e.g., Diller and Wallace 1999, Aubry 2000, Wilkins and Peterson 2000), their populations often are reduced or eliminated by timber harvest and related activities through direct perturbations to the forest and stream environment. Given that habitat conditions for *A. truei* are optimized in late-seral forests (Corn and Bury 1989; Welsh 1990, 1993; Welsh and Lind 1991), the long-term viability of this frog throughout the region of our study probably is linked to the presence and spatial accessibility of these forests and the interior microclimatic conditions they provide. We believe that in the KS Region *A. truei* is ecologically dependent (sensu Ruggiero et al. 1988) on these late-seral forests and their unique habitats. Further, our results indicate that *D. tenebrosus* is more of an ecological generalist (has a broader habitat niche) than *A. truei*, and thus its persistence is not as closely linked to late-seral conditions.

Habitat differences may have implications for understanding the respective roles of these 2

species in, and in response to, both ecological and anthropogenic processes. Habitat specialists like *A. truei* are inherently more sensitive to habitat disturbance or climatic change than a generalist like *D. tenebrosus*. Habitat fragmentation via timber harvesting or fire is thought to affect specialists more than generalists because it acts as an isolating mechanism for specialists that require interior environments (Lord and Norton 1990, Johnson 1998, Jules et al. 1999, Semlitsch 2000). Based on our research, we expect *D. tenebrosus* to continue to be widely distributed and abundant, while *A. truei* likely will continue to decline across the landscapes of the KS Region (and the greater Pacific Northwest) in response to these relatively new, more intensive anthropogenic disturbance regimes (e.g., Corn and Bury 1989, Dupuis and Steventon 1999, Welsh 2000).

ACKNOWLEDGMENTS

We thank the members of the field crews of the Pacific Southwest Forest and Range Experiment Station's Timber/Wildlife Research Unit for their help in collecting data: C. Barrows, W. Block, L. Brennan, K. Calabrese, S. Edwards, S. Goldwasser, P. Hall, M. Hamady, L. LaClaire, D. Lausche, P. Manley, W. McCleod, K. Milne, C. Ogan, P. Paton, R. Reynolds, A. Schaffer, K. Schmidt, J. Sterling, C. Taylor, D. Taylor, and G. Therien. We also thank J. A. Baldwin and B. R. Noon for advice on statistical methods. We are grateful to B. Harvey, L. Diller, C. Hawkins, N. Karraker, and 2 anonymous reviewers for helpful comments on earlier drafts of this paper. G. Hodgson, N. Karraker, and C. Wheeler helped with the tables and figures. The Nature Conservancy's North Coast Forest Preserve (now the University of California's Angelo Preserve) and Harwood Timber Company are gratefully acknowledged for allowing us to sample on their lands.

LITERATURE CITED

- ADAMS, M. J., AND R. B. BURY. 2002. The endemic headwater stream amphibians of the American Northwest: associations with environmental gradients in a large forested preserve. *Global Ecology and Biogeography* 11:169–178.
- AUTIG, R., AND E. D. BRODIE. 1972. Laboratory behavior of *Ascaphus truei* tadpoles. *Journal of Herpetology* 6:21–24.
- AUBRY, K. B. 2000. Amphibians in managed, second-growth Douglas-fir forests. *Journal of Wildlife Management* 64:1041–1052.
- BINGHAM, B. B., AND J. O. SAWYER. 1991. Distinctive features and definitions of young, mature, and old-growth Douglas-fir/hardwood forests. Pages 363–377 in L. F.

- Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- BLONDEL, J. 1987. From biogeography to life history: a multithematic approach illustrated by the biogeography of vertebrates. *Journal of Biogeography* 14:405-422.
- BROSOFESKE, K. D., J. CHEN, R. J. NAIMAN, AND J. F. FRANKLIN. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* 7:1188-1200.
- BROWN, H. A. 1975. Temperature and development of the tailed frog, *Ascaphus truei*. *Comparative Biochemistry and Physiology* 50A:397-405.
- . 1989. Developmental anatomy of the tailed frog (*Ascaphus truei*): a primitive frog with large eggs and slow development. *Journal of Zoology, London* 220:171-184.
- BROWN, J. H. 1995. Macroecology. University of Chicago Press, Illinois, USA.
- BURY, R. B. 1968. The distribution of *Ascaphus truei* in California. *Herpetologica* 24:39-46.
- , AND P. S. CORN. 1991. Sampling methods for amphibians in streams in the Pacific Northwest. U.S. Forest Service General Technical Report PNW-GTR-275.
- , P. S. CORN, K. B. AUBRY, F. F. GILBERT, AND L. L. C. JONES. 1991. Aquatic amphibian communities in Oregon and Washington. Pages 362-377 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- , AND C. A. PEARL. 1999. Klamath-Siskiyou herpetofauna: biogeographic patterns and conservation strategies. *Natural Areas Journal* 19:341-350.
- CAREY, A. B., AND T. A. SPIES. 1991. Wildlife habitat relationships in unmanaged Douglas-fir forests: A program of research. Pages 9-16 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. Wildlife and vegetation of unmanaged Douglas-fir forests. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- CHEN, J., J. F. FRANKLIN, AND T. A. SPIES. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219-237.
- , S. C. SAUNDERS, T. R. CROW, R. J. NAIMAN, K. D. BROSOFSKE, G. D. MROZ, B. L. BROOKSHIRE, AND J. R. FRANKLIN. 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49:288-297.
- CLAUSSEN, D. L. 1973a. The thermal relations of the tailed frog, *Ascaphus truei*, and the Pacific treefrog, *Hyla regilla*. *Comparative Biochemistry and Physiology* 44A:137-153.
- . 1973b. The water relations of the tailed frog, *Ascaphus truei*, and the Pacific treefrog, *Hyla regilla*. *Comparative Biochemistry and Physiology* 44A:155-171.
- CORKRAN, C. C., AND C. THOMS. 1996. Amphibians of Oregon, Washington and British Columbia. Lone Pine Publishing, Edmonton, Alberta, Canada.
- CORN, P. S., AND R. B. BURY. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39-57.
- DAUGHERTY, C. H., AND A. L. SHELDON. 1982a. Age-determination, growth, and life-history of a Montana population of the tailed frog (*Ascaphus truei*). *Herpetologica* 38:461-468.
- , AND ———. 1982b. Age-specific movement patterns of the tailed frog (*Ascaphus truei*). *Herpetologica* 38:468-474.
- DEMAINADIER, P. G., AND M. L. HUNTER, JR. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* 63:441-450.
- DILLER, L. V., AND R. L. WALLACE. 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. *Journal of Herpetology* 30:184-191.
- , AND ———. 1999. Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in North Coastal California. *Journal of Herpetology* 33:71-79.
- DUPUIS, L. A., AND D. STEVENTON. 1999. Riparian management and the tailed frog in northern coastal forests. *Forest Ecology and Management* 124:35-43.
- FEMINELLA, J. W., AND C. P. HAWKINS. 1994. Tailed frog tadpoles differentially alter their feeding behavior in response to non-visual cues from four predators. *Journal of the North American Benthological Society* 13:310-320.
- FRANK, E. C., AND R. LEE. 1966. Potential solar beam irradiation on slopes: tables for 30° to 50° latitudes. U.S. Forest Service Research Paper RM-18.
- FROELICH, H. A., D. H. McNABB, AND F. GAWEDA. 1982. Average annual precipitation 1960-1980 in southwestern Oregon. Cooperative Extension Services, Oregon State University, Corvallis, USA.
- FROST, E. J. 1997. Edge effects in old-growth forests of the Klamath Mountains: evidence from the understory flora. Pages 23-36 in J. K. Beigel, E. S. Jules, and B. Snitkin, editors. Proceedings of the first conference on Siskiyou ecology. The Siskiyou Regional Education Project, Cave Junction, Oregon, USA.
- FUTUYMA, D. J., AND G. MORENO. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics* 19:207-233.
- GRADWELL, N. 1971. *Ascaphus* tadpole: experiments on the suction and gill irrigation mechanisms. *Canadian Journal of Zoology* 49:307-332.
- GREGORY, S. V. 1997. Riparian management in the 21st century. Pages 69-85 in K. A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century. Island Press, Covelo, California, USA.
- HAILMAN, J. P. 1982. Extremely low ambient light levels of *Ascaphus truei*. *Journal of Herpetology* 16:83-84.
- HAWKINS, C. P., J. FEMINELLA, AND C. M. CRISSAFULLI. 1994. Patterns of abundance and growth of tailed frog populations near the Mt. St. Helens blast zone [abstract]. *Northwest Science* 68:129.
- , AND ———. 1997. Responses and recovery of stream dwelling tailed frog and giant salamander populations following the 1980 eruption of Mount St. Helens [abstract]. Pages 6-7 in J. S. Richardson and T. R. Wahbe, editors. Tailed frog workshop. University of British Columbia, Vancouver, Canada.

- , L. J. GOTTSCHALK, AND S. S. BROWN. 1988. Densities and habitat of tailed frog tadpoles in small streams near Mt. St. Helens following the 1980 eruption. *Journal of the North American Benthological Society* 7:246–252.
- , K. P. MURPHY, N. H. ANDERSON, AND M. A. WILBACH. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwest United States. *Canadian Journal of Fisheries and Aquatic Sciences* 40:1173–1185.
- HECNAR, S. J., AND R. T. M'CLOSKEY. 1997. Spatial scale and determination of species status of the green frog. *Conservation Biology* 11:670–682.
- HOLT, R. D. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. *Evolutionary Ecology* 1987:331–347.
- . 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities*. University of Chicago Press, Illinois, USA.
- , AND M. S. GAINES. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evolutionary Ecology* 1992:433–447.
- HOLTBY, L. B. 1988. Effects of logging on stream temperatures in Carnation Creek, British Columbia, and associated impacts on the coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:502–515.
- JENNINGS, M. R., AND M. P. HAYES. 1988. Habitat correlates of the distribution of California red-legged frog (*Rana aurora draytoni*) and foothill yellow-legged frog (*Rana boylei*): implications for management. Pages 144–158 in R. C. Szarim, K. E. Severson, and D. R. Patton, technical coordinators. *Management of amphibians, reptiles, and small mammals in North America*. U.S. Forest Service General Technical Report RM-166.
- JOHNSON, C. E. 1998. Species extinction and the relationship between distribution and abundance. *Nature* 394:272–274.
- JOHNSON, D. E. 1981. How to measure habitat—a statistical approach. Pages 53–57 in D. Capen, editor. *The use of multivariate statistics in studies of wildlife habitat*. U.S. Forest Service General Technical Report RM-87.
- JOHNSON, D. H. 1980. The comparison of use and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- JONES, J. A., AND G. E. GRANT. 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. *Water Resources Research* 32:959–974.
- JULES, E. S., E. FROST, L. MILLS, AND D. TALLMON. 1999. Ecological consequences of forest fragmentation in the Klamath Region. *Natural Areas Journal* 19:368–378.
- LAWTON, J. H., S. NEE, A. J. LETCHER, AND P. H. HARVEY. 1994. Animal distributions: patterns and processes. Pages 41–58 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, London, United Kingdom.
- LEONARD, W. P., H. A. BROWN, L. L. C. JONES, K. R. MCALISTER, AND R. M. STORM. 1993. *Amphibians of Washington and Oregon*. Seattle Audubon Society, Washington, USA.
- LEVIN, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- LORD, J. M., AND D. A. NORTON. 1990. Scale and the spatial concept of fragmentation. *Conservation Biology* 4:197–202.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, New Jersey, USA.
- MALANSON, G. P. 1993. *Riparian landscapes*. Cambridge University Press, Cambridge, United Kingdom.
- MAY, R. M. 1994. The effects of spatial scale on ecological questions and answers. Pages 1–17 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, London, United Kingdom.
- METTER, D. E. 1963. Stomach contents of Idaho larval *Dicamptodon*. *Copeia* 1962:435–436.
- . 1964. A morphological and ecological comparison of two populations of the tailed frog, *Ascaphus truei* Stejneger. *Copeia* 1964:181–195.
- . 1968. *Ascaphus truei*. *Catalogue of American Amphibians and Reptiles* 69.1–69.2.
- MITCHELL, S. 1999. A simple model for estimating mean monthly stream temperatures after riparian canopy removal. *Environmental Management* 24:77–83.
- MORRISON, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife–habitat relationship studies. *Journal of Wildlife Management* 65:613–623.
- MURPHY, M. L., AND J. D. HALL. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:137–145.
- NAIMAN, R. J., R. E. BILBY, AND P. A. BISSON. 2000. Riparian ecology and management in the Pacific coastal rain forest. *BioScience* 50:996–1111.
- NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1989. *Applied linear regression models*. Richard D. Irwin, Homewood, Illinois, USA.
- NUSSBAUM, R. A., E. D. BRODIE, AND R. M. STORM. 1983. *Amphibians and reptiles of the Pacific Northwest*. University Press of Idaho, Moscow, USA.
- O'NEIL, L. J., AND A. B. CAREY. 1986. Introduction: when habitats fail as predictors. Pages 207–208 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships*. University of Wisconsin Press, Madison, USA.
- PARKER, M. S. 1991. Relationship between cover availability and larval Pacific giant salamander density. *Journal of Herpetology* 25:355–357.
- . 1994. Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia* 1994:705–718.
- PERRY, D. A., AND M. P. AMARANTHUS. 1997. Disturbance, recovery, and stability. Pages 31–56 in K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st century*. Island Press, Covelo, California, USA.
- PLATTS, W. S., W. F. MEGAHAN, AND G. W. MINSHALL. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service General Technical Report INT-138.
- REEVES, G. H., L. E. BENDA, K. M. BURNETT, P. A. BISON, AND J. R. SEDELL. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17:334–349.

- RENCHER, A. C. 1992. Interpretation of canonical discriminant functions, canonical variates, and principal components. *American Statistician* 46:217-225.
- RESH, V. H., A. V. BROWN, A. P. COVICH, M. E. GURTZ, H. W. LI, G. W. MINSHALL, S. R. REICE, A. L. SHELDON, J. B. WALLACE, AND R. WISSMAR. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.
- RUGGIERO, L. F. 1991. Wildlife habitat relationships in unmanaged Douglas-fir forests: a program of research. Pages 5-7 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- , R. S. HOLTHAUSEN, B. G. MARCOT, K. B. AUBRY, J. W. THOMAS, AND E. C. MESLOW. 1988. Ecological dependency: the concept and its implications for research and management. *Transactions of the North American Wildlife and Natural Resources Conference* 53:115-126.
- SAS INSTITUTE. 1990. *SAS user's guide*. SAS Institute, Cary, North Carolina, USA.
- SAVAGE, J. M. 1960. The evolution of a peninsular herpetofauna. *Systematic Zoology* 9:184-212.
- SCHLOSSER, I. J. 1991. Stream fish ecology: a landscape perspective. *BioScience* 41:704-712.
- SEMLITSCH, R. D. 2000. Principles of management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64:615-631.
- SKELLY, D. K., E. E. WERNER, AND S. A. CORTWRIGHT. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80:2326-2337.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- SOUTHWOOD, T. R. E. 1988. Tactics, strategies, and tempests. *Oikos* 52:3-18.
- SPIES, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. Pages 111-121 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- , AND J. F. FRANKLIN. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-109 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- STEBBINS, R. C. 1985. *A field guide to western reptiles and amphibians*. Houghton Mifflin, Boston, Massachusetts, USA.
- STEVENS, J. 1986. *Applied multivariate statistics for the social sciences*. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.
- TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist* 111:1-7.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1-21.
- . 1991. Reply to Seaman and Jaeger: an appeal to common sense. Points of view: a controversy in statistical ecology. *Herpetologica* 46:357-361.
- TOWNSEND, C. R., AND T. A. CROWL. 1991. Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? *Oikos* 61:347-354.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901.
- . 1986. Summary: when habitats fail as predictors—the researcher's viewpoint. Pages 207-208 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000: modeling habitat relationships*. University of Wisconsin Press, Madison, USA.
- VAN TIENDEREN, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. *Evolution* 45:1317-1331.
- WAGNER, D. L., AND G. J. SAUCEDO. 1987. *Geologic map of the Weed quadrangle*. Division of Mines and Geology, Resources Agency of California, Sacramento, USA.
- WATERS, T. F. 1995. *Sediment in streams: sources, biological effects and control*. American Fisheries Society Monograph 7.
- WATERS, W. E., AND D. C. ERMAN. 1990. Research methods: concept and design. Pages 1-34 in C. B. Schreck and P. B. Moyle, editors. *Methods for fish biology*. American Fisheries Society, Bethesda, Maryland, USA.
- WELSH, H. H., JR. 1987. Monitoring herpetofauna in woodland habitats of northwestern California and southwestern Oregon: a comprehensive strategy. Pages 203-213 in T. R. Plumb and N. H. Pillsbury, editors. *Multiple-use management of California's hardwood resources*. U.S. Forest Service General Technical Report GTR-PSW-100.
- . 1990. Relictual amphibians and old-growth forests. *Conservation Biology* 4:309-319.
- . 1993. A hierarchical analysis of the niche relationships of four amphibians from forested habitats of northwestern California. Dissertation, University of California, Berkeley, USA.
- . 2000. California forest management and aquatic/riparian ecosystems in the redwoods. Pages 255-261 in R. Noss, editor. *The redwood forest: history, ecology, and conservation of the coast redwoods*. Island Press, Covelo, California, USA.
- , AND A. J. LIND. 1988. Old-growth forests and the distribution of the terrestrial herpetofauna. Pages 439-458 in R. Szaro, K. Severson, and D. Patton, editors. *Management of amphibians, reptiles, and small mammals in North America*. U.S. Forest Service General Technical Report RM-166.
- , AND ———. 1991. The structure of the herpetofaunal assemblage of the Douglas-fir forests of northwestern California and southwestern Oregon. Pages 394-413 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, technical editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Forest Service General Technical Report PNW-GTR-285. <http://www.fs.fed.us/pnw/pubs/gtr285/>
- , AND ———. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus* (Caudata: Plethodontidae), in northwestern California. *Journal of Herpetology* 29:198-210.
- , AND ———. 1996. Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in northwestern Cali-

- fornia. *Journal of Herpetology* 30:385–398.
- , AND L. M. OLLIVIER. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. *Ecological Applications* 8:1118–1132.
- , T. ROELOFS, AND C. FRISSELL. 2000. Aquatic ecosystems of the redwood region. Pages 165–199 in R. Noss, editor. *The redwood forest: history, ecology, and conservation of the coast redwoods*. Island Press, Covelo, California, USA.
- WIENS, J. A. 1989. Spatial scale in ecology. *Functional Ecology* 1989:385–397.
- WILKINS, R. N., AND N. P. PETERSON. 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. *Forest Ecology and Management* 139:79–91.
- ZWICK, P. 1992. Stream habitat fragmentation—a threat to biodiversity. *Biodiversity and Conservation* 1:80–97.

Received 23 November 2000.

Accepted 15 January 2002.

Associate Editor: Russell.