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THE INFLUENCE OF FOREST MANAGEMENT ON HEADWATER STREAM AMPHIBIANS AT MULTIPLE SPATIAL SCALES

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Abstract. Understanding how habitat structure at multiple spatial scales influences vertebrates can facilitate development of effective conservation strategies, but until recently most studies have focused on habitat relationships only at fine or intermediate scales. In particular, patterns of amphibian occurrence across broad spatial scales are not well studied, despite recent concerns over regional and global declines. We examined habitat relationships of larval and neotenic Pacific giant salamanders (*Dicamptodon tenebrosus*), larval and adult Pacific tailed frogs (*Ascaphus truei*) (hereafter "tailed frogs"), and torrent salamanders (*Rhyacotriton* spp.) at three spatial scales (2-m sample unit, intermediate, and drainage). In 1998 and 1999, we captured 1568 amphibians in 702 sample units in 16 randomly chosen drainages in the Oregon Coast Range. We examined species–habitat associations at each spatial scale using an information-theoretic approach of analysis to rank sets of logistic regression models developed a priori. At the 2-m sample unit scale, all groups were negatively associated with proportion of small substrate and positively associated with stream width or elevation. At the intermediate scale, Pacific giant salamanders, adult tailed frogs, and torrent salamanders were positively associated with presence of a 46-m band of forested habitat on each side of the stream, and larval tailed frogs were positively associated with presence of forest >105 years old. Aspect was important for Pacific giant salamanders and larval tailed frogs at the intermediate scale. At the drainage scale, all groups except torrent salamanders were positively associated with proportion of stream length having forested bands >46 m in width, but further analysis suggests narrower bands may provide adequate protection for some groups. Population- and community-level responses at broad spatial scales may be reflected in species-level responses at fine spatial scales, and our results suggest that geophysical and ecological characteristics, as well as measures of instream habitat, can be used together to prioritize conservation emphasis areas for stream amphibians in managed landscapes.

Key words: Ascaphus truei; Dicamptodon tenebrosus; forest management; headwater streams; information theory; Rhyacotriton variegatus; Rhyacotriton kezeri; riparian buffers; spatial scales; stream amphibians.

INTRODUCTION

Effective conservation of vertebrate diversity requires understanding influences of habitat structure at multiple spatial scales, yet there are few studies of multiscale habitat requirements of many taxa (but see Welsh et al. 1993, Lowe and Bolger 2002, Welsh and Lind 2002). Until recently, most studies of species–habitat relationships have focused on associations of single species with habitat characteristics measured at fine or intermediate spatial scales (Corn and Bury 1989). However, single-scale approaches are often inadequate for conservation because organisms perceive and select habitat in a hierarchical way (Kotliar and Wiens 1990). For example, an individual may select

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foraging habitat at a fine spatial scale, while mate selection occurs at a broader scale (Bissonette 1997). At still broader scales, habitat quality in areas separating subpopulations can influence dispersal and colonization of habitat patches (McCullough 1996, Wiens 1996).

Because stream amphibians have partially or fully terrestrial life stages, disturbance events that alter upslope and riparian habitats may influence abundance and viability through impacts on reproduction, foraging, dispersal, and overwintering habitat. At broad spatial scales, removal of vegetation and soil disturbance due to timber harvesting and road building could negatively impact stream amphibians at fine spatial scales by increasing water temperatures (Brown and Krygier 1970, Beschta et al. 1987) and water and sediment inputs into streams (Bormann and Likens 1979), and reducing allochthonous inputs, thereby affecting energy production and trophic dynamics (Gregory et al. 1991). Once linkages between habitat structure and constraints on amphibians at different scales are identified, more appropriate conservation strategies can be

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TABLE 1. Topogeographic characteristics of study drainages.

Forest management intensity category	Area (ha)	Elevation range (m)	Aspect (degrees)	Rock type
Low	119.4	105–306	340	sedimentary
Low	110.3	289–833	360	sedimentary
Low	138.7	204–484	10	sedimentary
Low	185.4	174–507	280	sedimentary
Low	108.6	341–982	360	sedimentary/volcanic
Low	140.6	366–902	315	sedimentary/volcanic
Moderate	148.0	217–598	90	sedimentary
Moderate	151.5	138–442	175	sedimentary
Moderate	114.0	435–807	335	sedimentary/volcanic
Moderate	93.8	315–807	100	sedimentary/volcanic
Moderate	139.6	237–711	150	sedimentary/volcanic
High	194.3	179–700	150	sedimentary
High	185.7	158–502	140	sedimentary
High	94.1	194–480	215	sedimentary
High	178.3	317–803	100	sedimentary/volcanic
High	197.4	208–406	180	sedimentary/volcanic

developed and implemented to meet ecological requirements of stream amphibians.

In the Pacific Northwest, habitat relationships of headwater stream amphibians have previously been studied at scales of stream reaches and forest stands (Murphy et al. 1981, Murphy and Hall 1981, Corn and Bury 1989, Kelsey 1995). At fine scales, stream amphibians have been positively associated with low stream temperatures and low levels of sediment (Corn and Bury 1989, Kelsey 1995, Diller and Wallace 1999, Dupuis and Steventon 1999). At intermediate scales, age of forests adjacent to streams has been important for stream amphibians. Generally, occurrence or abundance has been positively associated with old forests around streams (Bury and Corn 1988, Corn and Bury 1989, Welsh 1990, Welsh and Lind 1996; but see Diller and Wallace 1996, 1999).

Amphibian responses to geophysical characteristics have been investigated at broad spatial scales (Diller and Wallace 1996, 1999, Welsh and Lind 1996, Dupuis et al. 2000, Sutherland and Bunnell 2001, Adams and Bury 2002), but few of these studies have examined response to landscape structure (e.g., amount or configuration of forest patches in drainages). Results of a study of habitat relationships of headwater amphibians in 50–65-year-old forests suggested that geomorphic and geologic characteristics might override the influence of other habitat characteristics in determining amphibian abundance or occurrence (Wilkins and Peterson 2000). However, other studies have found occurrence of stream amphibians at broad spatial scales was related to density of large conifers (Welsh and Lind 1996) or distance to unharvested forest (Hunter 1998). Geophysical characteristics and habitat structure appear to be important predictors of habitat relationships at broad spatial scales and may interact to influence habitat suitability at finer spatial scales.

Our goal was to evaluate habitat relationships of headwater stream amphibians in the Oregon Coast Range at multiple spatial scales. We studied habitat relationships of larval and neotenic Pacific giant salamanders (*Dicamptodon tenebrosus*), larval and adult tailed frogs (*Ascaphus truei*), southern torrent salamanders (*Rhyacotriton variegatus*), and Columbia torrent salamanders (*Rhyacotriton kezeri*) at three spatial scales (2-m sample unit, intermediate, and drainage) in drainages representing a range of landscape conditions. Specifically, we examined (1) the role of biotic and abiotic habitat characteristics in predicting amphibian occurrence at the sample unit scale; (2) the importance of geophysical and forest management-related characteristics in predicting amphibian occurrence at intermediate and drainage scales; (3) patterns of amphibian occurrence and distribution across all three scales; and (4) how habitat models at each spatial scale could be used to develop conservation strategies for stream amphibians.

STUDY AREA

We conducted our study primarily on lands administered by the United States Bureau of Land Management (BLM) on the east side of the Oregon Coast Range between the Nestucca (45°17′ N) and Siuslaw (43°53′ N) Rivers. South of the Yamhill River (45°05′ N), the primary parent geology is the Tyee formation, sedimentary rock composed of tuffaceous and micaceous sandstone (Franklin and Dyrness 1973), with some igneous intrusions. North of the Yamhill River, both sedimentary and volcanic rocks occur (Franklin and Dyrness 1973) (Table 1).

The landscape surrounding the study area is a checkerboard of privately owned and publicly administered lands. Although the area is composed primarily of second-growth forests that naturally regenerated after fires
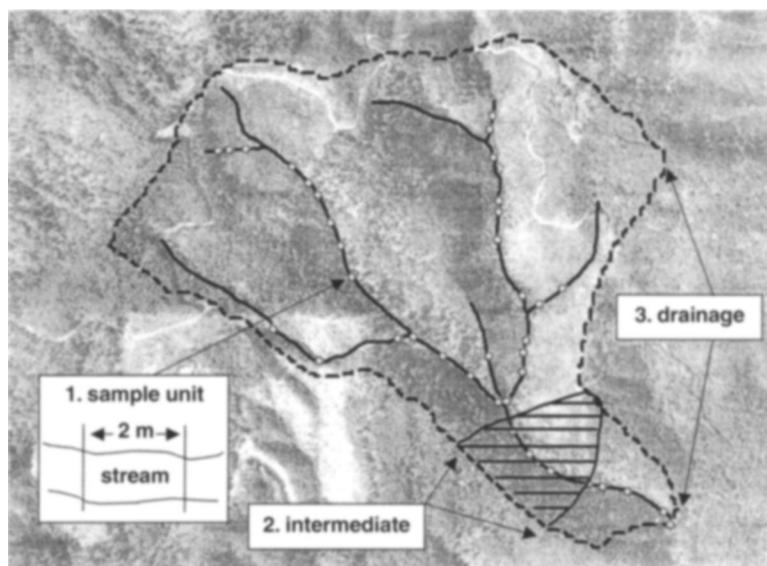
FIG. 1. Study drainage in the high management intensity category with an example of each of three spatial scales of analysis: (1) sample units (fine scale) were randomly selected 2-m lengths of stream; (2) the intermediate scale was defined by the combination of stand ages on each side of the stream (Table 2), in this example there is a 190-year-old stand on one side and a 20-year-old stand on the other; (3) drainages (broad scale) were defined by the catchment basins including all sample units.

or were planted following clearcutting, a mosaic of young, mature, and old-growth stands is present, with forest stands ranging in age from <5 to >150 years. The study area is in the western hemlock (*Tsuga heterophylla*) vegetation zone of western Oregon (Franklin and Dyrness 1973).

METHODS

Sampling design

We considered all third-order drainages in the Eugene and Salem Districts of the BLM on the eastern slope of the Coast Range as potential study sites. To assure representation of a range of forest management conditions, drainages were stratified into low, moderate, and high categories of forest management intensity based on the percentage of forest <26 and >55 years old in each drainage. In low intensity drainages, <30% of forests were <26 years old and >60% were >55 years old. In moderate intensity drainages, 40–60% of forests were <26 years old and 40–60% were >55 years old. At least 60% of forests in high intensity drainages were <26 years old and <30% were >55 years old. In all categories, <10% of drainage area was composed of forest 26–55 years old. We randomly selected five high-, five moderate-, and six low-intensity drainages for study. Study drainages ranged from 94 to 197 ha in area and 205 to 662 m in mid-drainage elevation (Table 1).

We conducted field work from late June to late August in 1998 and mid-June to early September in 1999. We grouped drainages according to proximity for sampling, and three to four drainages were sampled per week. We divided the field season into early and late (1998) or early, mid, and late (1999) time periods, randomly selected a group of drainages to sample each week, and sampled each drainage once in each time period.

We sampled amphibians and classified microhabitat in 35 to 50 2-m lengths of stream (sample units) in each drainage (total $n = 702$; Fig. 1). Each sample unit was visited once during the study. Sample units were randomly selected so that each 2-m stream length in a drainage had an equal probability of being chosen (Stoddard 2001). In less than an average of five cases per drainage were two sample units located <10 m apart. Potential sample units had visible surface flow, were <0.5 m deep, and were located in ephemeral, discontinuous, or perennial streams.

Our sampling approach for amphibians was based on a previously developed protocol (Bury and Corn 1991). Stream searches were initiated at the downstream edge of a sample unit. After capturing amphibians during an initial visual search, one person slowly moved upstream, searching under undercut banks and potential cover by moving rocks and coarse wood, holding a dip net downstream of the area searched to capture dislodged amphibians. For each capture, species and life stage were recorded prior to release.

Habitat variables

We measured habitat parameters that have been shown or hypothesized to be important for amphibian species inhabiting Oregon Coast Range streams and were easily obtained in the field or derived from maps

TABLE 2. Forest age classes used to classify patches into eight categories.

	Age class			Confidence interval	
Category	Bank 1	Bank 2	Coefficient	Lower	Upper
1	0–15	0–15	−1.60	−2.57	−0.62
2	0–15	16–55	−0.72	−2.08	0.64
3	0–15	>55	−0.27	−1.14	0.60
4	16–55	16–55	−2.05	−3.36	−0.74
5	16–55	>55	−0.70	−1.52	0.12
6	56-105	56-105	−0.23	−0.98	−0.51
7	56-105	>105	1.03	0.37	1.69
8	>105	>105	reference	reference	reference

Notes: Coefficient values and confidence intervals for age class are results of analyses for larval tailed frogs based on the model with age combination and heat load index. Category 8 is the reference level.

or geographic information system (GIS) data layers. Habitat variables were measured at spatial scales we believed to be meaningful in describing individual or population responses of stream amphibians. For analysis of associations at intermediate and drainage scales, sample size restricted the number of variables and models we could consider (Burnham and Anderson 2002). Therefore, we primarily examined habitat characteristics that are known to be strongly influenced by forest management practices at these scales (see Stoddard 2001). Correlation analysis was performed to identify if coefficients were large.

Two-meter sample unit scale

For each 2-m sample unit, variables related to microhabitat structure, water velocity, surrounding vegetation, stream width, and elevation were recorded. We classified each sample unit by percentage of slow (pool and glide) and fast (riffle and cascade) water, and slow : fast ratios were calculated (hereafter referred to as slow water; range 0–100%). We visually estimated percent cover of rock substrates for each size class and used the ratio of rock substrates with little or no cover value (bedrock and particle size <32 mm in maximum length) to substrates with greater cover value (particle size >32 mm in maximum length) as an index of substrate condition (hereafter referred to as small substrate; range 0–100%). Slow water and small substrate were log transformed. Mean stream width was calculated by averaging the lower, middle, and upper profiles of each sample unit (range 0.14–4.07 m). We visually estimated proportion of undercut bank, percent cover of coarse wood, and percent cover of overstory trees and shrubs in each sample unit (range for all 0–100%). Elevation of each sample unit was obtained from a 10-m digital elevation model (DEM) in GIS (range 105–789 m).

Intermediate scale

We defined the intermediate spatial scale as the area around one or more contiguous sample units having the same grouping of forest age classes adjacent to the stream (Fig. 1), and hereafter refer to this as a patch.

Each patch (n = 153) contained 1–34 sample units and was classified in one of eight age-combination categories (Table 2). We classified age-combination categories based on their likely functional significance to stream habitat or because they served as a surrogate for time since disturbance (Stoddard 2001). Each age-combination category was represented by 10–34 patches. For each patch, we used digital orthophotographs to determine presence or absence of forested bands >55 years old occurring <15 m, 15–30 m, 30–46 m, and >46 m on each side of the stream. Only the >46 m band width, which corresponds to the riparian buffer for permanently flowing, non-fish-bearing streams under the Northwest Forest Plan (USDA and USDI 1994), was used for generating a priori hypotheses for habitat association models.

Stream aspect was measured at each sample unit in a patch. These measures were transformed into heat load using

$$\text{Heat load index} = 1 - \cos(\theta - 45)/2$$

where θ is aspect in degrees (Beers et al. 1966). This index is scaled from 0 to 1; streams with values near zero receive little solar insolation (north, northeast) and those with values near 1 receive high levels of solar insolation (south, southwest). For each sample unit, gradient was calculated from a 10-m DEM in Arc/Info (ESRI, Redlands, California, USA) and side slopes were measured using a clinometer (range 0.6–38%). We calculated mean heat index, stream gradient, and side slope for sample units in each patch.

Drainage scale

We defined drainage as the catchment basin above the confluence with a fourth-order stream. Where logistical constraints prohibited sampling an entire third-order drainage, we selected a random start point on the main third-order stream in the study drainage. Habitat characteristics were measured for whole drainages (n = 16) based on the intersection of delineated watersheds and BLM GIS data layers. We categorized age structure of drainages by the ratio of the area of <15-year-old forest to >15-year-old forest. Road density

was calculated as the ratio of road length to drainage area (range 8–34 m/ha), and overall slope stability was calculated as the percentage of drainage area with side slopes >60% (range 1–43%). We determined the proportion of stream length in drainages with forested bands >46 m in width on both sides of the stream and >55 years old (range 5–100%).

Statistical analyses

We used logistic regression (PROC GENMOD; SAS Institute 1999) to determine the probability of occurrence of larval and neotenic (sexually mature, unmetamorphosed adults) Pacific giant salamanders, larval tailed frogs, adult tailed frogs, and torrent salamanders in relation to habitat characteristics measured at each of the three spatial scales. We combined capture results for southern and Columbia torrent salamanders because they occurred in low numbers and habitat requirements of the species appear similar; both are associated with small, low-order, streams with little fine sediment and high gradients (see Diller and Wallace 1996, Welsh and Lind 1996, Wilkins and Peterson 2000). Adult and larval tailed frogs were considered separately due to differences in habitat use between life stages (de Vlaming and Bury 1970, Hunter 1998). Data from the two field seasons were pooled. The response variable was amphibian presence-absence for the sample-unit scale, binomial count of occupied sample units in a patch for the intermediate scale, and binomial count of occupied sample units in a drainage for the drainage scale.

We developed an a priori set of candidate models based on available biological information on the species of interest and compared them using information-theoretic methods. We only considered models that had four or fewer variables because complex models with large numbers of variables are of limited practical value for conservation and management, additional variables typically have minimal explanatory value, and including additional variables would inflate the number of potential models beyond the number that can be reliably analyzed given our sample size (Burnham and Anderson 2002). By restricting variables to those likely to be of ecological and conservation significance, we considered models with all possible combinations of these variables to represent reasonable a priori hypotheses. For each species or life stage, 163 models were considered at the sample-unit scale and 16 models were considered at both the intermediate and drainage scales.

We ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC_c) (but appropriate for large sample sizes) for the sample-unit scale and a generalization of AIC for overdispersed data with small sample sizes ($QAIC_c$) for the intermediate and drainage scales. The existence of overdispersion was determined by assessing the fit of a global model for each species. ΔAIC_c or $\Delta QAIC_c$ (hereafter Δ) is the difference between the AIC_c or $QAIC_c$

value for a given model and the lowest value in a set. Nested models with $\Delta \leq 2$ for large sample sizes (i.e., $n/K > 40$ where K = number of parameters) and with $\Delta \leq 4$ for small sample sizes ($n/K < 40$) have empirical support as being plausible (Burnham and Anderson 2002). Therefore, we present models with $\Delta \leq 2$ for the sample unit scale ($n/K = 140.40$) and with $\Delta \leq 4$ for intermediate ($n/K = 12.75$) and drainage ($n/K = 3.20$) scales.

We used Δ values to compute Akaike weights (w), which are estimates of the relative likelihood of each candidate model given the data (Burnham and Anderson 2002). We assessed evidence of the importance of individual parameters by summing w values of all models in which the parameter occurs and normalizing these values across the set of variables for each taxon (importance weights) (Burnham and Anderson 2002). We considered importance weights >0.20 to be high. A null model with only an intercept term was included in the full set of models to determine if the variables considered were valuable in predicting amphibian occurrence.

At the sample-unit scale we accounted for uncertainty in model selection by calculating sizes of effects of variables from model-averaged estimates and confidence intervals (Burnham and Anderson 2002). We did not use model-averaged estimates at intermediate and drainage scales because variables measured at these scales were correlated and therefore interpretation of effects depends on which combination of variables occur in a model.

At the intermediate scale, our a priori hypotheses only considered one forest band width. After concluding from our initial analysis that a forested band >46 m in width on each side of the stream was important for amphibians, we explored potential influences of forest band width on amphibian occurrence. We used logistic regression (PROC GENMOD, SAS Institute 1999) to determine the probability of occurrence of each species in relation to four band widths, <15 m, 15–30 m, 30–46 m, and >46 m, and used Wald's test to determine significance of odds of occurrence relative to a reference level of >46 m. We used one-way analysis of variance (PROC ANOVA, SAS Institute 1999) to determine if mean values of side slope and stream gradient, which are potentially related to forest condition around a stream, differed by forest band width. Differences in mean values would suggest that amphibian responses could be related to these habitat characteristics and not to the width of forested habitat around a stream.

RESULTS

Amphibian occurrence

We captured 1568 amphibians in 702 sample units in 16 drainages. Neotenic and larval Pacific salamanders ($n = 1020$, 64% of total captures), were

TABLE 3. Results of logistic regression models for predicting amphibian occurrence at the sample unit spatial scale.

| | Variable | | | | | | | | | | | |
Species	Small substrate	Stream width	Elevation	Slow water	Undercut bank	Shrub cover	Overstory cover	Coarse wood	K†	Δ‡	w‡	Evidence ratio§
Pacific giant salamander	−	+				+			4	0.00	0.113	1.00
	−	+							3	0.17	0.104	1.09
	−	+		−		+			5	0.42	0.092	1.23
	−	+		−					4	0.66	0.081	1.39
	−	+			+	+			5	1.37	0.057	1.98
	−	+			+				4	1.40	0.056	2.01
	−	+	−			+			5	1.73	0.048	2.37
	−	+	−						4	1.82	0.046	2.48
Larval tailed frog	−	+		−	−				5	0.00	0.215	1.00
	−	+		−					4	0.48	0.169	1.27
	−	+	−	−					5	1.80	0.087	2.46
	−	+		−				+	5	1.94	0.082	2.64
Adult tailed frog	−	−	+	+					5	0.00	0.140	1.00
	−		+	+					4	0.39	0.115	1.22
	−	−	+						4	0.67	0.100	1.40
	−		+						3	1.35	0.071	1.97
	−		+	+				+	5	1.75	0.059	2.40
	−	−	+			+			5	1.98	0.052	2.69
Torrent salamander	−		+		+				4	0.00	0.104	1.00
	−		+						3	0.30	0.089	1.16
	−	−	+		+				5	0.88	0.067	1.55
	−		+				+		4	1.24	0.056	1.86
	−	−	+						4	1.25	0.056	1.86
	−		+		+		+		5	1.38	0.052	1.99
	−		+		+			−	5	1.55	0.048	2.17
	−		+	−	+				5	1.67	0.045	2.30
	−		+		+	+			5	1.80	0.042	2.46
	−		+					−	4	1.94	0.039	2.63
	−		+			+			4	2.00	0.038	2.71

Notes: All models with Δ < 2 are presented. Models (rows) are ordered by increasing Δ values for a species. Negative and positive signs indicate that a variable occurred in a model and the sign of the variable coefficient.

† K represents the number of parameters in a model.

‡ See *Methods: Statistical analyses* for definitions.

§ Evidence ratio or ratio of weights of two competing models is a multiplicative factor for the likelihood of the best model compared to an alternative model.

found in 373 of 702 (53%) sample units, and occurred in all drainages. Larval tailed frogs ($n = 348$, 22%) were found in 115 (16%) sample units in 13 (81%) drainages. Adult tailed frogs ($n = 43$, 3%) occurred in 32 (4.6%) sample units in nine (56%) drainages. Torrent salamanders ($n = 157$, 10%) were found in 67 (9.5%) sample units and occurred in all but one drainage (94%).

TABLE 4. Normalized importance weights for variables measured at the sample unit spatial scale.

Variable	Pacific giant salamander	Larval tailed frog	Adult tailed frog	Torrent salamander
Small substrate	0.29	0.28	0.28	0.27
Stream width	0.29	0.26	0.12	0.07
Elevation	0.05	0.04	0.28	0.30
Slow water	0.09	0.20	0.13	0.05
Undercut bank	0.06	0.11	0.04	0.12
Shrub cover	0.11	0.03	0.05	0.06
Overstory cover	0.05	0.05	0.04	0.07
Coarse wood	0.05	0.04	0.05	0.06

Note: Variables are ordered by the mean of the importance weights for each variable.

Sample unit scale

All competing models for Pacific giant salamanders included small substrate and stream width (Table 3). These were the only variables with importance values >0.20 for this species (Table 4). For larval tailed frogs, all competing models included small substrate, stream width, and slow water. Pacific giant salamanders and larval tailed frogs were negatively associated with proportion of small substrate and were positively associated with stream width. Based on model-averaged estimates, doubling the ratio of fine to coarse sediments (small substrate) was associated with a 22% decrease in odds of occurrence of Pacific giant salamanders (odds = 0.78; 95% CI, 0.73–0.84) and a 37% decrease in odds of occurrence of larval tailed frogs (odds = 0.63; 95% CI, 0.54–0.73). For each additional meter of stream width, odds of occurrence of Pacific giant salamanders increased by 72% (odds = 1.72; 95% CI, 1.31–2.24) and odds of occurrence of larval tailed frogs increased by 61% (odds = 1.61; 95% CI, 1.19–2.19). Doubling the ratio of slow to fast water decreased odds of occurrence of larval tailed frogs by 5% (odds = 0.95; 95% CI, 0.90–1.00).

TABLE 5. Results of logistic regression models for predicting amphibian occurrence at the intermediate scale.

Species	Forested band	Stream gradient	Heat load index	Age combination†	K	Δ	w	Evidence ratio
Pacific giant salamander	+	−	−		5	0.00	0.627	1.00
	+	−			4	1.91	0.241	2.60
Larval tailed frog		−	−	±	11	0.00	0.251	1.00
		−		±	10	0.01	0.250	1.01
				±	9	1.45	0.122	2.06
			−	±	10	1.80	0.102	2.46
	+	−	−	±	12	2.14	0.086	2.91
	+		−	±	11	2.19	0.084	2.99
	+			±	10	3.53	0.043	5.84
	+	−		±	11	3.83	0.037	6.79
Adult tailed frog	+				3	0.00	0.302	1.00
	+	+			4	0.02	0.298	1.01
	+	+	−		5	1.38	0.151	1.99
	+		−		4	1.40	0.149	2.02
Torrent salamander	+	+			4	0.00	0.488	1.00
	+	+	−		5	0.36	0.409	1.20

Notes: Models with $\Delta < 4$ are presented. See Table 3 for a description of the table format.
† Variable age combination had eight levels and sign of coefficient differed with level (see Table 2).

Small substrate and elevation occurred in all competing models for adult tailed frogs and torrent salamanders (Table 3) and were the only variables examined with importance values >0.20 for these groups (Table 4). Based on model-averaged estimates, doubling the ratio of fine to coarse substrates decreased odds of occurrence of adult tailed frogs by 33% (odds = 0.67; 95% CI, 0.53–0.84) and of torrent salamanders by 14% (odds = 0.86; 95% CI, 0.75–0.97). However, even the probability of finding a torrent salamander in a sample unit with no small substrate was low (0.06, based on the model with only substrate and elevation). A 100-m increase in elevation increased odds of occurrence of adult tailed frogs by 66% (odds = 1.66; 95% CI, 1.31–2.10) and odds of occurrence of torrent salamanders by 62% (odds = 1.62; 95% CI, 1.37–1.91).

The null model performed poorly for all amphibians at the sample-unit scale. The null model had $\Delta > 26.96$ and $w < 1.96 \times 10^{-7}$ for all groups, indicating that the habitat variables examined were valuable in explaining amphibian occurrence at this spatial scale. Percent cover of overstory and coarse wood did not occur in any of the strongly competing models.

Intermediate scale

At the intermediate scale, all competing models for Pacific giant salamanders, adult tailed frogs, and torrent salamanders included forested band (Table 5). Of 153 patches, 58 (38%) had forested bands >46 m in width. Forested band had the highest importance weight for Pacific giant salamanders and adult tailed frogs and was nearly the highest for torrent salamanders (Table 6). The odds of finding a Pacific giant salamander in a stream with >46-m forested bands were 213% (odds = 3.13; 95% CI, 2.00–4.76) higher than the odds of

finding this species in a stream without forested bands of this size. Similarly, the increase in odds of occurrence was 360% (odds = 4.60; 95% CI, 1.42–14.86) for adult tailed frogs and 178% (odds = 2.78; 95% CI, 1.30–5.88) for torrent salamanders. The probability of finding an adult tailed frog or a torrent salamander in a stream without a forested band was only 0.02. This probability increased for torrent salamanders to 0.05 and to 0.08 for adult tailed frogs when the stream had forested bands. Stream gradient occurred in the best models for Pacific giant salamanders and torrent salamanders and in a strongly competing model for adult tailed frogs ($\Delta = 0.02$), although the direction of responses differed among species (Table 5). Based on these models, as gradient increased by 10%, the odds of occurrence decreased by 40% (odds = 0.60; 95% CI, 0.41–0.89) for Pacific giant salamanders and increased by 84% (odds = 1.84; 95% CI, 0.84–4.05) for adult tailed frogs and 159% (odds = 2.59; 95% CI, 1.53–4.40) for torrent salamanders. Heat load index also occurred in the best model for Pacific giant salamanders (Table 5). After accounting for other variables in the model, moving from a northeast-facing

TABLE 6. Normalized importance weights for variables measured at the intermediate scale.

Variable	Pacific giant salamander	Larval tailed frog	Adult tailed frog	Torrent salamander
Forested band	0.38	0.11	0.51	0.38
Stream gradient	0.34	0.20	0.28	0.42
Heat load index	0.27	0.28	0.20	0.20
Age combination	0.01	0.40	0.01	0.00

Note: Variables are ordered by the mean of the importance weights for each variable.

TABLE 7. Results of logistic regression models for predicting amphibian occurrence at the drainage scale.

| | Variable | | | | | | | |
Species	Forested band	Slope > 60%	Young forest	Roads	K	Δ	w	Evidence ratio
Pacific giant salamander	+				3	0.00	0.568	1.00
	+	+			4	2.78	0.141	4.02
	+			−	4	3.39	0.104	5.45
	+		−		4	3.62	0.093	6.10
Larval tailed frog	+				3	0.00	0.392	1.00
	+	−			4	1.20	0.215	1.82
	+	−	−		5	2.61	0.106	3.70
	+		−		4	2.69	0.102	3.84
	+			−	4	3.49	0.069	5.71
Adult tailed frog	+				3	0.00	0.473	1.00
	+	−			4	2.22	0.156	3.03
	+			−	4	2.29	0.150	3.14
	+		−		4	3.62	0.077	6.12
Torrent salamander					2	0.00	0.409	1.00
				−	3	2.54	0.115	3.56
	+				3	2.63	0.110	3.73
				−	3	2.70	0.106	3.86
			−		3	3.02	0.090	4.53

Notes: Models with Δ < 4 are presented. See Table 3 for a description of the table format.

stream to a southwest-facing stream resulted in a 54% decrease in odds of occurrence (odds = 0.46; 95% CI, 0.21–0.98).

Age of forest along streams (age combination) had low importance values (≤0.01) for Pacific giant salamanders, adult tailed frogs, and torrent salamanders (Table 6), but occurred in all competing models (Table 5) and had the highest importance weight for larval tailed frogs (Table 6). Occurrence of larval tailed frogs was positively associated with streams having forests >105 years old on one or both sides and was negatively associated with streams that did not (Table 2). Odds of occurrence decreased most when 0–15 or 16–55-year-old forests occurred on each side of the stream (categories 1 and 4, Table 2). Based on the model with heat load index and age combination, odds of finding a larval tailed frog in a stream with 56–105-year-old forest on one side and forest >105 years old on the other side (category 7, Table 2) are 1282% greater (odds = 13.82; 95% CI, 5.58–45.15) than odds of finding a larval tailed frog in a stream surrounded by 0–15-year-old forest (category 1, Table 2) and 2079% greater (odds = 21.79; 95% CI, 6.62–100.48) than odds of finding a larval

TABLE 8. Normalized importance weights for variables measured at the drainage spatial scale.

Variable	Pacific giant salamander	Larval tailed frog	Adult tailed frog	Torrent salamander
Forested band	0.66	0.53	0.61	0.25
Slope > 60%	0.14	0.23	0.15	0.21
Young forest	0.10	0.17	0.11	0.27
Roads	0.10	0.07	0.14	0.27

Note: Variables are ordered by the mean of the importance weights for each variable.

tailed frog in a stream bordered by 16–55-year-old forests (category 4, Table 2). Heat load index and stream gradient also occurred in the best model for larval tailed frogs (Table 5). Based on the model with age combination and heat load index, moving from a northeast-facing stream to a southwest-facing stream decreased odds of finding a larval tailed frog by 61% (odds = 0.39; 95% CI, 0.15–1.03). As gradient increased by 10%, odds of occurrence decreased by 4% (odds = 0.96; 95% CI, 0.92–1.01).

Null models for all species had high Δ values and low w's. For Pacific giant salamanders and larval tailed frogs, null models had Δ > 34.99 and w < 1.59 × 10^{-8}. Null models for adult tailed frogs and torrent salamanders had Δ > 5.87 and w < 0.02.

Drainage scale

Forested band occurred in all competing models for Pacific giant salamanders, larval tailed frogs, and adult tailed frogs at the drainage scale, was the only variable in models with the lowest Δ value for these groups (Table 7), and had importance values >0.50 for each group (Table 8). Based on models with Δ = 0, each increase of 10 percentage points in stream length with >46-m forested bands increased odds of occurrence of Pacific giant salamanders by 27% (odds = 1.27; 95% CI, 1.13–1.42), of larval tailed frogs by 24% (odds = 1.24; 95% CI, 1.12–1.38) and of adult tailed frogs by 27% (odds = 1.27; 95% CI, 1.11–1.44). For each of these groups, odds of occurrence roughly doubled with an increase of 30 percentage points in amount of stream length having forested bands. However, probability of occurrence was low for all species except Pacific giant salamanders; when percent of stream length in a drainage was 30%, probability of occurrence was 0.46 for
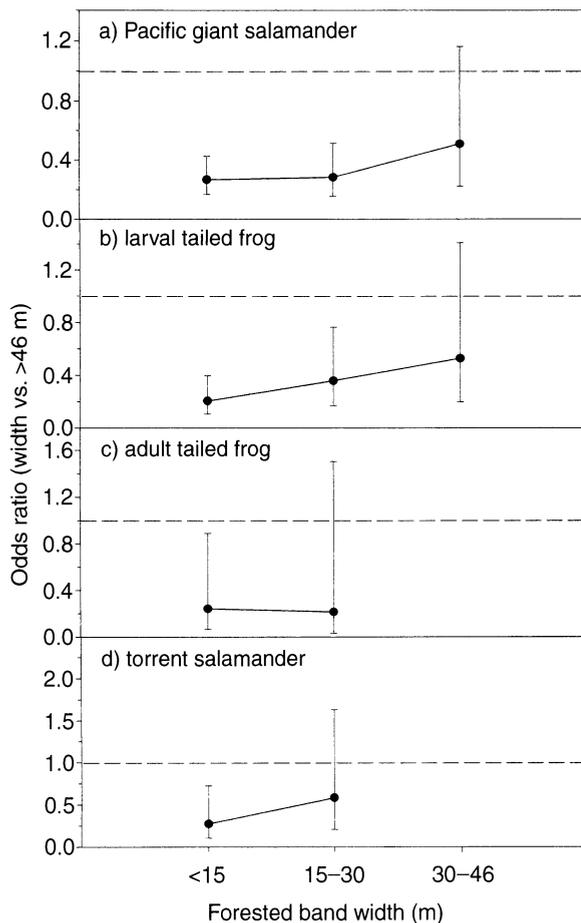
FIG. 2. Relationships between odds ratios for stream amphibians and forested band width. Points represent the ratio of odds of finding each species in a stream (intermediate spatial scale) bordered by forested bands of various widths compared to odds of occurrence in streams with forested bands >46 m in width (and 95% CI). The dashed line (odds ratio = 1) represents the point at which odds of occurrence do not differ. Odds ratios for torrent salamanders and adult tailed frogs were calculated using data from only two band width age classes because these species did not occur in stands having 30–46 m forested bands.

Pacific giant salamanders, 0.12 for larval tailed frogs, and 0.03 for adult tailed frogs.

The null model was selected as the best model for torrent salamanders at the drainage spatial scale (Table 7). This suggests that torrent salamanders do not respond at this scale to changes in variables we included in our analysis. Out of 16 models, null models were ranked ninth (Δ = 8.50) for Pacific giant salamanders, 14th (Δ = 13.74) for larval tailed frogs, and eighth (Δ = 6.20) for adult tailed frogs.

Forest band width

In an exploratory analysis of the influence of forest band width on amphibian occurrence at the intermediate scale, we found the relative odds of finding amphibians in streams showed an increasing trend as band width increased (Fig. 2). For example, odds of finding

a larval tailed frog in a stream surrounded by forested bands >46 m in width were approximately five times greater than the odds of occurrence in a stream surrounded by forested habitat <15 m in width (odds ratio = 0.2045; Fig. 2). Only odds of occurrence in the <15 m and 15–30 m band widths were statistically different from odds of occurrence in band widths >46 m for Pacific giant salamanders (<15 m, χ^2 = 31.01, P < 0.0001; 15–30 m, χ^2 = 17.24, P < 0.0001) and larval tailed frogs (<15 m, χ^2 = 22.26, P < 0.0001; 15–30 m, χ^2 = 7.07, P = 0.0078). For adult tailed frogs and torrent salamanders, only odds of occurrence in streams with band widths <15 m were statistically different from odds of occurrence in streams with >46 m band widths (Fig. 2; adult tailed frogs, χ^2 = 4.56, P = 0.0328; torrent salamanders, χ^2 = 6.84, P = 0.0089). Adult tailed frogs and torrent salamanders did not occur in any streams surrounded by forested bands 30–46 m in width. Mean values of side slope and stream gradient at the intermediate spatial scale did not differ by band width (side slope, F = 2.33, P = 0.08; stream gradient, F = 1.76, P = 0.16), suggesting odds ratios in Fig. 2 reflect influences of forest band widths and not influences of other habitat characteristics.

DISCUSSION

The combined influences of habitat structure and geophysical location were important in determining amphibian occurrence. In most cases, the importance of these variables can be related to known life-history requirements. Results at fine spatial scales appear to reflect constraints on individuals (e.g., the importance of large substrate) whereas those at broader scales may reflect biological constraints manifested at the population level (e.g., aspect and presence or amount of forested riparian areas that influence stream microclimate).

Amphibian responses at one scale were generally compatible with those at other spatial scales. For example, the likelihood of finding Pacific giant salamanders and larval tailed frogs was greater in wider streams (sample unit scale) with lower gradients (intermediate scale). Conversely, torrent salamanders were more likely to occur in higher elevation streams (sample unit scale) having higher gradients (intermediate scale). The occurrence of larval tailed frogs in larger streams and adults in smaller streams has been documented (Hunter 1998) and may be explained by breeding ecology. Because male tailed frogs cannot attract or locate females to mate by calling (Stebbins and Cohen 1995), adults may move upstream to smaller, higher elevation streams to congregate during the breeding season (Kelsey 1995). Hatchlings and tadpoles are thought to drift or be washed down the stream network (Metter 1964, Daugherty and Sheldon 1982), and tadpoles may distribute themselves by age class based on thermal preferences (de Vlaming and Bury 1970). Occurrence or abundance of Pacific giant salamanders often is posi-

PLATE 1.　Torrent salamander *Rhyacotriton variegatus*, Oregon Coast Range. Photo credit: M. Stoddard.

tively associated with factors related to stream size, such as depth and subdrainage area (e.g., Hunter 1998). In general, this species has broader habitat requirements than other stream amphibians and may be able to tolerate the greater temperature extremes that may exist in wider streams with less canopy cover (Nussbaum et al. 1983). Torrent salamanders (see Plate 1), however, are generally associated with small, high elevation, high gradient streams and seeps with cold, highly oxygenated water (Nussbaum et al. 1983). Because they have highly reduced lungs and breathe primarily through their skin (Stebbins and Cohen 1995), torrent salamanders require this type of habitat to respire efficiently.

Contrary to results for other taxa examined in this study, we found that torrent salamanders were not associated with characteristics measured at the drainage scale. This may reflect low sensitivity to broad spatial scale characteristics, but it is possible that characteristics besides those we measured at the drainage scale, such as type of surficial geology, may better predict torrent salamander occurrence. Wilkins and Peterson (2000) suggested that streams with basaltic substrates should have higher priority for conservation because amphibian abundances were greater in these streams than in streams with sedimentary substrates. However,

stream amphibians have been shown to be abundant in areas where sedimentary geology is widespread (Adams and Bury 2002), and therefore using geology type to identify areas of conservation value may be appropriate only in certain regions.

Our data suggest that regulating sediment load has important conservation implications for stream amphibians. At the finest spatial scale, occurrence of all amphibians was negatively associated with small substrate. Fine sediments can fill interstitial spaces that are used as oviposition sites and refugia by amphibians (Bury and Corn 1988, Corn and Bury 1989) and coarse substrates are used as cover from predators, such as salmonids and Pacific giant salamanders (Metter 1964, Good and Wake 1992). Increases in fine sediments, along with increases in stream temperatures, have been hypothesized to be causal factors underlying decreases in stream amphibian populations in watersheds managed for timber production (Bury and Corn 1988, Corn and Bury 1989). Streamside or upslope logging and road building resulted in increased sedimentation in streams in several studies (Beschta 1978, Murphy et al. 1981, Beschta et al. 1987), although presence and amount of sediment was highly variable depending on geomorphology and management practices used. In one study in western Oregon, sediment yields tripled in a

drainage that was 82% clearcut, and these yields remained elevated for five years after harvest (Beschta 1978). This change in sediment yield is greater than the degree of change in small substrate that we interpret in our results (doubling fine : coarse substrate), suggesting that decreases in probability of occurrence of some amphibian species may be greater in heavily managed forests than those we present.

Our findings also suggest that maintaining mature forests around streams plays an important role in conservation of stream amphibians at broad spatial scales. The relationship between forest condition around streams and occurrence of stream amphibians may be related to the role that streamside vegetation plays in the moderation of stream temperatures (Brown and Krygier 1970, Beschta et al. 1987) and riparian microclimate (Brosofske et al. 1997, Dong et al. 1998, Chen et al. 1999). Maintaining cool stream temperatures is important for larval tailed frogs, which have a narrow range of thermal tolerance (Brattstrom 1963, de Vlaming and Bury 1970, Brown 1975), and for torrent salamanders, which are associated with cool water (Nussbaum and Tait 1977, Good and Wake 1992). Air temperature and humidity may affect use of upslope habitat by metamorphosed stream amphibians, which rely partially on cutaneous respiration and therefore require cool, moist microclimates when foraging or dispersing away from the streambed. Disturbance of riparian and upslope habitat therefore could affect individuals by altering foraging habitat, populations by restricting movements to breeding sites, and metapopulations by disrupting connectivity among patches thereby limiting dispersal.

Forested riparian habitat may be particularly important for adult tailed frogs and torrent salamanders. Although these groups can occur in high densities in some areas (Diller and Wallace 1996), they often occur in relatively low numbers in others (Steele et al. 2003). Consequently, we speculate that even with highly suitable habitat conditions, small changes in habitat suitability may affect them dramatically. Results from our study show these groups are most likely to occur at high elevations in small, steep streams with low levels of sediment. Forest management activities that increase sedimentation or stream temperatures, or disturb dispersal habitat (particularly for tailed frogs) by removing riparian vegetation around small streams should be minimized if a goal is to conserve adult tailed frogs and torrent salamanders.

We caution that results of our comparisons of forested band widths may have been compromised by small sample sizes. As a result, large error bars on relative odds may have obscured biologically significant differences among band widths. In addition, we sampled only during the summer months, when precipitation and stream levels were low and amphibians may have been concentrated in streams. During wetter months, distributions of amphibians may change as water levels rise, and metamorphosed amphibians likely use riparian and upslope habitats more often to forage or disperse. Management implications from our analysis may therefore be conservative with regard to width of forested bands needed in riparian areas. In coniferous forests in the Pacific Northwest where maintaining populations of stream amphibians is a conservation priority, we recommend maintaining forested bands >46 m in width bordering streams having high-quality instream habitat (e.g., low levels of small substrate) and desirable geophysical characteristics (e.g., north-facing aspects).

Geophysical characteristics of streams or drainages were important for all taxa at the intermediate scale. In particular, Pacific giant salamanders and torrent salamanders were strongly associated with stream gradient. Our results for torrent salamanders are consistent with those of Corn and Bury (1989) who documented higher densities of southern torrent salamanders in logged streams with high gradients than in those with low gradients and hypothesized that stream gradient can mitigate the effects of logging by facilitating transport of fine sediments downstream. Corn and Bury (1989) also found Pacific giant salamanders occurred in high densities in high-gradient logged streams; in contrast, we observed a negative relationship between gradient and occurrence of this species. Gradient always occurred with forested band when this variable occurred in a strongly competing model both for Pacific giant salamanders and torrent salamanders, suggesting the effect of one variable may depend on the other, and therefore both should be considered when establishing conservation measures for these species.

Aspect was particularly important at the intermediate spatial scale for larval tailed frogs and Pacific giant salamanders, usually in concert with the presence of a forested band along the stream. Occurrence or abundance of some stream amphibians has been positively associated with north-facing aspects (Diller and Wallace 1996, 1999, Wilkins and Peterson 2000, Adams and Bury 2002). The influence of aspect may be attributed to differences in the amount of solar radiation reaching streams, which may affect stream microclimate. Larval tailed frogs and Pacific giant salamanders may be most likely to persist in north-facing streams, and these areas could be given conservation priority. However, in some situations small populations on south-facing aspects also may have conservation importance, and these populations may be more sensitive to habitat manipulation.

Our findings corroborate previous research on amphibian habitat associations, but also provide some insight into potential linkages between amphibian responses across scales. Understanding these linkages is particularly important in the Pacific Northwest where conservation efforts for sensitive species, such as southern torrent salamanders and tailed frogs, must be implemented in heavily-managed landscapes. Manage-

ment-related factors that operate at broad scales apparently can affect individuals by altering instream habitat, and the sum of effects on individuals may have consequences for population viability. However, factors such as gradient, aspect, and geology may mitigate the potential negative influences of these activities on stream habitat at both fine and broad scales. An effective conservation strategy might involve developing a decision tree and using characteristics identified as important in studies such as ours to prioritize conservation areas. Information on habitat quality and influences of disturbance can be used to identify conservation priorities on managed landscapes for other species as well.

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