AN ABSTRACT OF THE THESIS OF

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Most recent research on stream amphibians in the Pacific Northwest has focused on associations with reach-level or stand-level environmental features. Little is known about landscape-level distributions of these species or landscape-level aspects of their life-histories. I used a watershed-wide sample and logistic regression to develop models and maps of probability of occurrence throughout the Blue River watershed stream network using widely-available and/or easily-derivable explanatory variables in pixelized GIS format. I also developed an innovative multi-scale model-building process to discern the strength of association of site-level variables in the presence of larger-scale, context variables. Finally, I investigated size distributions of stream amphibians within the stream network. Cascade torrent salamander larvae occurred only in a narrow range of stream sizes in the stream network. Tailed frog life stages differed in their occurrence within the stream network. Average sizes of Pacific giant salamander larvae were larger in larger streams. The strength of association of abstract, large-scale variables in the presence of detailed instream variables in multi-scale models indicated that some aspects of the environment which more directly affect the distribution of stream amphibians were not measured.

Watershed-level Patterns among Stream Amphibians in the Blue River Watershed, West-Central Cascades of Oregon

by

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APPROVED:

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Chair of Department of Forest Science

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Matthew G. Hunter, Author

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INTRODUCTION

This study was initiated as a first step to develop an amphibian monitoring strategy for the Blue River Landscape Project (Cissel 1997), and to investigate landscape-level aspects of stream amphibian life-histories in mountain watersheds. Information derived from this effort will be used to develop a multi-scale, long-term amphibian monitoring strategy for the watershed. It is hoped that this first attempt to understand watershed-level distributions and life-histories of stream amphibians will initiate many similar studies, both for the purposes of understanding landscape-level life-histories of these species, and to develop monitoring approaches that will help guide management of aquatic and terrestrial ecosystems at the watershed level. Stream amphibians present in this watershed are the Cascade torrent salamander (*Rhyacotriton cascadae*), Pacific giant salamander (*Dicamptodon tenebrosus*), and tailed frog (*Ascaphus truei*).

MANAGEMENT CONTEXT

The Blue River watershed is within the Central Cascades Adaptive Management Area designated by the Northwest Forest Plan (NFP) (USDA and USDI 1994). Each Adaptive Management Area (AMA) designated in the NFP was assigned a particular emphasis. The emphasis for this AMA includes “intensive research on ecosystem and landscape processes and its application to forest management in experiments and demonstrations at the stand and watershed level; approaches for integrating forest and stream management objectives and on implications of natural disturbance regimes...” (USDA and USDI 1994, p D-12). The Blue River Landscape Project (BRLP) was initiated to “develop, demonstrate and test an integrated landscape management strategy to achieve ecological and social objectives based upon historical disturbance regimes for the Blue River watershed," with the intent to meet NFP objectives. Many of the concepts developed in the Augusta Creek Project (Cissel et al. in press) are incorporated and refined in the BRLP. One of those concepts is the use of historic fire regimes to guide rates of timber harvest, size of treated areas, and levels of tree retention in harvest areas and along streams. Another key component is the designation of headwater aquatic reserves in which complete headwater basins are protected in a few locations throughout the watershed. The BRLP is being evaluated in two primary ways: 1) Comparison to NFP objectives, and 2) Comparison to a simulated, unmodified implementation of the NFP.

A characteristic feature of the BRLP, is the long time period (up to 400 years) and large spatial extent (10,000 to 50,000 ha) for which management alternatives are developed and evaluated. "Ecosystem Management", now prevalent throughout the United States (Grumbine 1997, Swanson 1996), encourages an integrated approach to management of many resources at many temporal and spatial scales. If amphibian populations are going to be considered in watershed-level planning and evaluation, distribution and life-histories will need to be understood at that scale. The kind of information that would be useful for planning and evaluation at that scale include 1) distribution within watersheds, 2) a spatial and temporal understanding of seasonal movements, 3) distribution of important breeding and non-breeding sites, 4) rates of recolonization of disturbed sites. However, even anecdotal observations are lacking for some of these states and processes.

RESEARCH CONTEXT

Most habitat studies of stream amphibians in the Pacific Northwest have investigated the associations of presence, density, biomass, and/or diversity of these species with site-level variables such as stream substrate composition or adjacency of previous timber harvest (e.g. Bury and Corn 1991, Bury et al. 1991, Corn and Bury 1989, Diller and Wallace 1996, Hawkins et al. 1983, Murphy and Hall 1981, Murphy et al. 1981, Welsh and Lind 1991, Welsh and Lind 1996). Sample units generally have been small patches of stream habitat, 5-20 meters in length. These studies purposely controlled the size of stream sampled, some more loosely than others, and typically have not controlled or measured any larger-extent variables. Stream sizes sampled have typically been described as 1st to 3rd order, or as being within a certain range of widths (such as <2 m). Studies such as these give insight into hiding cover associations, relationship of substrate composition with amphibian density, local effects of timber harvest, and variation in these associations at the resolution of a sub-reach or of several channel units (Figure 1).

At the other end of the spectrum, species' ranges have long been of interest and updates have been published as new information was acquired (Blaustein et al. 1995, Bury et al. 1991, Leonard et al. 1993, Nussbaum et al. 1983). These delineate the outer limits of the known range of each species, and occasionally identify disjunct subpopulations. The outer boundary of the true ranges are thought to change slowly and likely reflect very long-term interactions of the species with climate, geologic events, and associated vegetation and hydrologic regimes (Figure 1). For example, Good and Wake (1992) speculated that the distribution and speciation of the *Rhyacotriton* complex was related to volcanic activity and glacial movements.

However, I am aware of no published work that has investigated patterns of change and/or variation in amphibian populations or life-history attributes at a medium scale within the range of a species. Aspects of amphibian life-histories that occur at medium to large spatial and temporal scales include moderate-grain patchiness of occurrence; distributional limits of nest-placement and life stages within stream networks; strategies for resisting or responding to disturbance; time to metamorphosis; extent, direction, and distribution of dispersal of metamorphs; timing of food source availability; and direction, breadth and rate of gene flow (Figure 1). Physical phenomena that operate at the landscape scale, and may be associated with these life histories include seasonal presence of surface water; occurrence and frequency of debris flows; geomorphic and geologic landforms that provide a setting and material source for streams (such as steep slopes and shallow soils vs. gentle slopes and deep soils); variation in peak flows (e.g. streams receiving peak discharges from snow melt, vs. rain-on-snow events, vs. primarily rain)(Perkins 1997); and major vegetation zones (conifer-dominated forest, vs. conifer-broadleaf forest, vs. broadleaf forest, versus open forest, versus savannah, etc.)(Figure 1).

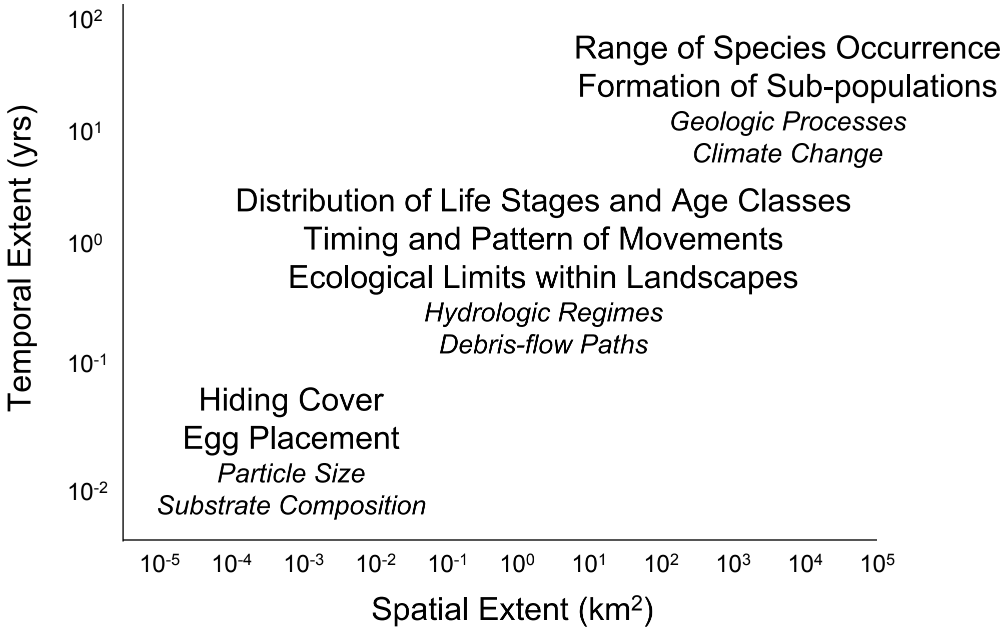


Figure 1. Conceptual association of amphibian life-history attributes and physical phenomena at several spatial and temporal scales.

Few studies have examined associations of amphibians with measures of physical characteristics, such as stream size, geologic landforms, and elevation, that change predictably or visibly over landscapes within the range of a species. While amphibians are frequently rumored to have "patchy" distributions, no examples are available which demonstrate patchiness of stream amphibians at any resolution. Comprehensive treatments of amphibian natural history (Stebbins and Cohen 1995) and biology (Duellman and Trueb 1994) devote merely a few paragraphs to landscape-level movements of amphibians.

Examples of information needs at these scales are scattered through the literature on these species. Corn and Bury (1989) stated “Future studies of aquatic amphibians in the Pacific Northwest should include intensive studies of whole drainage basins, and further research is needed on the natural history of all species.” Again, Bury and Corn (1991) stated “Studies of single watersheds are needed to determine the distributions of amphibian populations from headwaters to higher order streams.” Torrent salamanders are known to inhabit small streams and seeps (Nussbaum et al. 1983, Good and Wake 1992, Leonard et al. 1993, Murphy 1979), but quantitative measures from small to large streams are lacking. Corn and Bury (1989), among others, have questioned whether electroshocking methods are biased toward larger-sized giant salamanders or whether there are demographic differences in giant salamanders in streams of different sizes. A watershed-level study would be required to answer that question. In addition, Vannote et al. (1980), stated in the “River Continuum Concept” that a host of physical and biological phenomena change from headwaters to larger streams; however, amphibian distribution over this gradient has not been studied.

Knowledge of many basic attributes of stream amphibian life histories, namely their distribution, nest locations, and movements, is incomplete at the watershed level. No data are available that allow a landscape or watershed-level estimate of distribution. There are no published data that describe the timing, extent, duration, and direction of seasonal, landscape-level movements of these species. There is no information describing the watershed-level distribution of important breeding areas or larval rearing areas. There is no information describing the effects of instream disturbances such as debris flows, rates of recolonization, and differences between “natural” and road- or harvest-induced events. While a single study would not be able to address all these needs, investigating the watershed-level distribution of each species, their numbers, life stages, and size distribution would allow future investigators to formulate more specific hypotheses of life-histories at the landscape level for each species, and of the effects of landscape management strategies.

LIFE HISTORIES OF PACIFIC NORTHWEST STREAM AMPHIBIANS

Stream amphibians are flowing-water breeders. In the Pacific Northwest, the term "stream" alone does not adequately capture the type of aquatic ecosystem inhabited by these species. Many lowland, very low-gradient streams effectively become warm, lentic habitats during summer and function as breeding habitat for more "still-water breeders" rather than for these species. However, in the Blue River watershed, and most mountainous streams within the range of these species, streams are generally cool and in motion, and define the ecosystem occupied by these species. In mountainous areas, even some small ponds created by beaver (*Castor canadensis*) are cool enough to be occupied by Pacific giant salamanders (pers. obs.).

Each of these species passes through two life stages: a larval form and a metamorphosed form. Paedogenesis (attainment of sexual maturity while retaining many larval features such as external gills and specific bone structures) is known only for giant salamanders, though this may occur rarely in torrent salamanders (unpublished data).

Very little is known about egg placement in these species. Only about 5 nests of giant salamanders (*Dicamptodon* spp.) have been observed (Henry and Twitty 1940, Nussbaum 1969b, Marc Hayes pers. comm.); 3 nests of torrent salamanders (*Rhyacotriton* spp.) (Nussbaum 1969a, Karraker 1997); and about 10-15 nests of tailed frogs (Gaige 1920, Metter 1964, Metter 1967, Franz 1970, Brown 1975, Adams 1993). No nests of any stream amphibian species have been described in detail from the Oregon Cascades, though Metter (1967) mentioned finding two tailed frog nests there. In general, these amphibian nests have been hidden under large rocks, logs, or in deep bedrock cracks. While these observations cannot be considered normative for the species, they indicate a selection of relatively stable environments for egg placement within an otherwise highly dynamic system.

Based on only three torrent salamander nests, these species may be either communal egg-layers or may lay individual clutches, and probably do not attend the eggs (Nussbaum 1969a, Karracker 1997). Giant salamanders appear to lay single-parent clutches which are guarded by the female (Nussbaum 1969b, Marc Hayes pers. comm.). Tailed frogs may lay single or communal nests and do not attend the eggs (Adams 1993, Nussbaum et al. 1983).

Incubation periods are reported to be as short as 30 days for tailed frogs, up to 200 days for giant salamanders, and as long as 290 days for torrent salamanders (Nussbaum et al. 1983, Nussbaum and Tait 1977). Hatchlings emerge from nest sites after several months of yolk absorption within the stream substrate, although the exact timing may vary with stream temperature (Metter 1964, Brown 1990, Adams 1993). Time to metamorphosis also varies depending on local temperatures. In the Coast Range of Oregon, age at metamorphosis is about 1-2 years for tailed frogs (Bury and Corn 1991, Metter 1967, Adams 1993), 3 years for giant salamander (*D. tenebrosus*, Bury and Corn 1991), and 3.0-3.5 years for torrent salamanders (*R. variegatus*, Nussbaum and Tait 1977). In areas with colder temperatures, such as the north Cascade Range and the Rocky Mountains, metamorphosis takes place at about 3-4 years for tailed frogs (Brown 1990, Metter 1964, 1967). Time to metamorphosis for torrent salamanders reaches about 4.5 to 5 years in the Cascades (Nussbaum and Tait 1977, Good and Wake 1992), and about 3-4 and 2-4 years respectively in the Blue River watershed for Pacific giant salamanders and tailed frogs (unpublished data).

Each species seems to have a different mode of dispersal after metamorphosis, but little is known about the temporal and spatial pattern of their movement. Metamorphosed Pacific giant salamanders have been found on hillslopes both near and far from streams, even to ridgetops, but mass movements have not been observed. Tailed frog metamorphs have been observed dispersing upslope in large numbers during fall rains (Larry Gangle III, pers. comm.) and have occasionally been caught in large numbers in upslope pit traps in conifer forests (Bury and Corn 1988). The timing and duration of these migrations likely vary with weather sequences and geographic location. Until recently, metamorphosed torrent salamanders had not been found more than a few meters away from streams (Nussbaum et al. 1983). However, Good and Wake (1992) reported a few observations at more than 50 m from water, and Vesely (1996) recorded metamorphosed torrent salamanders more than 20 m from any aquatic habitat. Welsh (1990) used very weak evidence to suggest that dispersal occurs mainly by larvae in streams. However, upslope habitats adjacent to streams occupied by torrent salamanders have not been investigated during all times of year that might serve as dispersal periods (such as late fall, winter, and during snow melt). Therefore, the occurrence of upslope migration by this species is neither certain nor eliminated.

The rate of travel, duration of travel, and resulting destination of any dispersing stream amphibian metamorphs are completely unknown. Do the individuals remain within their natal headwater basin or cross ridgetops to neighboring headwaters? Do they migrate rapidly to other streams, or do they spend their first winter hidden upslope in decayed logs and subterranean macropores? Answers to these questions currently are not available. In any case, metamorphs of all species apparently require an additional 1-3 years of maturation before becoming reproductively active (Nussbaum et al. 1983, Good and Wake 1992). At this point, if not before, they return to the streams where adults find mates and breed. As mentioned previously, it is not uncommon for some Pacific giant salamanders to experience paedomorphosis, in which case they remain in the stream and become reproductively capable without experiencing metamorphosis.

OBJECTIVES

My goal was to depart from the reach-level investigations of most recent studies of stream amphibians, and begin to explore patterns and processes at a watershed level. My overall objective was to determine if there were watershed-level patterns of distribution of stream amphibians within the Blue River watershed, and if so, to visually display the findings. Several variables whose values changed in a known, predictable manner over the landscape (such as watershed area and elevation) were used to test hypotheses of patterns being present. Hypotheses were tested through development of watershed-level statistical models of occurrence and by producing visual displays of the results (objective 1). Potential explanations of the results were explored through objectives 2 and 3.

1. Develop statistical models of the probability of occurrence of larval Cascade torrent salamanders, larval Pacific giant salamanders, and larval and metamorphosed tailed frogs in 5-m stream-lengths during summer in the Blue River watershed, using widely-available or easily-derivable data layers, such that a map can be produced of an estimated mean probability of occurrence.
2. Explore associations of potential explanatory variables at multiple scales with the presence of larval Cascade torrent salamander, larval Pacific giant salamander, and larval and metamorphosed tailed frog in 5-m stream-lengths during summer in the Blue River watershed.
3. Determine if there are any discernible trends in size distribution of larval Cascade torrent salamander, larval Pacific giant salamander, and larval and metamorphosed tailed frog in the stream network of the Blue River watershed.

METHODS

STUDY AREA

The study was conducted in the Blue River watershed, a tributary of the McKenzie River in the west-central Cascades of Oregon (Figure 2). The confluence of Blue River with the McKenzie River is at the town of Blue River, 60 km east and 11 km north of Eugene, Oregon. The Blue River watershed drains approximately 23,900 ha. Blue River was dammed in 1968, approximately 2.8 km above its confluence with the McKenzie River (Johnson et al. 1983). At full pool, Blue River Reservoir is about 8-km long and creates about 378 ha of surface water which extends up Blue River about 200 m above the confluence with Lookout Creek.

The Blue River watershed is primarily composed of conifer forest, the majority of which is managed by the Blue River Ranger District, Willamette National Forest. Elevations range from 317 m at the mouth of Blue River, to 1630 m at the peak of Carpenter Mountain. Topography in the watershed is fairly gentle in a few areas, but is generally quite steep (Figure 3). The following climate information is summarized from a meteorological station at low elevation (426 m) in the H. J. Andrews Experimental Forest, within the Blue River watershed, recorded for years 1972-1984 (Bierlmaier and McKee 1989): Average daily air temperature was 0.6^{o} C in January, 17.8^{o} C in July, 8.5^{o} C yearly average, extremes higher than 37.8^{o} C and as low or lower than -12.2 to -6.7^{o} C; average yearly rainfall was 230.16 cm, 71 percent of which fell from November to March, wettest month was December (average 43.71 cm of rain), driest month was July (average 1.88 cm of rain). Average temperatures at higher elevation are usually lower, although a temperature inversion is common in this area in the mornings during clear sunny days. Average precipitation at higher elevation is usually higher. One precipitation gauge at 1203 m on the H. J. Andrews Experimental Forest collected 21 percent more than a gauge at 460 m. A persistent snowpack usually forms during winter above 1050 m and may last into June.

Figure 2. Location of the study area and samples. The Blue River watershed is filled in black in the map of Oregon counties. Sample locations for 1995 and 1996 are plotted on the 1996 Blue River Ranger District GIS stream layer.

Plant association series (Hemstrom et al. 1987) were mapped by Blue River Ranger District personnel from aerial photos and field data (Figure 4). Most of the land area (excluding Blue River Reservoir) in the watershed (74%) is composed of plant associations in the western hemlock (*Tsuga heterophylla*) series, in which Douglas-fir (*Pseudotsuga menzesii*) is currently the canopy dominant and western hemlock and western redcedar (*Thuja plicata*) occur as co-dominants, subdominants, and as the primary regenerating species. Most streams in the watershed course through and are surrounded by this series. Higher elevations, particularly above 1100 m are composed primarily of plant associations in the Pacific silver fir (*Abies amabilis*) series (comprising 22% of the land area). In this series Douglas-fir is currently the canopy dominant at lower elevations, while Pacific silver fir is dominant at higher elevations. Pacific silver fir is the primary regenerating species in all stands in this series. Because of the high slope position of this series in this watershed, only 1st- and occasionally 2nd-order streams are found in this series. Small patches of the Douglas-fir series (comprising 2% of the land area) are present at low elevations on generally south-facing slopes or in mini rain shadows. In these patches, Douglas-fir is the dominant overstory and regenerating species. The highest ridges in this watershed are capped with patches of the mountain hemlock (*Tsuga mertensiana*) series, in which a mixture of firs and hemlocks are typically present in the canopy and regenerating layer. This series comprises about 2% of the land area in the watershed and to my knowledge hosts no stream channels.

Timber harvest, in the form of selective cutting, began in the watershed in the 1930s (Blue River Ranger District, in prep). The first 20 years of timber harvest was primarily on lower slopes in the most western drainages: Simmond's Creek, Quartz and North Fork Quartz Creek, and other small tributaries of and hillslopes flanking Blue River below its confluence with Tidbits Creek. Most often logs were hauled downslope to bulldozed roads adjacent to the creek bottom. Old haul roads and cull logs can still be seen along some tributaries. Most of this early harvest took place when the land was privately owned. Clearcut regeneration and extensive road-building began in the 1950s. Clearcutting continued through about 1990. More recent timber harvest methods are

Figure 3. Distribution of hillslope steepness in the Blue River watershed.

Figure 4. Distribution of plant association series in the Blue River watershed.

characterized by a wide range of overstory retention levels. Harvest units with unusually high overstory retention have been implemented on the H. J. Andrews Experimental Forest, in the Lookout Creek drainage.

STUDY DESIGN

The area of interest in this study was the Blue River watershed. This watershed was large enough to contain a range of stream sizes over which to sample, and small enough to allow a sample size adequate to characterize patterns within the watershed. To obtain a sample I utilized semi-random and random sampling of streams of all sizes, from headwater intermittent streams to the main stem of Blue River above the reservoir (Figure 2). The length of the search area (5 m) and sample size (about 150 sites per summer) were adjusted such that I could accomplish the task each summer (3 sites sampled per day). I needed many sample points to cover a range of stream sizes and geographic locations, and to be sure to have sufficient sites where the least abundant species (Cascade torrent salamander) would be found.

SITE SELECTION

In 1995, I divided the watershed into a number of units that seemed ecologically relevant and feasible to sample within the time available, with the intention to geographically disperse the sampling effort. I derived approximately 36 units by stratifying the watershed by subdrainage and 305-m (1000-ft) elevation bands. Subdrainages designated were typically major tributaries of Blue River with some exceptions. With a table of random numbers, I assigned the order in which each of the 36 subdrainage-elevation band units would be sampled.

In each elevation band within each subdrainage I attempted to search at least three 5-m stream lengths. For the larger subdrainages with multiple tributaries of similar size (such as Tidbits Creek), I sampled additional reaches. My selection of a stream within a subdrainage-elevation unit was guided by the following: 1) Topography suggested that an active stream channel was likely, 2) More accessible streams were preferred over less accessible streams with similar characteristics, 3) First- to second-order streams were generally preferred.

Once on the stream, I selected what seemed to be a representative section of stream to search. I considered a section of stream representative if it contained channel unit types in similar proportion to the nearby reach (as described in Bury and Corn 1991). I typically avoided sampling bedrock slides unless that habitat was common along the stream. The judgment of representativeness was subjective.

In 1996, I improved the method of site selection to reduce the potential for bias in the stream site sample. I used a three-step, multi-scale, random selection process to locate sample areas along streams. I first overlaid an approximately 1-km square grid across the watershed. The size of the grid cells was chosen such that each square was large enough to encompass several tributary junctions, and small enough to allow sampling of three different sites in one day within the chosen cell. A random number was assigned to each of the 287 cells in the watershed and the list of cells sorted by the random number, thus creating an ordered list of cells in which to sample. A chosen cell was divided into a 10 by 10 grid of smaller cells. Randomly generated numbers from 00-99 were used to select several (usually three or four) points within the cell . The closest location to a point along the closest stream channel was used as the destination for placing a sampling area. My best estimates of these locations were marked on low-elevation, color aerial photos. Locating points in the field was easiest for large streams with less canopy and more difficult for small streams with complete canopy. A combination of topographic maps and aerial photos, with their associated features, helped me locate the points. Once at the approximate location, a list of random numbers from zero to 15, and a coin, were used to establish the upper end of the 5-m sampling area. The random number determined the distance in meters, and a flip of the coin determined whether I measured up or down from my approximate field location. The final point designated the upper end of the 5-m sample area. If the 5-m length chosen contained any surface water whatsoever, that surface water was sampled. If the 5-m length contained no surface water, the original “dry” point was recorded, and the nearest stream reach containing surface water was located. If >5 m of potential sample area was present at the new location, I repeated the final step of the random selection process to place the 5-m search area.

A few exceptions exist to the previously-described methodology. In 1995 I avoided a few sites that were searchable, but would have been very difficult to search because of heavy brush, log, or slash cover. In 1996 I searched all searchable sites. Sites considered unsearchable were those with more than 25% of the surface water inaccessible due to dense log cover (4 instances in 1996), extremely thick and immovable vegetation and/or slash cover (4 instances in 1996), or water that was too deep or turbulent (2 instances in 1996).

SITE CHARACTERIZATION

I characterized numerous physical and some biological attributes of each 5-m survey area and its context (Table 1). Physical attributes included wetted channel substrate composition, water temperature, wetted channel dimensions, channel unit composition, channel slope, surface water configuration, air temperature, cover over stream, evidence of past harvest or stream buffer, and azimuth of flow.

ANIMAL SEARCH

In all cases I searched the surface and near-surface water in a 5-m length of stream bed for all amphibian species and life stages. Near-surface water included water present under the top layer of otherwise dry particles.

Each 5-m survey area was searched from downstream to upstream. The primary method for detecting amphibians was visual observation. In portions of the stream with non-turbulent water, substrate was probed, moved, or removed in order to locate hiding amphibians. Amphibians detected visually were coaxed into a dipnet. In turbulent waters where visual detection was difficult or impossible, nets were set usually downstream from substrate, and the substrate was then disturbed. Animals dislodged either washed into the net or were subsequently captured. Nets were typically set in expected escape routes during searches regardless of the turbulence or calmness of the water. Substrate was searched down to where sand-sized or smaller particles were dominant or filled available interstices among larger particles. In addition, subsurface seeps, either in the active channel or nearby, were searched. This involved either digging horizontally into a pile of material, or excavating a trench along the route of the seep.

Each amphibian was placed into a plastic ziplock bag. Once settled against the side or bottom of the bag, snout to vent lengths (SVL) and total lengths (TL) were measured on each amphibian. SVL was measured from the tip of the snout to the anterior extent of the vent slit. Body length was substituted for SVL on tailed frog tadpoles. Each individual was identified to species and the stage of development recorded (larvae, transforming, metamorphosed). Other details were recorded on each amphibian and cover object but are not included in these analyses.

In 1996 a net fixed across the entire wetted channel was initially used at the downstream end to insure that no amphibians escaped from the 5-m section (a net was not used at all in 1995). After about 30 surveys I discontinued use of the net because it was time-consuming to situate, and no amphibians were ever found in or blocked by the net. I assume the lack of amphibians in the block net is due to the thoroughness of my searches from downstream to up.

VARIABLES DERIVED FROM GIS DATA SOURCES

Nine variables were developed for use in analysis of amphibian association with widely-available or easily-derivable data layers (identified with asterisks in Table 1). Each of these variables was derived from or converted to a 30- x 30-m grid format, conforming to the resolution of the available USGS 7.5-minute Digital Elevation Model (DEM). These variables were chosen because of their associations with environmental features known to be important to amphibians (e.g. basin size with stream size, elevation with temperature and moisture), and because they are available to or easily-derivable by most resource management organizations.

Table 1. Comprehensive list and description of variables used for the analysis. Variables are grouped by similarity of spatial extent. Variables derived from or converted to 30- x 30-m resolution GIS data are identified with an asterisk (*).

VARIABLE	DEFINITION	SOURCE OF DATA
TEMPORAL POSITION		
YR	Year	Calendar
JLD	Julian Date (1-365)	US Government Calendar
MTIME	Time midway through search (decimal hours)	Converted field start and end times to decimal hours, then averaged.
LARGE CONTEXT		
Geophysical Context		
*WSHA	Watershed Area (ha): the cumulative horizontal land area drained by any point on a stream.	30-m DEM, run sequentially through several ArcInfo GRID algorithms (FLOWDIRECTION, FLOWACCUMULATION). Number of 30- x 30-m cells flowing through a point were multiplied by 0.09-ha/cell to derive watershed area in ha for each point.
*MNSL33	Mean Slope Context (%): average of slopes for all 30-x30-m cells within approximately 1-km radius.	30-m DEM, run sequentially through several ArcInfo GRID algorithms (SLOPE, FOCALMEAN).
*BSSL	Basin Slope Percent: average slope for all 30- x 30-m cells within watershed of point on stream	30-m DEM; first, two separate grids produced from ArcInfo GRID algorithms (FLOWDIRECTION and SLOPE). Then, the FLOWACCUMULATION algorithm was run on the FLOWDIRECTION grid, weighted by the SLOPE grid. Resulting grid contained total of slope values for each grid within the watershed of each point. The final grid was produced by dividing the SLOPE grid by the FLOWACCUMULATION grid produced for WSHA, prior to its conversion to hectares.
*REGIND	Indicator variable: Topographic region, 0=gentle, 1=steep	The gentle region was defined by a line connecting the mouth of Quentin Creek, S to N-most point on Lookout-McKenzie divide, WNW to SW-most point on Lookout-Budworm divide, N encompassing central-N Lookout Cr. slopes, McRae, Wolf, Mann, and Quentin Cr. drainages. The steep region was any area outside the outlined gentle region.
Vertical Position		
ELEVM	Elevation above sea level (m)	Estimated from 1"/mile (1.6 cm/km), 80-ft (24-m) contour interval topographic map of Ranger District.
*DELEVM	Elevation above sea level (m)	30-m DEM. Obtained directly from the grid.
Horizontal Orientation		
AZ	Azimuth of stream flow(0-359 degrees)	Field compass reading
NTOS	North to South percent	Degrees from north (either W or E) / 180
*DAZ	Azimuth from DEM: 0, 45, 90, 135, 180, 225, 270, 315.	30-m DEM, run through an ArcInfo GRID algorithm (FLOWDIRECTION). Flowdirection grid (which identified directional flow from each cell in one of 8 possible directions) converted to azimuth.
*NSAZ	North to South degrees: only 5 possible values (0, 45, 90, 135, 180); values 45, 90, and 135, may represent 315, 270, and 225 respectively.	30-m DEM, run through an ArcInfo GRID algorithm (FLOWDIRECTION). Flowdirection grid (which identifies directional flow from each cell in one of 8 possible directions) converted to represent one of 5 values in degrees.

Table 1, Continued

VARIABLE	DEFINITION	SOURCE OF DATA
	LOCAL CONTEXT	
	Harvest Effects	
*MOSTYPE	Occurrence of harvest adjacent to stream . Indicator variable, referring to the majority classification for cells within a 3-cell radius (approximately 100 m) of each point: 0=Unharvested, 1=Harvested.	ArcInfo polygon coverage was derived indicating harvested and unharvested polygons (I considered all clearcut, shelterwood, and seed-tree methods implemented since 1950 as harvested). Polygon 'Harvest' coverage was converted to grid with 30-x30-m cells, such that each cell had value of 0 or 1. ArcInfo GRID command MAJORITY was used to determine the majority value among all cells within a 3-cell radius of each point.
HARV1Y	Indicator variable, referring to the presence of previous timber harvest on at least one side of the stream at the point being searched: 0=No, 1=Yes.	Field observation.
HARV2Y	Indicator variable, referring to the presence of previous timber harvest on both sides of the stream at the point being searched: 0=No, 1=Yes.	Field observation.
CONBUF	Indicator variable, referring to the presence of a conifer stream buffer adjacent to the stream for those sites with adjacent harvest: 0=No, 1=Yes.	Field observation.
UHUY	Indicator variable, referring to the presence of unharvested forest upstream from the search area: 0=No, 1=Yes.	GIS vegetation layer and aerial photos.
UHU	Shortest stream distance from sample point to unharvested forest in upstream travel only (m).	Measured with distance tool in ArcView
UHDY	Indicator variable, referring to the presence of unharvested forest upstream from the search area: 0=No, 1=Yes.	GIS vegetation layer and aerial photos.
UHD	Shortest stream distance from sample point to unharvested forest in downstream travel only (m).	Measured with distance tool in ArcView
UHA	Shortest stream distance from sample point to unharvested forest in any combination of upstream or downstream travel (m).	Measured with distance tool in ArcView
*WSHARV	Watershed harvest: percent of land area which is harvested in basin above the sample point.	Harvest grid produced prior to the MAJORITY grid for MOSTYPE was used as the weighting grid when FLOWACCUMULATION was run on the FLOWDIRECTION grid. Resulting grid was the number of cells in the watershed of each point that were harvested. This grid was divided by the FLOWACCUMULATION grid produced for WSHA, prior to its conversion to hectares.
	IMMEDIATE CONTEXT	
	Cover Over Stream	
LCOV	Percent cover at 0-5 m in height, over the wetted channel, including a maximum angle of 30 degrees from the water edge and the upper and lower extension of the sample area.	Visual estimate.
MCOV	Same as above, 5-15 m	Visual estimate.
HCOV	Same as above, >15 m	Visual estimate.
XCOV	Maximum value of the above measurements	Derived in database with conditional statements.

Table 1, Continued

VARIABLE	DEFINITION	SOURCE OF DATA
	Presence of Deciduous Riparian	
RIPDEC	Binary classification (0/1), 1=presence of contiguous deciduous riparian canopy over stream sample area and at least 50 m above and below the site.	Visual evaluation
	Air Temperature	
AIRC	Air temperature in Celsius degrees	Measured with glass thermometer 1-2 m above the stream.
	Surface Water Configuration	
PCHY	Indicator variable, referring to the surface water configuration in the immediate vicinity of the search area: 0=Continuous; we could see continuous surface water up and downstream from our survey site. 1=Patchy; surface water present, but in patches typically 1 to 5 channel units in length, separated by dry stream bed.	Visual evaluation
DISJ	Indicator variable, referring to the surface water configuration of the stream segment below the point at which the search area was located: 0=Continuous; lengths of dry stream bed >100 m not observed. 1=Disjunct; separated from lower portion of network by >=100 m of dry stream bed.	Visual evaluation
	STREAM MORPHOLOGY	
	Channel Slope	
GRAD5	Gradient over 5-m search area	Measured with clinometer.
	Channel Unit Composition	
POOL	Percent of surface water within the 5-m section with level surface, typically small width-to-depth ratio, often clear and non-turbulent except immediately below a cascade.	Visual estimate
GLIDE	Percent of surface water within the 5-m section with a very slight gradient, a moderate width-to-depth ratio, few or no particles protruding above the water surface in mid-channel, and visibility fair, but with some surface distortion.	Visual estimate
RIFF	Percent of surface water within the 5-m section with noticeable gradient, a large width-to-depth ratio, numerous emergent particles, and at least mildly-turbulent, moving water with limited visibility.	Visual estimate
CASC	Percent of surface water within the 5-m section coursing over and then free-falling from relatively large particles such as logs or boulders.	Visual estimate
	Wetted Channel Dimensions	
AVWD	Average width of water present at time of search (cm)	Visual estimate, calibrated with physical measure
AVDP	Average depth of water present at time of search (cm)	Visual estimate, calibrated with physical measure
WDRAT	AVWD/AVDP	Calculated in SAS
LGTH	Total length of surface water searched in 5-m search area (m)	Measuring Tape

Table 1, Continued

VARIABLE	DEFINITION	SOURCE OF DATA
INSTREAM ENVIRONMENT		
Biota		
RHCALTY	Indicator of detection of Cascade torrent salamander: 1=detected, 0=not detected	Hand search, visual observation
DITELTY	Indicator of detection of Pacific giant salamander: 1=detected, 0=not detected	Hand search, visual observation
ASTRLTY	Indicator of detection of larval tailed frog : 1=detected, 0=not detected	Hand search, visual observation
ASTRMY	Indicator of detection of metamorphosed tailed frog: 1=detected, 0=not detected	Hand search, visual observation
CRAY	Indicator of detection of any crayfish species: 1=detected, 0=not detected.	Hand search, visual observation
FISH	Indicator of detection of any fish species: 1=detected, 0=not detected	Hand search, visual observation
Water Temperature		
WATC	Water temperature in Celsius degrees	Glass thermometer placed in stream for at least 5 minutes
Wetted Channel Substrate Composition		
LOG	Percent log >=10cm diameter	Visual estimate.
BED	Percent bedrock.	Visual estimate.
BLD	Percent boulder (>=256 mm b-axis)	Visual estimate.
CBL	Percent cobble (65-256 mm b-axis)	Visual estimate.
PBL	Percent pebble (32-65 mm b-axis)	Visual estimate.
GRV	Percent gravel (2-32 mm b-axis)	Visual estimate.
SND	Percent sand (1-2 mm b-axis)	Visual estimate.
SILT	Percent silt (<1 mm b-axis). Note, this did not include silt present on top of otherwise visible particles).	Visual estimate.
LITT	Percent new and decomposing organic material, including “logs” <10 cm diameter.	Visual estimate.
FINES	Percent fine substrate.	Values summed: GRV+SND+SILT.
COARSE	Percent coarse substrate	Values summed: BLD+CBL.

[1] All DEM grids were run through the ArcInfo GRID "FILL" process before other algorithms were processed. Therefore, all references to DEMs are assumed to be 'filled' DEMs.

ANALYSIS

The analysis consisted of three parts corresponding to the three objectives. First I developed watershed-level models which estimated probability of occurrence of amphibians in 5-m stream lengths throughout a DEM-derived stream network in the Blue River watershed, using widely-available or easily-derivable data layers in a 30- x 30-m grid format. These models were then used to produce maps which gave visual indication of the general distribution trends of each species and/or life stage in streams of the watershed. Second, in an attempt to explore more direct explanations for the watershed-level patterns observed, I executed a series of model-building exercises for each species. These were used to gain insight into the comparative strength of association of presence of each species and/or life stage with variables representing phenomena at several scales. Third, I briefly examined the association of amphibian size distribution with position in the stream network. All analyses were conducted for Cascade torrent salamander larvae, Pacific giant salamander larvae, tailed frog larvae, and metamorphosed tailed frogs. Metamorphosed Cascade torrent salamanders and Pacific giant salamanders were rarely encountered and were not included in the analyses. In all cases, individuals in the process of transformation (metamorphosis) were included in analyses of the larval form.

Watershed-level models

Examination of Raw Data

Plots of moving-window averages of amphibian presence, linear rate, and density were produced over watershed area, elevation, and other landscape-level variables to gain initial insight into relationships of amphibian presence with these variables. These plots represent average y-axis values for consecutive and overlapping "windows" of groups of data points along the x-axis. The number of data points used in the average defines the window "width". Average y-values are plotted over median x-values in this case. General interpretation of trends and variation are made from these graphs.

Model-Building

Logistic regression was used to investigate associations of amphibian presence with several geographic, geomorphic, and hydrologic variables (those identified with an asterisk in Table 1). I also included time of day, Julian date, and year in the selection process in case these variables needed to be standardized. I used a multi-step process to derive a single "best" model. I first conducted a manual stepwise process to select an initial model ($p<0.05$ to enter and stay in). Quadratic and log-transformed (base 10) terms for all continuous variables were included as potential variables in this process. Interactions were checked after the stepwise process was complete. If significant interactions were found, the stepwise process was resumed until no more significant variables or interactions were detected. Lastly, I examined model-checking diagnostics available in PROC LOGISTIC (SAS Institute Inc. 1997), to assess model fit and influential observations.

The stepwise process I used was not that provided in the LOGISTIC procedure in SAS. Unfortunately, that automated procedure selects variables for inclusion based on the Score Chi-square value, and removal based on Wald's Chi-square (Manuela Huso, pers. comm.). Neither criterion uses Type 3 test statistics (equivalent to the "drop in deviance" test), which are more reliable than the Wald's Test (Ramsey and Schafer 1997). Therefore, I wrote a program in SAS code that produces Type 3 p-values from the GENMOD procedure (SAS Institute Inc. 1997) for all candidate variables in each step. I used these values as guidance for inclusion or exclusion of variables, rather than the Wald or Score statistics.

From Models to Maps

The statistical models developed for each species were used to calculate a "response" grid which was displayed as the estimated mean probability of occurrence associated with each cell, given the values of explanatory variables at each cell. The logistic regression equations developed actually calculate the natural log of the odds of occurrence. This value was transformed to a probability of occurrence by the formula EXP(Y)/(1+EXP(Y)), where Y is the natural log of the odds calculated from the statistical models.

The resulting response grid was then reclassified in ArcView into several 10-unit increments of probability of occurrence (for example, 0-10%, 10-20%, etc.). This reclassified grid was then converted to arcs, or lines (vector format), using the STREAMLINE function in ArcInfo. This new line coverage was then read again into ArcView in order to format the maps for presentation, using graduated line thickness as the indicator of increasing probability of occurrence.

Exploring Multi-scale Associations

Logistic regression was used to explore associations between presence of amphibians and variables at multiple scales. All variables listed in Table 1 were included as potential explanatory variables in this analysis except for the biotic indicators. Variables were arranged into five groups representing five spatial scales (Table 1). An additional group included the temporal variables. A model-building process was conducted five times for each species and/or life stage. The first model-building process included only the physical "instream" variables. Subsequent processes included a slightly broader context of variables in addition to all the previous variables. Therefore, the model-building process using large-context variables included all possible variables in the analysis. Temporal variables were included in the pool of potential explanatory variables in every model-building process. I used the same manual stepwise selection process described for watershed model-building, except that interactions between variables were not tested. While it was expected that interactions do exist among some variables, most models included many significant variables without including interactions. Including interaction terms in this process may have had the potential to reduce the ability to detect more general relationships and may have injected additional uncertainty into interpretation of results. Alternatively, it could have resulted in valuable insight. However, to simplify the process, I chose to ignore interactions for this analysis.

Coefficients from each model were translated to more interpretable forms (odds ratios or maximum effect values) and organized in tables. Results of model-building processes were summarized for each species. In addition, a composite description was made of the type of stream that had the highest odds of occurrence for each species and/or life stage. The composite descriptions serve only as a reference for habitat with a high probability of occurrence, and do not represent the only habitat occupied by the species.

Size Distribution

A histogram was used to assess broad differences in size distribution in small, medium, and large streams. A moving-window average scatterplot was used to investigate general trends in minimum, maximum, and average amphibian sizes across a range of basin sizes.

RESULTS

CHARACTERISTICS OF THE LANDSCAPE AND STREAMS

Geomorphology

While some intermediate landforms are present in the watershed, notably the Quentin Creek drainage, most areas in the watershed are generally more steep or more gentle (Figure 5). This perception of a bimodal distribution of slopes in the watershed is borne out in a histogram of all 30- x 30-m cells from a digital elevation model (Figure 6).

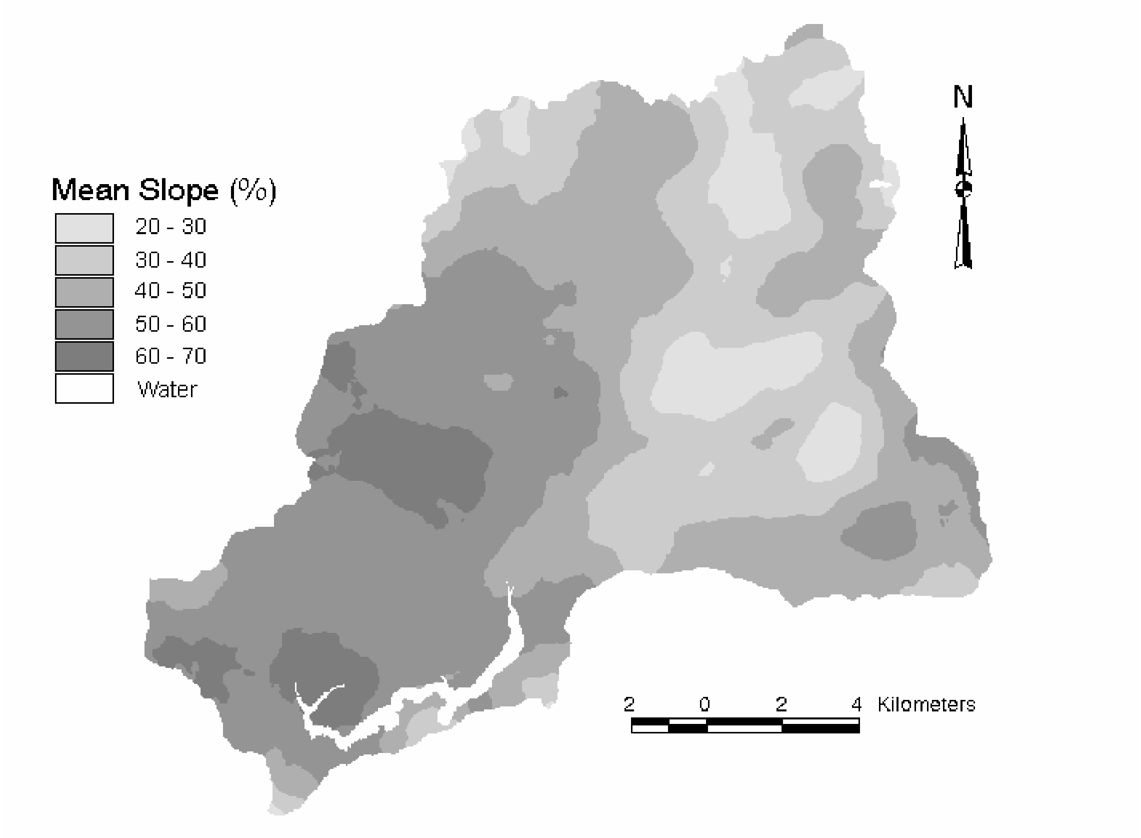


Figure 5. Map of several groupings of MNSL (1-km mean slope context, see Table 1) in the Blue River watershed.

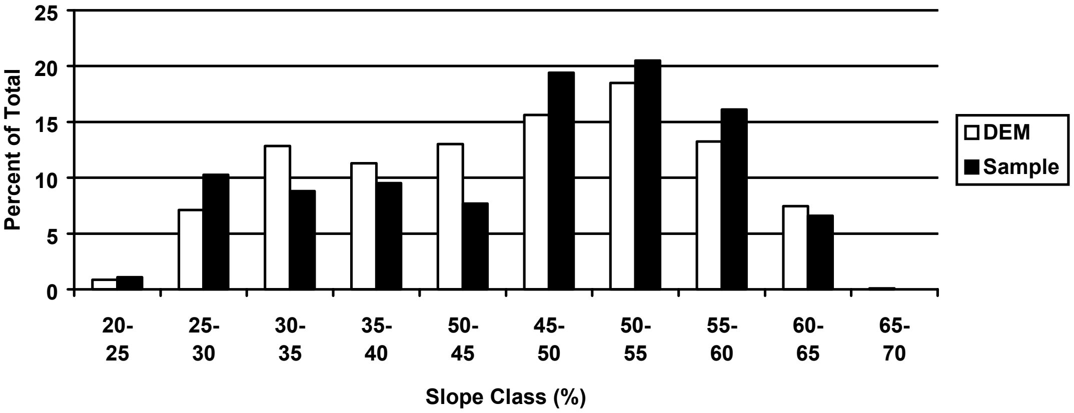


Figure 6. Frequency distribution of MNSL (1-km mean slope context, see Table 1) for all 30- x 30-m Digital Elevation Model (DEM) cells in the Blue River watershed and for the 273 samples from summers 1995 and 1996.

These slope characteristics are perceived by soil scientists and hydrologists to be directly related to edaphic characteristics and hydrologic regimes, respectively (Blue River Ranger District, in prep)(Table 2). The region of generally gentle slopes also is correlated roughly with the supposed extent of glaciation, and an associated deep deposit of unconsolidated glacial material (Swanson and James 1973).

Table 2. Associations of hydrologic regimes and edaphic characteristics with hillslope steepness (taken from Blue River Ranger District GIS soil layer for Blue River watershed, 1996).

Characteristic	Gentle	Steep
Flashiness of Streams	Low	High
Soil Depth	Deep	Shallow
Erosiveness	Low	High
Sediment Transport Capacity	Low	High

Distribution of Timber Harvest

About one-third of the Blue River watershed has experienced timber harvest. Percent of harvest in each drainage area above each sample point varied from 0 to 100%, with most basins having <40% harvest (Figure 7).

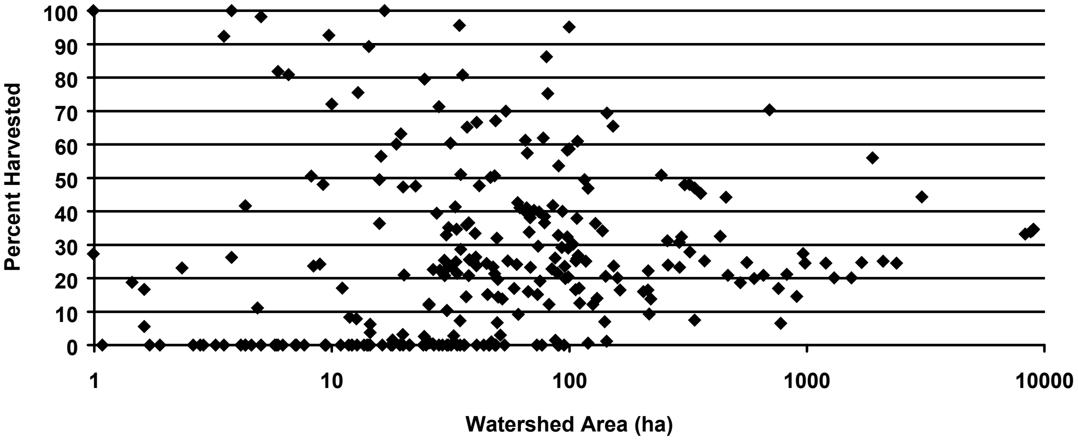


Figure 7. Comparison of percent basin harvested with size of basin. Three points are not displayed (values refer to the x- and y-axes, respectively): (0.27, 0), (11746,32), (11790,32).

Streams

Streams are assumed to have been sampled in approximate proportion to their occurrence in the watershed. Two things explain the difference in DEM distribution and sample distribution of watershed area (Figure 8). One is that stream channels are typically not initiated in basin sizes less than about 2 ha (pers. obs.), except in areas where springs are present (where water emerges to the surface apart from a stream channel). The second reason is that sites represented in my sample are only those that had some surface water present. The upper reaches of many headwater streams are dry in summer (Figures 9 and 10). Ideally, to evaluate the representativeness of my sample, I would want to plot my sample distribution adjacent to the actual distribution of ‘wet’ stream channel. However, this distribution is not known, and my sample is the best representation available of that distribution.

Note that in Figure 10, some channels with continuous surface water were present even in very small basins late in the summer, while some channels with larger basins were dry even in mid- and early summer. It appears that there is tremendous variation in subsurface flow paths and underground basin surfaces which influence the rate and duration of the appearance of surface water at specific locations in the watershed.

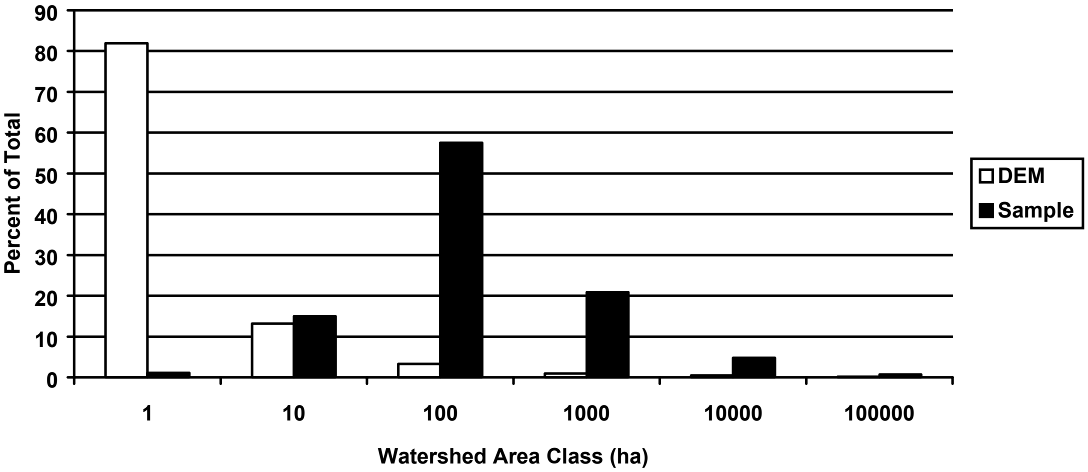


Figure 8. Proportion of watershed 30- x 30-m cells and sample sites in each basin size class. The upper limits of each class are displayed on the X-axis. My sample included only those sites with surface water present.

One phenomenon I commonly noticed in the watershed was the occurrence of flowing surface water upstream from large patches of dry stream bed (represented as “disjunct” in Figure 10). In all cases the temporary disappearance of surface water appeared to be due to an accumulation of unconsolidated material in a gentle-gradient valley bottom below a steeper segment of stream with high instream exposure of bedrock. This configuration is nicely displayed in Watersheds 1, 2, and 3 in the H. J. Andrews Experimental Forest. The apparent mechanisms forming this pattern are hillslope failures, debris flows, or merely high water flows, which do the work of moving material downstream from steeper reaches to more gentle-gradient reaches where material is deposited.

While this pattern of streambed composition is common, it is not present on all streams. Further, while surface water upstream from a dry stream bed is not unusual in this watershed, both the stream channel and surface water eventually disappear farther upstream (Figure 9)(sometimes simultaneously in spring-fed channels).

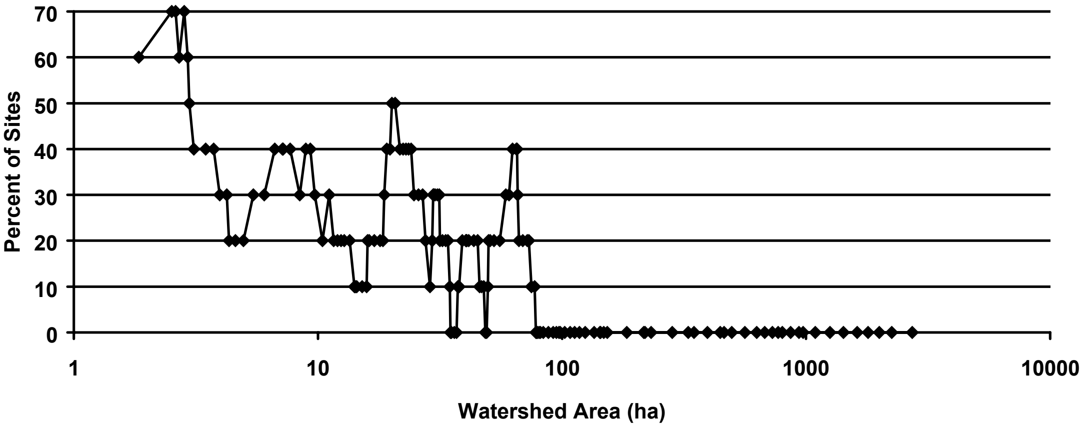


Figure 9. Percent of 5-m stream channel lengths completely dry, summer 1996, represented by a 10-site, moving window average of binary response (completely dry or not) over median watershed area. Note that some sites considered not completely dry may have had patchy surface water, as illustrated in Figure 10.

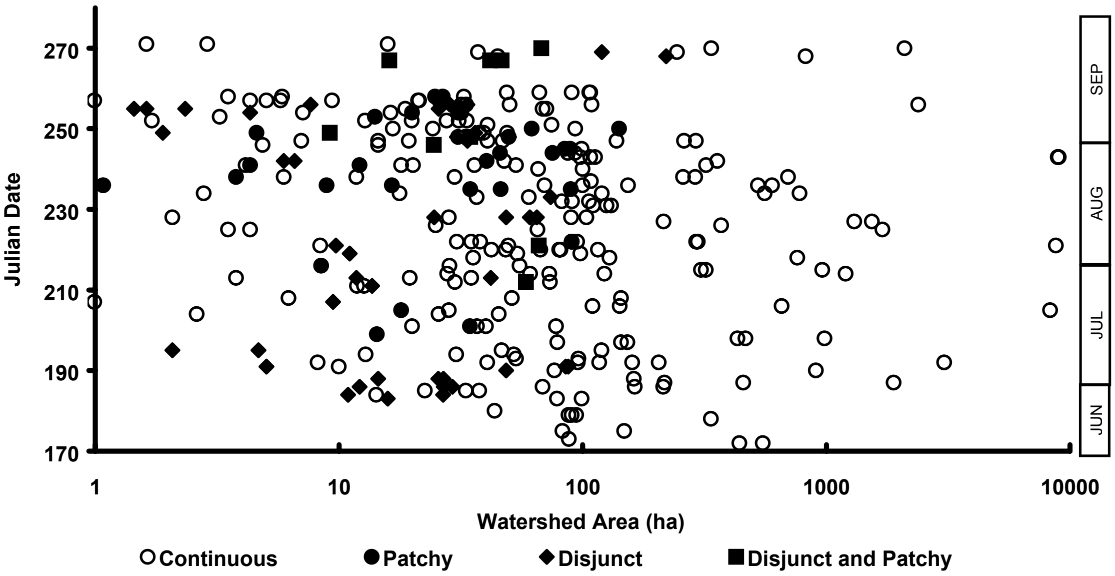


Figure 10. Qualitative assessment of surface water, summers 1995 and 1996. Sites represented here are only those sites where at least some water was present and amphibian searches were conducted. Total of 273 sites. Three points are not displayed (values refer to the x- and y-axes, respectively): (0.27, 254), (11746, 242), (11790, 242). See Table 1 for definitions of surface water types (under variables PCHY and DISJ).

MODELING WATERSHED DISTRIBUTION

The range over which each variable was measured is listed in Table 3 (definitions are in Table 1). These define the maximum range over which models are relevant in the Blue River watershed, for summers 1995 and 1996.

Table 3. Ranges over which variables were measured.

Variable[1]	Range
DEM Elevation (m)	394-1453
Azimuth of stream flow (degrees from N)	0, 45, 90, 135, 180, 225, 270, 315
North to south azimuth (degrees from N)	0, 45, 90, 135, 180
Watershed area (ha)	0.270-11790.180
1-km mean slope context (% slope)	23.439-64.459
Topographic region (gentle or steep)	0, 1
Basin slope percent (%)	13.023-71.974
Occurrence of harvest adjacent to stream	0, 1
Percent of watershed harvested (%)	0-100
Length of surface water (m)	1-5
Time midway through search (hrs)	9.45-18.42
Julian date	178-271
Year	1995, 1996

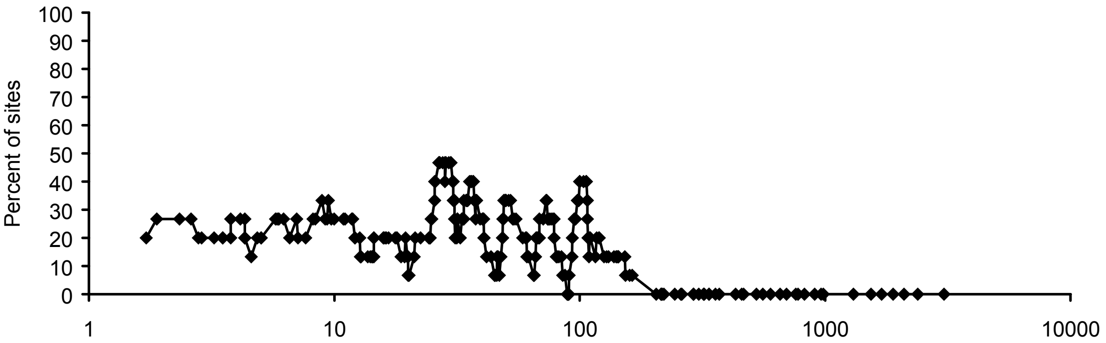
[1] See Table 1 for definitions.

Cascade torrent salamander larvae

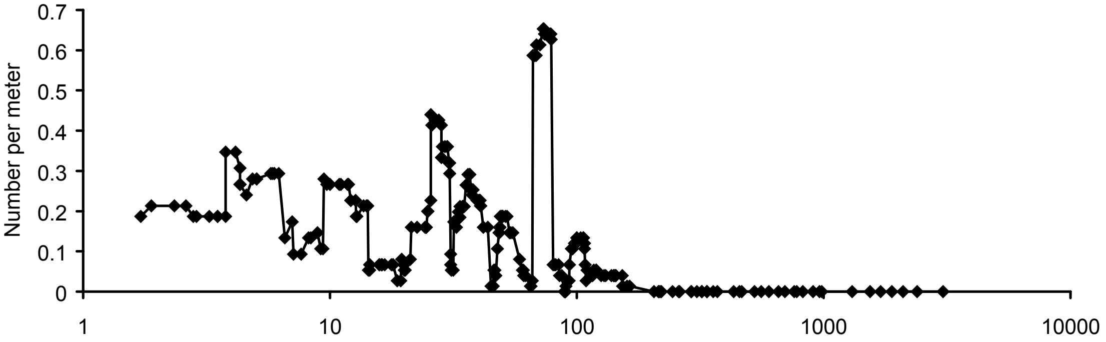
Cascade torrent salamander larvae were found at 19% (52 of 273) of sites searched (Figure 11). Average frequency of occurrence, linear rate, and density of Cascade torrent salamander larvae in 5-m stream lengths, are displayed in Figure 12 over a range of basin sizes. Cascade torrent salamander larvae were found only in small streams. The maximum basin size measured for a site containing Cascade torrent salamander larvae was 141 ha (one-half section is about 130 ha). Average frequency of occurrence, average linear rate (number per length of stream), and average density decreased with increasing basin size (Figure 12). The frequency of occurrence of Cascade torrent salamander larvae in streams in the Blue River watershed was greatest at about 900 m elevation (Figure 13). Each of these general observations from the moving-window plots were borne out in the logistic regression analysis.

Figure 11. Locations where Cascade torrent salamander larvae were and were not detected in 5-m stream lengths in summers 1995 and 1996 in the Blue River watershed.

(a) Percent of sites where present.



(b) Number of individuals per meter length of stream.



(c) Number of individuals per square meter of surface water.

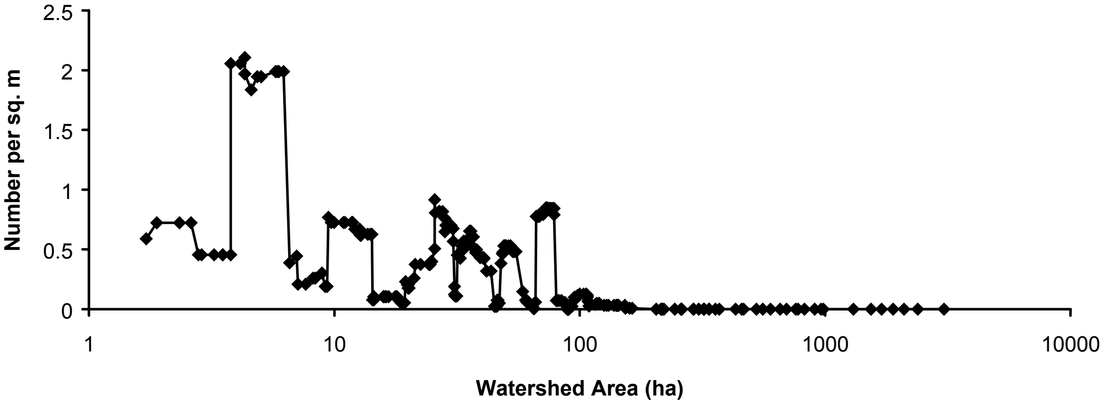


Figure 12. Occurrence of Cascade torrent salamander larvae over a range of basin sizes. Points represent a 15-site average over median watershed area. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points, from smallest to largest watershed area.

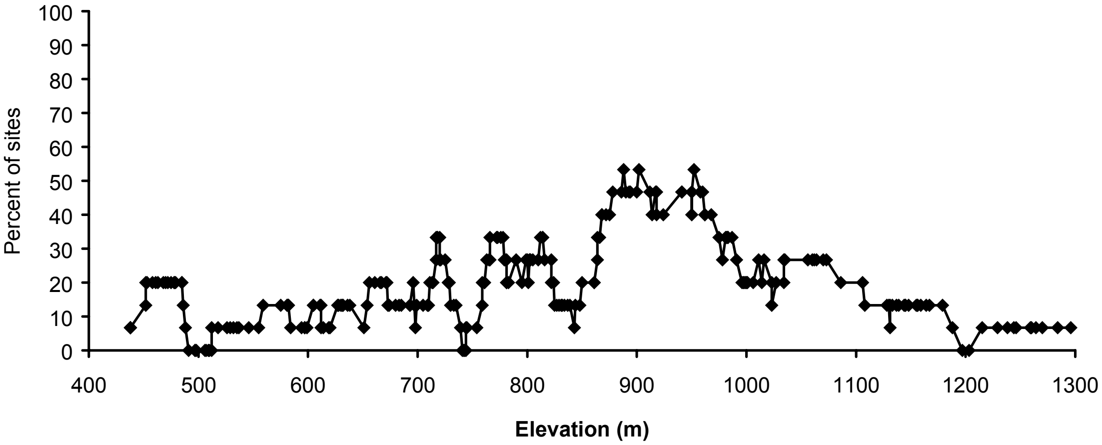


Figure 13. Occurrence of Cascade torrent salamander larvae over a range of elevations. Points represent a 15-site average over median elevation. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points, from lowest to highest elevation.

The watershed model for Cascade torrent salamander larvae (Table 4a) included four variables. Three were linear and one had a quadratic effect with respect to the natural log of the odds of occurrence. Following were the effects of each variable after accounting for others in the model. A 1-m increase in length of surface water searched was associated with a 3.1x increase in the odds of detection. A 10-unit increase in the 1-km radius mean slope percent was associated with a 2.2x increase in the odds of occurrence. A 10-ha increase in watershed area was associated with a 11% decrease in the odds of occurrence. The maximum positive effect of elevation was at about 870 m. Estimated mean probabilities of occurrence of Cascade torrent salamanders in the Blue River watershed stream network were calculated from coefficients listed in Table 4a and are displayed in Figure 14.

Table 4. Results of watershed-level model-building process using only widely-available or easily-derivable data layers in pixel form. Variables and coefficients are for the logit model (natural log of the odds of occurrence). The logit (Y) is converted to probability of occurrence by EXP(Y))/(1+EXP(Y)) to produce maps in Figures 14, 18, 21, and 25. Variables are in linear form unless noted as quadratic (Q) or base 10 log-linear (LL).

a) Cascade torrent salamander larvae

Variable	Coefficient	P-value
DEM elevation	0.02205	0.00009
DEM elevation (Q)	-1.268E-05	0.00009
Intercept	-19.0595	
Length of surface water	1.1328	0.02
1-km mean slope context	0.07883	0.00001
Watershed area	-0.01109	2E-06

Akaike's Information Criterion=223.3
Degrees of Freedom=267
Deviance=211.3

b) Pacific giant salamander larvae

Variable	Coefficient	P-value
DEM azimuth	-0.02220	0.002
DEM azimuth (Q)	4.847E-05	0.02
DEM elevation	0.007841	0.07
DEM elevation (Q)	-4.896E-06	0.05
Intercept	-6.4636	
Length of surface water	0.4034	0.2
Watershed area (LL)	1.5507	3E-09
Time of day, mid-survey	0.1704	0.02

Akaike's Information Criterion=260.0
Degrees of Freedom=265
Deviance=244.0

c) Larval tailed frog

Variable	Coefficient	P-value
DEM elevation	0.003102	0.04
Intercept	-25.33	
Watershed area (LL)	14.796	2E-07
Watershed area (QLL)	-2.73315	0.00005
1-km mean slope context	0.04772	0.058

Akaike's Information Criterion=120.5
Degrees of Freedom=268
Deviance=110.5

d) Metamorphosed tailed frog

Variable	Coefficient	P-value
DEM elevation	0.01438	0.006
DEM elevation (Q)	-5.639E-06	0.05
Intercept	-13.1341	
Length of surface water	0.4912	0.2
1-km mean slope context	0.04770	0.003
North-south degrees	-0.006179	0.03

Akaike's Information Criterion=259.5
Degrees of Freedom=267
Deviance=247.5

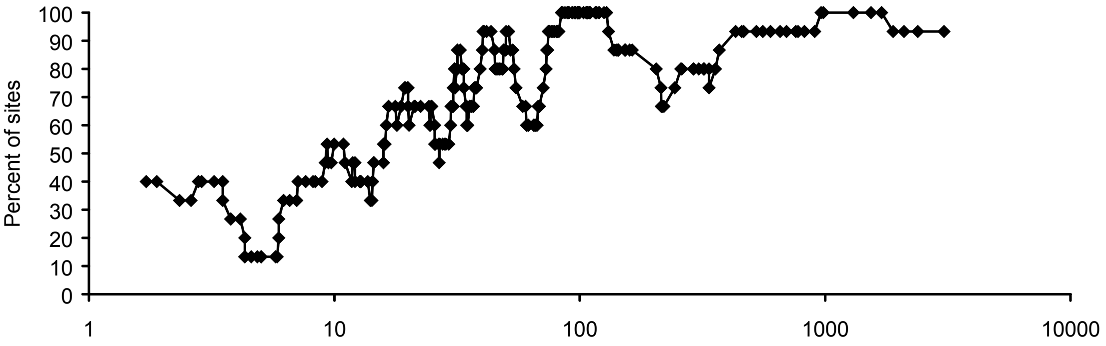
Figure 14. Estimated mean probability of occurrence of Cascade torrent salamander larvae in 5-m stream lengths in the Blue River watershed during summers of 1995 and 1996, for basins >= 7 ha, assuming water is present in the channel.

Pacific giant salamander larvae

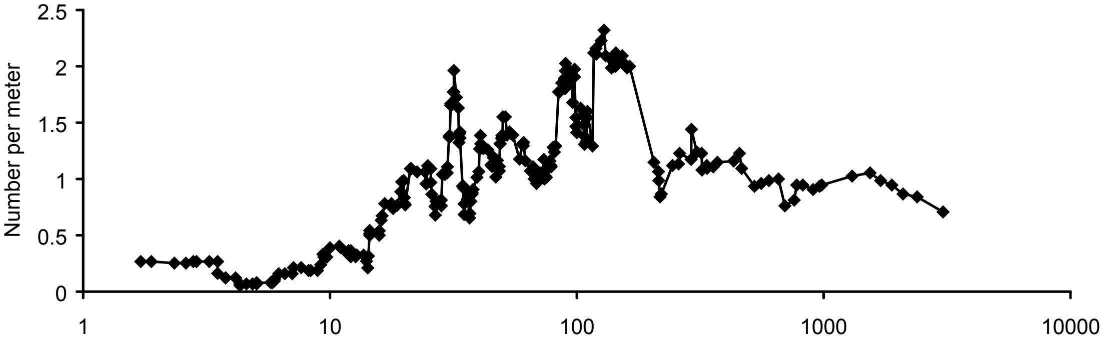
Pacific giant salamander larvae were found at 71% (194 of 273) of sites searched (Figure 15). Average frequency of occurrence, linear rate, and density of Pacific giant salamander larvae in 5-m stream lengths, are displayed in Figure 16 over a range of basin sizes. Pacific giant salamander larvae were found in all basin sizes sampled in the watershed. Therefore, this study did not detect a downstream limit of basin size for this species. Frequency of occurrence steadily increased downstream. In contrast, average linear rate increased from small to mid-sized basins then decreased slightly in larger basins. Interestingly, average density peaked in basins of about 20-100 ha in size and was smaller in streams with the smallest and largest basins. It appears that the increase in area sampled in downstream reaches (as indicated by width in Figure 17) more than compensated for the decrease in number of individuals present in the larger streams, thereby resulting in a high frequency of detection of Pacific giant salamander in 5-m lengths searched on larger streams. This has important implications for interpretation of results of both the watershed and multi-scale model-building processes.

Figure 15. Locations where Pacific giant salamander larvae were and were not detected in 5-m stream lengths in summers 1995 and 1996 in the Blue River watershed.

(a) Percent of sites where present.



(b) Number of individuals per meter length of stream.



(c) Number of individuals per square meter of surface water.

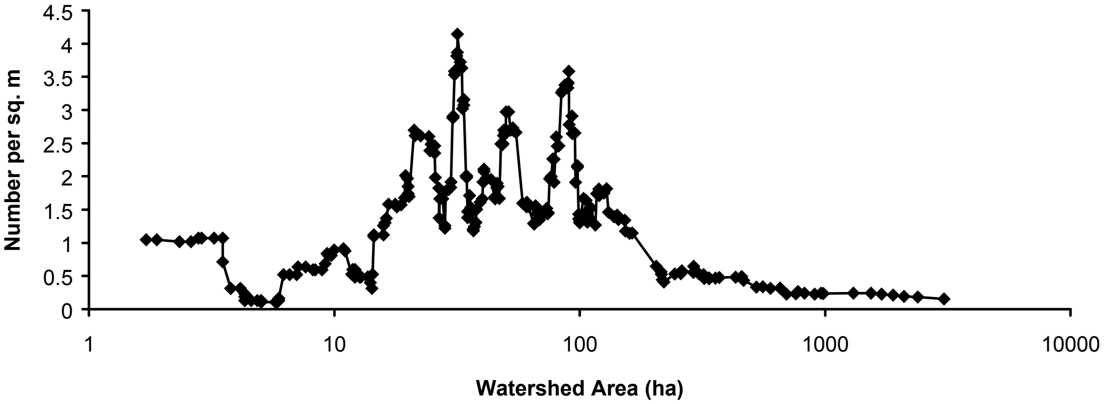


Figure 16. Occurrence of Pacific giant salamander larvae over a range of basin sizes. Points represent a 15-site average over median watershed area. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points, from smallest to largest watershed area.

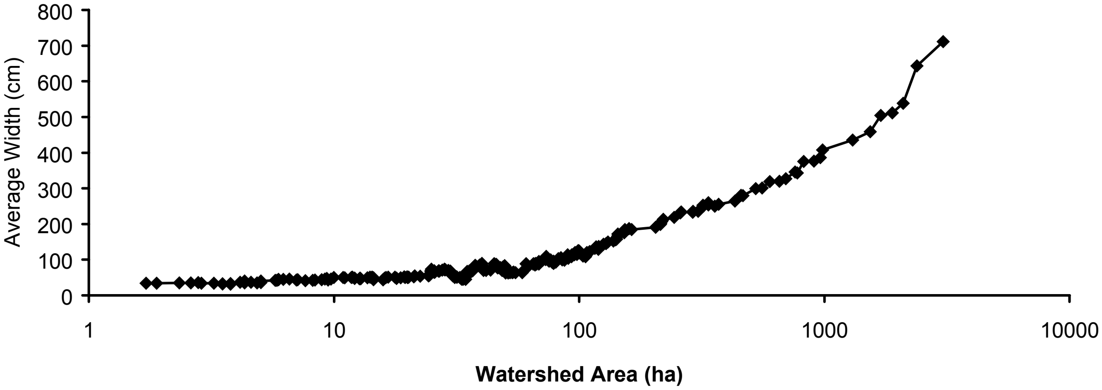


Figure 17. Average wetted channel width over a range of basin sizes in the Blue River watershed, summers 1995 and 1996. Points represent a 15-site average over median watershed area. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points, from smallest to largest watershed area.

The watershed model for Pacific giant salamander larvae (Table 4b) included five variables. Two were linear, one was log-transformed (base 10), and two had quadratic effects with respect to the natural log of the odds of occurrence. Following were the effects of each variable after accounting for others in the model. While not significant, the length of surface water searched was included in the model merely to allow standardization of the output to a 5-m length of surface water. A 1-hr increase in time of day (between about 0800 and 1800) was associated with a 19% increase in the odds of detection. A 10-fold increase in watershed area (such as from 1 to 10, or 100 to 1000) was associated with a 4.7x increase in the odds of occurrence. The maximum negative effect of azimuth was at about 229°. The maximum positive effect of elevation was at about 801 m.

Estimated mean probabilities of occurrence of Pacific giant salamanders in the Blue River watershed stream network were calculated from coefficients listed in Table 4b and are displayed in Figure 18. Clearly, Pacific giant salamander larvae can be expected almost everywhere in all streams in the watershed.

Figure 18. Estimated mean probability of occurrence of Pacific giant salamander larvae in 5-m stream lengths in the Blue River watershed during summers of 1995 and 1996, for basins >= 7 ha, assuming water is present in the channel.

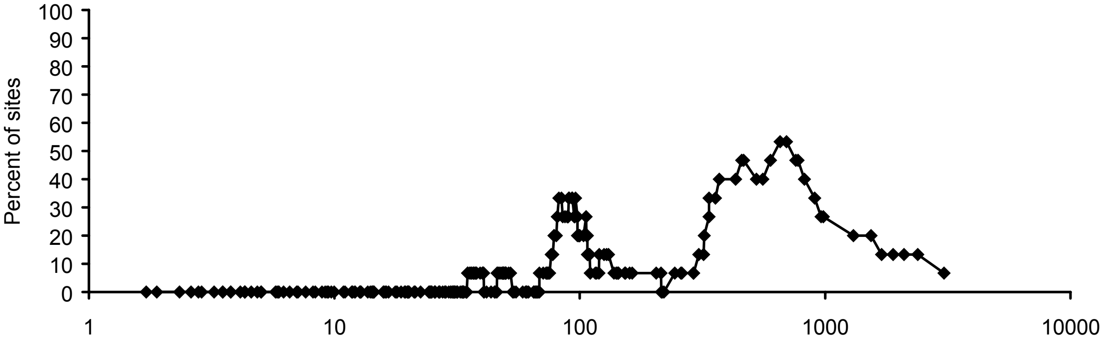
Tailed frog larvae

Tailed frog larvae were found at only 8% (21 of 273) of sites searched (Figure 19). Average frequency of occurrence, linear rate, and density of tailed frog larvae in 5-m stream lengths, are displayed in Figure 20 over a range of basin sizes. The distribution pattern of tailed frog larvae was striking. They were not present in the smallest streams and were rarely detected in the largest streams, but were most frequent in moderate-sized streams. Tailed frog larvae were not detected in basin sizes less than 37 ha, and the highest frequency of occurrence was below portions of the stream network where intermittent or patchy surface water is common (Figures 9 and 10).

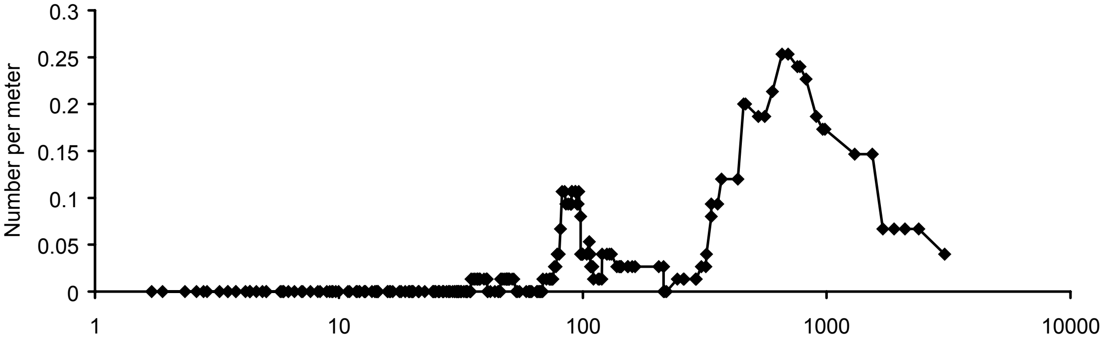
The watershed model for larval tailed frogs (Table 4c) included three variables. Two were linear and one had a quadratic effect with the log (base 10) transformed term with respect to the natural log of the odds of occurrence. Length of surface water searched was not included in this model because no larvae were found in patchy surface water, and the logistic regression procedure could not compute parameter estimates for this variable. Following are the effects of each variable after accounting for others in the model. A 10-unit increase in 1-km radius mean slope percent was associated with a 61% increase in the odds of occurrence. A 100-m increase in elevation was associated with a 36% increase in the odds of occurrence. The maximum effect of watershed area was at about 509 ha. Estimated mean probabilities of occurrence of larval tailed frogs in the Blue River watershed stream network were calculated from coefficients listed in Table 4c and are displayed in Figure 21. The predominant occurrence of tailed frog larvae in moderate-sized streams, just below the smallest streams is quite apparent in this map.

Figure 19. Locations where larval tailed frogs were and were not detected in 5-m stream lengths in summers 1995 and 1996 in the Blue River watershed.

(a) Percent of sites where present.



(b) Number of individuals per meter length of stream.



(c) Number of individuals per square meter of surface water.

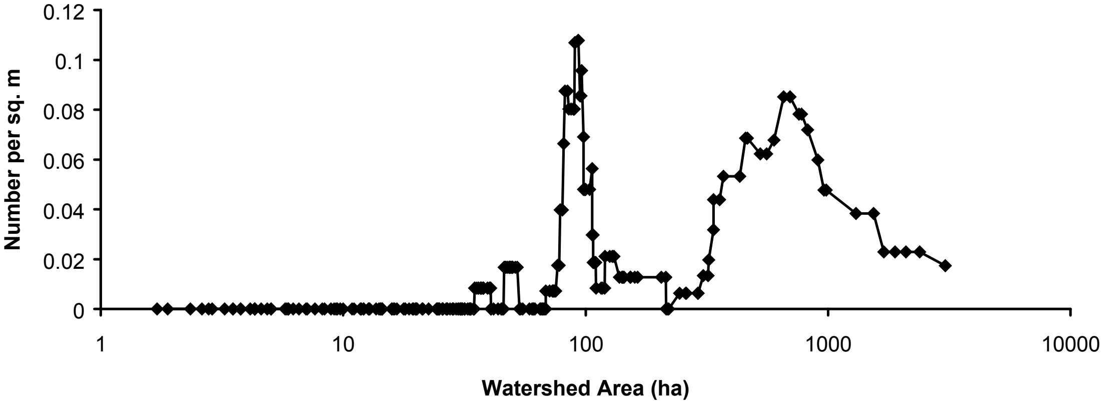


Figure 20. Occurrence of tailed frog larvae over a range of basin sizes. Points represent a 15-site average over median watershed area. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points, from smallest to largest watershed area.

Figure 21. Estimated mean probability of occurrence of tailed frog larvae in 5-m stream lengths in the Blue River watershed during summers of 1995 and 1996, for basins >= 7 ha, assuming water is present in the channel

Metamorphosed tailed frogs

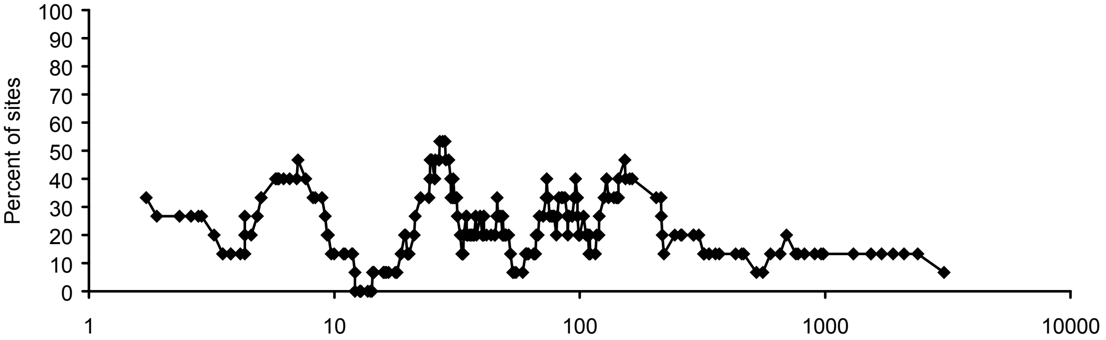
Metamorphosed tailed frogs were found at 23% (62 of 273) of sites searched (Figure 22). Average frequency of occurrence, linear rate, and density of metamorphosed tailed frogs in 5-m stream lengths, are displayed in Figure 23 over a range of basin sizes. Metamorphosed tailed frogs were found in all basin sizes sampled. In contrast to tailed frog larvae, there seemed to be no clear trend in frequency of occurrence over the range of basin sizes. However, there appeared to be a slight decrease in average linear rate, and a clear decrease in density over the range of basin sizes. A plot of frequency of occurrence over elevation indicated an increasing probability of occurrence in higher elevation streams (Figure 24).

The watershed model for metamorphosed tailed frogs (Table 4d) included four variables. Three were linear and one had a quadratic effect. Following were the effects of each variable after accounting for others in the model. A 1-m increase in length of surface water searched (maximum of 5) was associated with a 63% increase in the odds of occurrence. A 10-unit increase in 1-km radius mean percent slope was associated with a 61% increase in the odds of occurrence. A 45-degree increase from north (either west or east) was associated with a 24% decrease in the odds of occurrence. Odds of occurrence in a south-facing stream (180 degrees) were estimated to be 33% of those of a north-facing stream (0 degrees). The maximum positive effect of elevation was at about 1274 m.

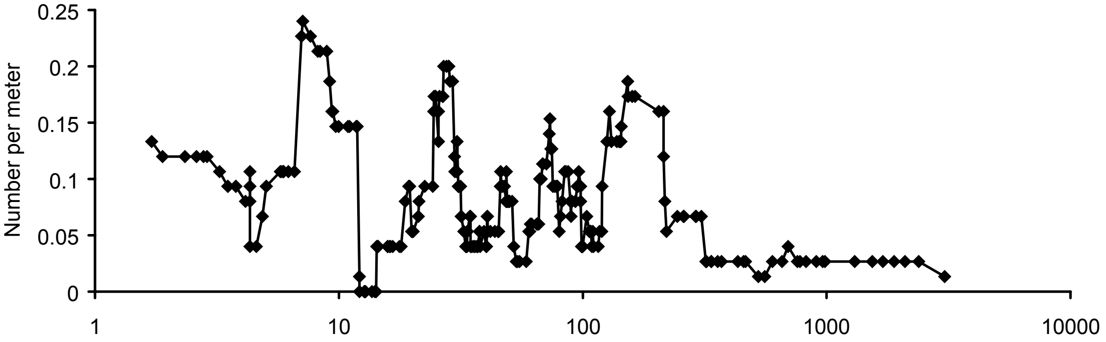
Estimated mean probabilities of occurrence of metamorphosed tailed frogs in the Blue River watershed stream network were calculated from coefficients in Table 4d and are displayed in Figure 25. The predominance of metamorphosed tailed frogs in small streams at high elevations in this watershed is quite apparent. A comparison with the general distribution of larval tailed frogs in the watershed (Figure 21) reveals that the highest frequency of occurrence of larval tailed frogs occurred below portions of the network with high probability of occurrence of metamorphosed tailed frogs.

Figure 22. Locations where metamorphosed tailed frogs were and were not detected in 5-m stream lengths in summers 1995 and 1996 in the Blue River watershed.

(a) Percent of sites where present.



(b) Number of individuals per meter length of stream.



(c) Number of individuals per square meter of surface water.

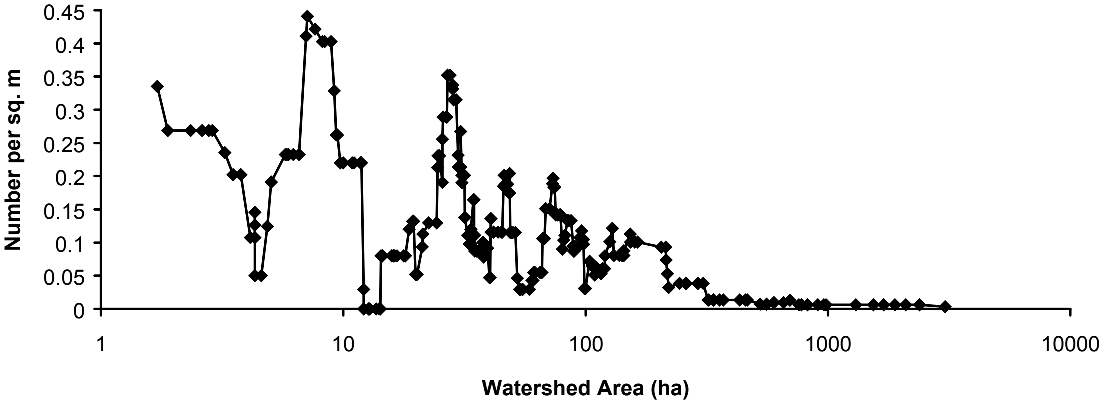


Figure 23. Occurrence of metamorphosed tailed frog over a range of basin sizes. Points represent a 15-site average over median watershed area. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points, from smallest to largest watershed area.

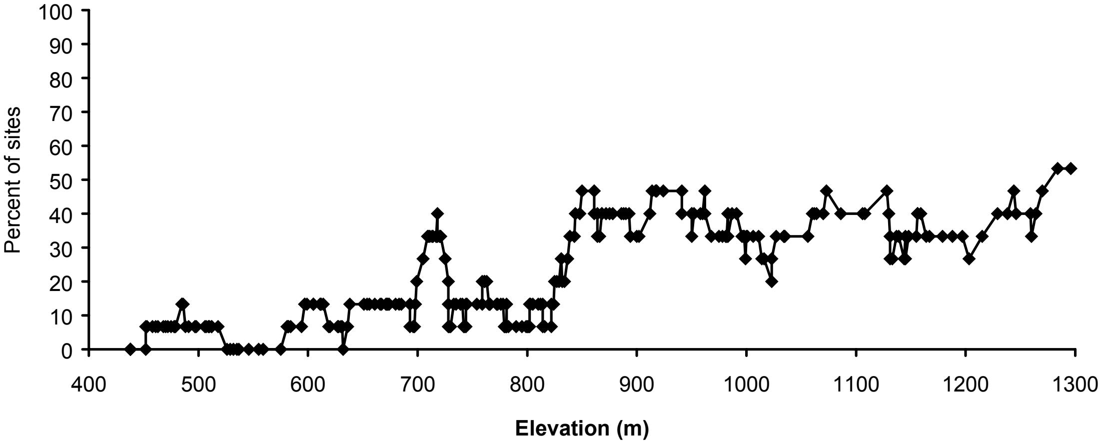


Figure 24. Percent of sites detecting metamorphosed tailed frog within a 15-site moving window over a range of elevations. Only sites with at least some surface water were searched for amphibians and are represented here (i.e. dry sites are not included). The line connecting the points serves only to guide the reader in the consecutive order of the points.

Figure 25. Estimated mean probability of occurrence of metamorphosed tailed frog in 5-m stream lengths in the Blue River watershed during summers of 1995 and 1996, for basins >= 7 ha, assuming water is present in the channel.

MULTI-SCALE CORRELATIONS WITH PRESENCE

Cascade torrent salamander larvae

Unique models were built for three of five model-building processes (Table 5). In the fifth and last process, when all variables were included in the pool of potential explanatory variables, variables from 4 of 5 groups were included. Also in the fifth process, several immediate-context and large-scale variables entered the model, and it appears that these changed the relationship of other explanatory variables to the response and eliminated others. The strong presence of moderate- and large-extent variables in the final model indicated that aspects of the Cascade torrent salamander's life history operating at those scales were likely important in determining the distribution of this species. Alternatively, instream variables may have been measured imprecisely, or other important instream variables were not measured.

A composite description of a stream which had high odds of occurrence of Cascade torrent salamander larvae in a 5-m length of surface water searched in summers 1995 and 1996 in the Blue River watershed would be: very small basin size, at about 800-900 m elevation in a region of steep topography, with an average depth about 4-5 cm (so average maximum depth of about 8-10 cm), wetted channel substrate composed of at least moderate amounts of cobble and boulder, channel units composed of low to moderate amounts of riffle, but mostly other channel-unit types, moderate high canopy cover with some mid-level cover adjacent to the stream. Searches later in the day, but in the coldest waters meeting the previous description were most productive.

Table 5. Results of the multi-scale model-building processes for Cascade torrent salamander larvae.[1] Only variables significant ($p<=0.05$) in at least one model are shown.

		Maximum Spatial Extent of Potential Variable Pool				
Variable (units)	Variable Group[2]	Instream	Morphology	Immediate Context	Local Context	Large Scale
Water temperature (°C)	S	Q, 0.005 (+) 10.3	Q, 0.05 (+) 9.9	Q, 0.05 (+) 9.9	Q, 0.05 (+) 9.9	L, 0.0007 (1) 0.65x
Percent pebble (%)	S	Q, 0.05 (+) 23	ns	ns	ns	ns
Percent silt (%)	S	Q, 0.04 (+) 15	ns	ns	ns	ns
Percent coarse particles (%)	S	ns	ns	ns	ns	LL, 0.01 (10x) 6.4x
Average depth (cm)	M	▨	Q, 0.002 (+) 4.9	Q, 0.002 (+) 4.9	Q, 0.002 (+) 4.9	Q, 0.008 (+) 4.1
Stream gradient (%)	M	▨	LL, 0.008 (10x) 4.66x	LL, 0.008 (10x) 4.66x	LL, 0.008 (10x) 4.66x	ns
Length of surface water (m)	M	▨	L, 0.04 (1) 3.31x	L, 0.04 (1) 3.31x	L, 0.04 (1) 3.31x	ns
Percent riffle (%)	M	▨	L, 0.003 (10) 0.98x	L, 0.003 (10) 0.98x	L, 0.003 (10) 0.98x	Q, 0.02 (+) 35
>15-m cover (%)	IC	▨	▨	ns	ns	Q, 0.01 (+) 55
5- to 15-m cover (%)	IC	▨	▨	ns	ns	L, 0.005 (10) 1.02x
Elevation (m)	LS	▨	▨	▨	▨	Q, 0.002 (+) 853
1-km mean slope context (%)	LS	▨	▨	▨	▨	L, 3E-07 (10) 3.10x
Watershed area (ha)	LS	▨	▨	▨	▨	L, 0.03 (10) 0.88x
Time of day, mid-survey (hr)	T	ns	L, 0.05 (1) 1.17x	L, 0.05 (1) 1.17x	L, 0.05 (1) 1.17x	L, 0.03 (1) 1.24x
Year	T	ns	ns	ns	ns	I, 0.0006 (1) 7.13x
Akaike's Information Criterion		255.2	225.6	same	same	198.2
Model Degrees of Freedom		264	260	same	same	253
Deviance		241.2	207.6	same	same	166.2

[1] For each model-building step and variable, four pieces of information are given. The first line lists the type of effect (Q=quadratic, L=linear, LL=log-linear [base 10], I=indicator variable), and the p-value for the effect. For quadratic effects, the second line indicates the direction of the convexity (in parentheses, + = up, - = down) and the value of the explanatory variable which gives maximum effect in that direction. For all other effects the second line specifies a unit increase (in parentheses) and the mean associated multiplicative change in odds of occurrence. "ns" indicates the variable was not significant ($p>0.05$).

[2] S=Instream, M=Morphology, IC=Immediate Context, LC=Local Context, LS=Large Scale

Pacific giant salamander

Unique models were built for all five model-building processes (Table 6). Four of 5 variable groups were represented in the last model-building process which included all potential variables. Large-scale variables were not prominent in the model that included all variables. In contrast, both instream and stream morphology variables were prominent in models where they were present as potential variables.

A composite description of a stream which had high odds of occurrence of Pacific giant salamander larvae in a 5-m length of surface water searched in summers 1995 and 1996 in the Blue River watershed would be: A generally north-flowing stream, with low to moderate composition of cascade, low gradient, water temperature at about 12-15$^{\mathrm{o}}$ C, moderate to high percent boulder cover in the wetted channel, deep water (only measured up to 60 cm), and cool air temperatures. Searches during early August may have been least productive.

Tailed frog larvae

All five model-building processes produced unique models (Table 7). At least one variable from each group was included in the model which allowed all variables as potential explanatory variables. It appears that aspects of the life-history of tailed frogs at multiple scales may be important in determining distribution of larvae in watersheds.

A composite description of a stream with high odds of occurrence of larval tailed frog in a 5-m length of surface water searched in summers 1995 and 1996 in the Blue River watershed would be: A moderate-sized stream, with a basin size of a few hundred hectares, with only very small amounts of particles as small as or smaller than pebbles, but rather a predominance of boulder and cobble, with wetted channel dimensions of about 13 cm average depth (so average maximum depth of about 25-30 cm) and 3.5-4.0 m average width, moderate mid-level vegetation cover within a harvested stand, but only about 100-150 m away from unharvested forest.

Table 6. Results of multi-scale model-building processes for Pacific giant salamander larvae.[1] Only variables significant (p<=0.05) in at least one model are shown.

		Maximum Spatial Extent of Potential Variable Pool				
Variable (units)	Variable Group[2]	Instream	Morphology	Immediate Context	Local Context	Large Scale
Water temperature (°C)	S	Q, 0.002 (+) 14.3	Q, 6E-06 (+) 12.5	Q, 7E-06 (+) 12.7	Q, 6E-05 (+) 12.8	Q, 3E-06 (+) 13.3
Percent boulder (%)	S	LL, 4E-07 (10x) 4.32x	LL, 0.002 (10x) 2.93x	LL, 0.0003 (10x) 4.12x	LL, 0.0003 (10x) 4.20x	LL, 3E-05 (10x) 4.64x
Percent cobble (%)	S	LL, 0.0008 (10x) 5.75x	LL, 0.04 (10x) 3.55x	LL, 0.003 (10x) 9.08x	LL, 0.002 (10x) 9.67x	ns
Percent litter (%)	S	L, 0.01 (10) 0.50x	ns	ns	ns	ns
Percent log (%)	S	LL, 0.02 (10x) 4.17x	ns	ns	ns	ns
Percent pebble (%)	S	ns	L, 0.03 (10) 0.71x	ns	ns	ns
Percent bedrock (%)	S	ns	ns	L, 0.02 (10) 1.31x	L, 0.003 (10) 1.43x	ns
Percent cascade (%)	M	▨	Q, 0.02 (+) 17	Q, 0.007 (+) 18	Q, 0.003 (+) 16	Q, 0.004 (+) 19
Percent glide (%)	M	▨	L, 0.02 (10) 1.31X	L, 0.02 (10) 1.31x	L, 0.02 (10) 1.31x	
Stream gradient (%)	M	▨	L, 0.03 (10) 0.72x	L, 0.008 (10) 0.65x	L, 0.007 (10) 0.64x	L, 0.001 (10) 0.59x
Average depth (cm)	M	▨	LL, 0.0001 (10x) 14.1x	LL, 0.0004 (10x) 14.2x	LL, 0.0002 (10x) 15.2x	LL, 3E-06 (10x) 29.2x
>15-m cover (%)	IC	▨	▨	L, 0.05 (10) 0.89x	ns	ns
Air temperature (°C)	IC	▨	▨	ns	ns	L, 0.03 (1) 0.89x
Harvest on at least one side, and with conifer buffer	LC	▨	▨	▨	I, 0.03 0.24x	ns
Harvest on at least one side, and without conifer buffer	LC	▨	▨	▨	I, 0.03 2.41x	ns
DEM azimuth (°)	LS	▨	▨	▨	▨	Q, 0.002 (-) 210
Julian date	T	Q, 0.005 (-) 222	ns	Q, 0.03 (-) 215	Q, 0.03 (-) 216	ns
Akaike's Information Criterion		257.4	218.5	214.1	213.8	202.6
Model Degrees of Freedom		262	258	255	254	256
Deviance		239.4	196.5	186.1	183.8	180.6

[1] For each model-building step and variable, four pieces of information are given. The first line lists the type of effect (Q=quadratic, L=linear, LL=log-linear [base 10], I=indicator variable), and the p-value for the effect. For quadratic effects, the second line indicates the direction of the convexity (in parentheses, + = up, - = down) and the value of the explanatory variable which gives maximum effect in that direction. For all other effects the second line specifies a unit increase (in parentheses) and the mean associated multiplicative change in odds of occurrence. "ns" indicates the variable was not significant (p>0.05).

[2] S=Instream, M=Morphology, IC=Immediate Context, LC=Local Context, LS=Large Scale

Table 7. Results of multi-scale model-building processes for tailed frog larvae.[1] Only variables significant (p<=0.05) in at least one model are shown.

		Maximum Spatial Extent of Potential Variable Pool				
Variable (units)	Variable Group[2]	Instream	Morphology	Immediate Context	Local Context	Large Scale
Water temperature (°C)	S	ns	Q, 0.02 (+) 12.6	Q, 0.02 (+) 12.5	ns	ns
Percent boulder (%)	S	L, 0.0001 (10) 1.71	ns	ns	ns	ns
Percent cobble (%)	S	L, 0.004 (10) 1.56	ns	ns	ns	ns
Percent fine particles (%)	S	ns	LL, 0.0009 (10x) 0.10x	LL, 0.0002 (10x) 0.06x	LL, 0.0003 (10x) 0.08x	LL, 0.002 (10x) 0.09x
Percent pebble (%)	S	ns	ns	ns	ns	LL, 0.01 (10x) 0.08x
Average depth (cm)	M	▨	Q, 0.0001 (+) 12.6	Q, 9E-06 (+) 12.9	Q, 5E-05 (+) 13.0	ns
Width/depth ratio	M	▨	Q, 6E-05 (+) 29.2	Q, 4E-06 (+) 30.0	Q, 9E-06 (+) 29.3	Q, 0.0002 (+) 26.6
>15-m cover (%)	IC	▨	▨	LL, 0.008 (10x) 0.23x	LL, 0.02 (10x) 0.21x	ns
5- to 15-m cover (%)	IC	▨	▨	Q, 0.0009 (+) 43	Q, 0.001 (+) 43	Q, 0.03 (+) 48
Stream distance in any direction to unharvested forest (m)	LC	▨	▨	▨	Q, 0.03 (+) 116	Q, 0.005 (+) 109
Watershed area (ha)	LS	▨	▨	▨	▨	QLL, 0.0007 (+) 397
Akaike's Information Criterion		135.2	111.5	104.7	104.0	99.9
Model Degrees of Freedom		269	261	258	258	258
Deviance		129.2	95.5	82.7	82.0	77.9

[1] For each model-building step and variable, four pieces of information are given. The first line lists the type of effect (Q=quadratic, L=linear, LL=log-linear [base 10], I=indicator variable), and the p-value for the effect. For quadratic effects, the second line indicates the direction of the convexity (in parentheses, + = up, - = down) and the value of the explanatory variable which gives maximum effect in that direction. For all other effects the second line specifies a unit increase (in parentheses) and the mean associated multiplicative change in odds of occurrence. "ns" indicates the variable was not significant (p>0.05).

[2] S=Instream, M=Morphology, IC=Immediate Context, LC=Local Context, LS=Large Scale

Metamorphosed tailed frog

All five model-building processes produced unique models (Table 8). The final model, which allowed all variables as potential explanatory variables, contained variables from four of five variable groups. Large-extent variables figured prominently in this model, indicating that some unmeasured environmental variables, such as ground-level humidity, are important to metamorphosed tailed frogs at this scale.

A composite description of a stream with high odds of occurrence of metamorphosed tailed frog in a 5-m length of surface water searched in summers 1995 and 1996 in the Blue River watershed would be: A high elevation stream in a region of relatively steep topography, with at least a moderate percent of the glide channel unit, and a small proportion of cascades, a moderate presence of boulders in the wetted channel, within or very near to unharvested forest.

Table 8. Results of multi-scale model-building processes for metamorphosed tailed frog.[1] Only variables significant ($p<=0.05$) in at least one model are shown.

		Maximum Spatial Extent of Potential Variable Pool				
Variable (units)	Variable Group[2]	Instream	Morphology	Immediate Context	Local Context	Large Scale
Water temperature (°C)	S	L, 0.04 (1) 0.87x	ns	ns	ns	ns
Percent boulder (%)	S	LL, 5E-05 (10x) 3.40x	LL, 6E-05 (10x) 3.60x	LL, 6E-05 (10x) 3.83x	LL, 9E-05 (10x) 3.71x	Q, 0.01 (+) 35
Percent cascade (%)	M	▨	Q, 0.05 (+) 8	Q, 0.03 (+) 8	Q, 0.04 (+) 9	Q, 0.0005 (+) 11
Percent glide (%)	M	▨	LL, 0.02 (10x) 1.99x	LL, 0.02 (10x) 1.96x	LL, 0.03 (10x) 1.91x	ns
Stream gradient (%)	M	▨	LL, 0.0003 (10x) 4.87x	LL, 0.0005 (10x) 4.87	LL, 0.0005 (10x) 4.79	ns
>15-m cover (%)	IC	▨	▨	Q, 0.03 (+) 57	ns	ns
Stream distance in any direction to unharvested forest (m)	LC	▨	▨	▨	L, 0.0001 (100) 0.59x	L, 0.0007 (100) 0.63x
DEM elevation (m)	LS	▨	▨	▨	▨	L, 2E-08 (100) 1.52x
1-km mean slope context (%)	LS	▨	▨	▨	▨	L, 0.009 (10) 1.57x
Akaike's Information Criterion		276.3	267.4	263.5	254.3	236.2
Model Degrees of Freedom		268	265	263	264	264
Deviance		270.3	255.4	247.5	240.3	220.2

[1] For each model-building step and variable, four pieces of information are given. The first line lists the type of effect (Q=quadratic, L=linear, LL=log-linear [base 10], I=indicator variable), and the p-value for the effect. For quadratic effects, the second line indicates the direction of the convexity (in parentheses, + = up, - = down) and the value of the explanatory variable which gives maximum effect in that direction. For all other effects the second line specifies a unit increase (in parentheses) and the mean associated multiplicative change in odds of occurrence. "ns" indicates the variable was not significant ($p>0.05$).

[2] S=Instream, M=Morphology, IC=Immediate Context, LC=Local Context, LS=Large Scale

Biotic Interactions

I had originally attempted to use indicator variables for the presence of fish and crayfish in the multi-scale modeling exercise as the second in a total of six processes. However, occurrence of some species was exclusive or nearly exclusive to occurrence of others, making model coefficient estimation impossible or highly questionable. Therefore, in order to display the relative frequency of occurrence of each species in relation to others I prepared an occurrence matrix to display relationships between presence and absence of biota (Table 9). The most obvious results were the completely exclusive occurrences of fish and Cascade torrent salamander, the completely exclusive occurrences of crayfish and metamorphosed tailed frogs, the nearly exclusive occurrence of crayfish and Cascade torrent salamander, and the frequent occurrence of Cascade torrent salamander when metamorphosed tailed frogs were present. While none of these biota are truly completely exclusive of the other in the watershed, this table illustrates that there was little overlap among some species.

Table 9. Occurrences of biota in 273 areas searched. Presence is indicated by 1, absence by 0. Marginal totals are given for each species and/or life stage.

		248	25									
Crayfish	1	36	10	46								
	0	212	15	227	46							
Metamorphosed Tailed Frog	1	59	3	62	0	62						
	0	189	22	165	46	211	62					
Larval Tailed Frog	1	16	5	19	2	13	8	21				
	0	232	20	208	44	198	54	252	21			
Pacific Giant Salamander Larvae	1	170	24	158	36	149	45	174	20	194		
	0	78	1	69	10	62	17	78	1	79	194	
Cascade Torrent Salamander Larvae	1	52	0	50	2	35	17	48	4	14	38	52
	0	196	25	177	44	176	45	204	17	65	156	221
		0	1	0	1	0	1	0	1	0	1	
		Fish		Crayfish		Metamorphosed Tailed Frog		Larval Tailed Frog		Pacific Giant Salamander Larvae		

AMPHIBIAN SIZE DISTRIBUTION

Cascade torrent salamander larvae occurred over a small range of basin sizes and did not show any trends in size distribution over this range. The sample size for tailed frog larvae was small, and no trends were apparent. While metamorphosed tailed frogs were found throughout the watershed, there were no noticeable trends in size. Only Pacific giant salamander larvae occurred over a wide range of basin sizes and showed distinct trends in size distribution over watershed area. Therefore, only data on Pacific giant salamander larvae are presented.

The size distribution of Pacific giant salamander larvae was more highly skewed to small sizes in the smallest streams, and less so in larger streams (Figure 26). Larger streams had a larger proportion of large larvae than in the small streams (Figure 26).

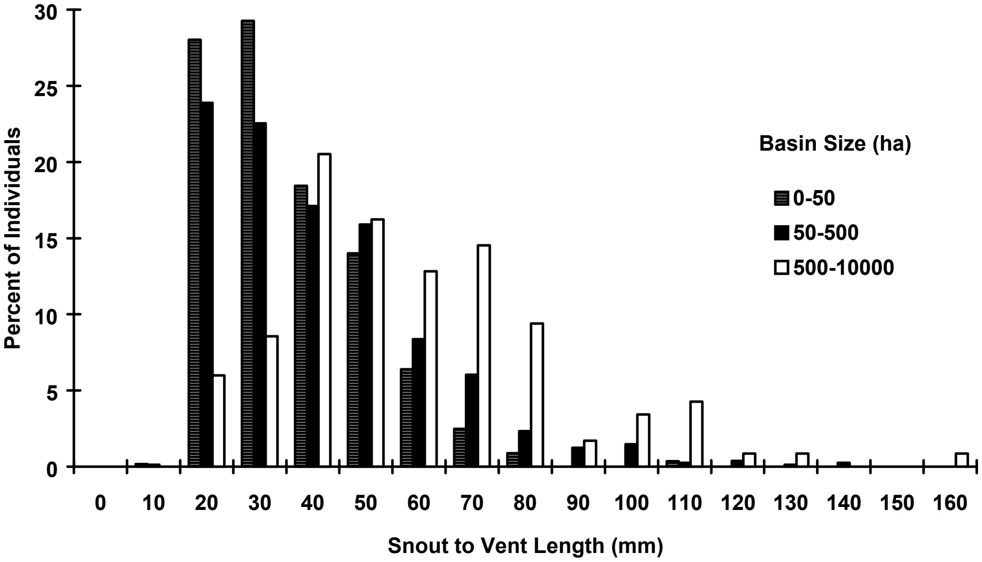


Figure 26. Size distribution of Pacific giant salamander larvae in three basin size ranges. Bars represent percent of individuals of a given size class within the corresponding basin size.

Average sizes of Pacific giant salamander larvae increased with basin size (Figure 27). While minimum sizes remained fairly constant over the range of basin sizes, the maximum size of larvae encountered increased from small streams to larger streams. The elevated average sizes in very small basins are in part due to the unusual presence of a single, large neotene in one of these very small streams.

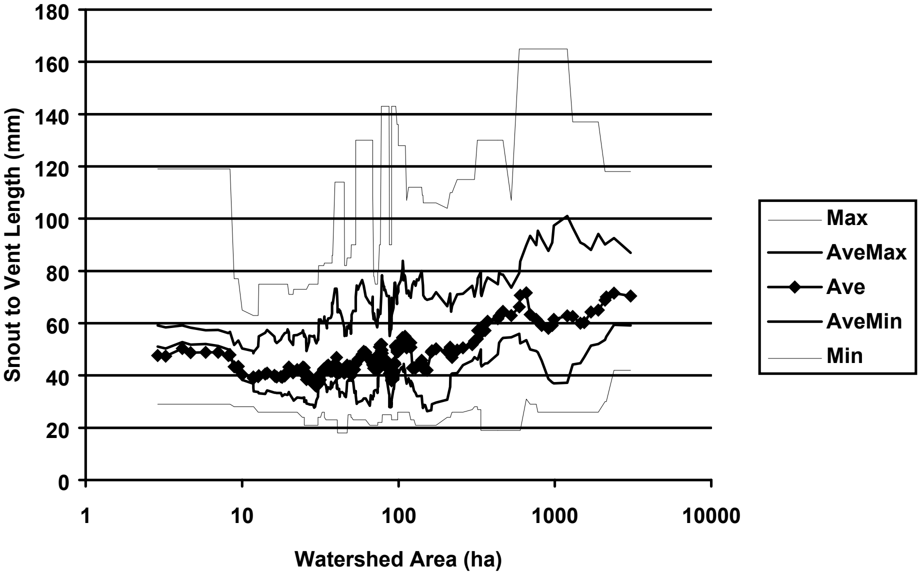


Figure 27. Sizes of Pacific giant salamander larvae. Points represent an 11-site moving window. Snout to vent lengths displayed are the maximum and minimum, the average of each site maximum and minimum, and the average of all larvae detected at all 11-sites represented by the single point. Plotted over median watershed area among the 11 sites.

DISCUSSION

My results represent a first step in investigating watershed-level life histories and associations of stream amphibians. My study is the first to 1) randomly sample amphibians within a complete watershed stream network, 2) develop statistical models of the mean probability of occurrence of amphibians throughout a watershed stream network, 3) produce maps of estimated mean probability of occurrence of amphibians within a watershed stream network, and 4) explore multi-scale associations of amphibian presence using logistic regression. Important findings in this study include 1) specific stream sizes occupied by Cascade torrent salamander larvae in a stream network, 2) differential distribution of tailed frog life stages in a stream network, and 3) longitudinal trends in size distribution of Pacific giant salamander larvae. In addition, many lessons were learned regarding sampling within watersheds, and in interpreting results of model-building.

In the following sections I evaluate the watershed-level modeling and multi-scale model-building processes, recommend approaches to interpretation of my results, discuss outcomes of these processes, discuss implications of these results to landscape-level life-histories of stream amphibians, and discuss implications to stream amphibian research and management.

WATERSHED-LEVEL MODELING

The process used to sample, model, and map watershed-level distributions of stream amphibians in the Blue River watershed using widely available or derivable data layers was quite successful. While landscape-level sampling, modeling, and mapping of terrestrial birds has recently been attempted (e.g. Hansen et al. 1993, Wallin unpubl.data), I am aware of no similar attempts for aquatic organisms. Detailed instream habitat conditions in forested mountain landscapes are not currently available through remote sensing over large geographic areas as they are for vegetation. Therefore mapping estimated watershed distributions of stream amphibians based on spatially-explicit representations of instream habitat variables currently is not possible.

However, I found strong correlations of stream amphibian distributions in stream networks with geomorphic and geographic variables, which in turn were highly correlated with some instream habitats.

Very few examples or even hypotheses of landscape-level trends in distribution of stream amphibians exist. However, several that have been put forth were confirmed in this study. For example, Cascade torrent salamanders were found most often in the smallest streams, as observed by Nussbaum et al. (1983), Leonard et al. (1993), Applegarth (1994), Good and Wake (1992). Applegarth (1994) suggested that Cascade torrent salamanders "may be limited to the rather narrow zone of transient snowpack." While I wouldn't interpret the zone as narrow (350-1100 m, Harr 1981, 1986), I did find Cascade torrent salamanders to reach their highest probability of occurrence in small streams within the central and upper portions of this transient snow zone. The predominant occurrence of torrent salamanders in steeper topography, as observed in this study, is consistent with the observations of Good and Wake (1992).

Patterns observed for larval and metamorphosed tailed frogs have not previously been reported. As expected, Pacific giant salamander larvae were found throughout the watershed. However, the trends in frequency of occurrence have not previously been reported.

A single result of the modeling effort was less than fully satisfactory: the probability of occurrence estimated for tailed frog larvae in the mainstem of Lookout Creek (<10%). Stan Gregory and others have commonly found tailed frog larvae in riffles of the mainstem of Lookout Creek (Randy Wildman pers. comm.), yet my estimates based on watershed-level sampling are that <10% of all 5-m sections of the mainstem would support tailed frog larvae. The reason for this potential discrepancy seems two-fold: 1) No random sample points fell on middle and lower Lookout Creek, but more than five were on Blue River, and 2) the mainstem of Lookout Creek is quite different from other stream segments of similar size. Therefore, the potential inadequacy of the model on lower Lookout Creek was not a problem with the modeling process per se, but due to an underrepresentation of that particular stream in the sample taken.

The riparian area of Lookout Creek is quite heavily forested. A large cold tributary, Mack Creek, where tailed frogs are common, flows into Lookout Creek at mid-length. Small to large floodplains, side-channels, and vegetated banks are common along most of Lookout Creek, except the very lowest reach. Boulder-cobble riffles are common. All these characteristics favor presence of tailed frog larvae in this segment. In contrast, Blue River, between Tidbits and Quentin Creeks, is only partially forested along its banks. Most of the tributaries are south-flowing basins, not as cold as Mack Creek. Most of Blue River along this segment is constrained in a narrow bedrock canyon, where bedload movement during high flows is likely severe, and refuges are few. Riffle habitats are frequently composed of very large boulders and bedrock, and boulder-cobble riffles are often quite shallow and exposed to the sun.

The mapped probability of occurrence of tailed frog larvae I think is quite representative of the Blue River watershed except for the mainstem of Lookout Creek. Here, probabilities of occurrence are likely between 10% and 30% (Randy Wildman, Department of Fisheries and Wildlife, Oregon State University, suggested 25% to 30%). A stratified random sampling design may have prevented this chance bias. However, inclusion of mainstem Lookout Creek in the sample also may have biased results for the remainder of the watershed.

MULTI-SCALE ASSOCIATIONS

This multiple model-building process was quite time-consuming to conduct because no automated mechanism was available to conduct step-wise logistic regression using “drop-in-deviance” chi-square tests. Nevertheless, this process revealed strengths of association and consistency (or lack thereof) of habitat-level variables with the response variable, in the face of "competition" (through correlation) with other variables at multiple scales. Further, several of the more abstract, large-scale variables were significant components of models predicting presence of stream amphibians, even after accounting for measured instream habitat variables. This indicates that other unmeasured environmental features may be important in determining watershed-level distribution of stream amphibians. These additional features may be other instream variables, such as annual instability of cobble-sized particles or presence of good nesting structures, or may be variables associated with terrestrial stages of the amphibians, such as quality of dispersal or aestivation habitat. It also is clear from this exercise that it could be quite easy to draw different conclusions regarding importance of particular environmental features to amphibian distribution if different variables are included in the pool of potential explanatory variables.

Overall, detailed interpretations of model-building results were most straightforward for the less common species (Cascade torrent salamander larvae, metamorphosed and larval tailed frogs) and most unclear for the very common and widespread Pacific giant salamander. Comparisons with other studies were typically difficult because of differences in sampling methods, ranges over which variables were measured, and type of response examined. In the following discussions I have sometimes compared associations of variables with the odds of occurrence observed in this study, to associations of these variables with density observed in other studies. However, it is unknown in many cases whether this comparison is meaningful, since these two measures could be independent, depending on the sampling resolution and instream distribution patterns of these species. Nevertheless, in the following paragraphs I have cautiously attempted to interpret my results and compare them to associations reported by others.

Cascade torrent salamander larvae

Quadratic associations of water temperature with occurrence of Cascade torrent salamanders in the instream and morphology models indicated highest odds of occurrence were in streams of about 10°C. Welsh and Lind (1996) reported that the highest abundances of southern torrent salamanders (*R. variegatus*) in northwestern California occurred in waters with temperatures of 8-13°C. Welsh and Lind (1996) also postulated a weakly-fitting quadratic regression equation in which the highest densities of southern torrent salamanders were estimated to be at about 10°C. However, in the last stage of my multi-scale model-building process, water temperature was included, but had a negative linear relationship with the log odds of occurrence.

This change in form of the effect is likely due to the inclusion of elevation in the large-scale model. Elevation is negatively correlated with water temperature in this basin, and entered the large-scale model with a quadratic effect as water had previously. Once elevation explained that pattern of occurrence, the effect of water temperature took on a different role, that of identifying the cooler sites.

The significance of the quadratic effects of percent pebble and percent silt in the instream model is uncertain. Values as high as 23% pebble and 15% silt are frequent only in small streams in this watershed, where summer low flows are inadequate to transport the material. However, high amounts of these finer particles are generally associated with reduced odds of occurrence of torrent salamanders, as is indicated by the positive association with coarse particles in the large-scale model. Therefore the quadratic effects of percent pebble and silt may represent a compromise between small streams, where torrent salamanders are most often found, and an extreme situation with high levels of these substrates, where torrent salamanders are not often found.

The average depth resulting in the greatest effect on odds of occurrence was about 4-5 cm (indicating an average maximum depth of about 8-10 cm). Lee (1997) reported a positive correlation of Cascade torrent salamander density with average water depth in summer in old-growth forests, in streams with average summer depths of 0.6 cm, average maximum summer depths of 1.1 cm, and a range of depths from 0 to 8.5 cm. Lee's results are generally consistent with mine since most of her sites had depths less than 5 cm. However, it appears that a quadratic model would have fit her data (Figure 3.5 in Lee 1997) just as well, if not better than a linear model.

The log-linear relationship with stream gradient in the morphology model indicates that small increases over small values of gradient (such as 1% to 10%) are associated with relatively large changes in the odds of occurrence compared to similar absolute changes at higher values of gradient (such as 50% to 60%). This merely indicates that Cascade torrent salamander larvae occurred most often in streams with at least moderate gradients (which were often small streams), and rarely in streams with very small gradients (which were often large streams). Diller and Wallace (1996) also reported a positive relationship of gradient with presence of the southern torrent salamander. The disappearance of gradient in the large-scale model is likely due to the inclusion of watershed area, which is negatively correlated with gradient. The positive association with length of surface water in the search area indicates the seemingly obvious, that the few sites with less than a full 5-m length of surface water had a reduced odds of torrent salamander occurrence.

Percent riffle was included once as a negative linear (morphology model) variable and once as a quadratic term (large-scale model). Riffles have been reported as having both positive (for high gradient riffles, Diller and Wallace 1996) and negative (Welsh and Lind 1996) associations with densities of southern torrent salamanders. Inconsistencies among sampling methods and lack of random sampling methods confound explanation of these different results. However, the interpretations of these authors along with my own observations indicate that relatively high-gradient channel units may provide the only extensive interstitial space (used as hiding cover) available in sediment-rich, low-gradient streams. In contrast, higher-gradient streams with step-pool morphology scour fine sediments from small pools which then deposit in riffle units. While very fine sediment is washed from riffle units and deposited in pool units during low flows, this small amount of sediment does not fill in all the interstitial space created during high flows. Therefore interstitial space in summer is more widespread in higher-gradient streams and often quite abundant in pools.

Reports of associations with canopy cover also are inconsistent. Welsh and Lind (1996) indicated a positive association of canopy cover with density of southern torrent salamanders, while Diller and Wallace (1996) found no significant association of canopy cover with presence of southern torrent salamanders, and Lee (1997) reported a negative correlation of riparian overstory with Cascade torrent salamander density. In my study, vegetation cover variables did not enter until large-scale variables were included. In that context, high-level cover had the greatest effect at moderate levels (versus high or low) and medium-height cover had a very small positive association. The results of this study may be a reflection of the hydrologic regime and geomorphic context rather than an actual effect of canopy cover. In the Blue River watershed, flashy stream channels in steeper topography and rockier soils often have more extensive rocky banks and lower slopes. These steep banks are often devoid of conifers but often support moderate-sized deciduous trees. This canopy configuration, therefore, may reflect ground-level or underground riparian and stream bank conditions that may be more important than the actual canopy cover.

Torrent salamanders have been reported from near sea level (Nussbaum et al. 1983) to 1469 m elevation (southern torrent salamander, L. Diller, unpublished data, in Welsh and Lind 1996). Streams sampled in the Blue River watershed extended to near the maximum elevational limit reported (see Table 3). Therefore, a quadratic association of Cascade torrent salamander occurrence with elevation was expected. Virtually no comparable data have been reported. Welsh and Lind (1996) reported a weak negative relationship between elevation and presence of southern torrent salamanders (sample range up to 1115 m, minimum elevation sampled not given). Lee (1997) reported a negative correlation of Cascade torrent salamander densities with elevation in 10 old-growth stands in both spring and summer (range 503 m to 1146 m). However, this sample size is rather small, and elevational patterns of occurrence may not be the same as elevational patterns of density.

The strong association with steep topography (1-km mean slope context) has not been previously reported from a field experiment, although Good and Wake (1992) stated "Because *Rhyacotriton* prefers rapidly flowing, well aerated streams and springs, it is restricted to the vicinity of areas with considerable physical relief. These salamanders are absent from flat areas and areas with only low, gently sloping hills where such streams are lacking". I postulated that topography and associated geology might effect the instream substrate, which in turn would influence the presence of Cascade torrent salamander. However, the occurrence of the torrent salamander was overwhelmingly associated with steep topography, even after accounting for substrate composition. Therefore it may be that some characteristics of stream banks or streamsides in steep topography (such as deep accumulations of colluvium) may act as important habitats for metamorphosed Cascade torrent salamanders. Alternatively, streams located in steep topography may contain a higher density and quality of channel unit step structures which may act as nest sites for this species.

The negative association with watershed area was expected and is corroborated by anecdotal (Good and Wake 1992, Leonard et al. 1993, Nussbaum et al. 1983) and scientific (Murphy 1979) reports.

The inclusion of time of day in the torrent salamander models may indicate a need to randomize, stratify by, or use time of day as a covariate in studies of this species. It is unknown whether these results are anomalies of the data sets, diel patterns of surface occurrence, or some sort of sampling bias. Diel patterns of activity have been reported for Pacific giant salamander (Parker 1994), but not for torrent salamanders. However, no effect of time of day was detected for Pacific giant salamanders.

Pacific giant salamander larvae

Pacific giant salamanders are widespread in the Pacific Northwest (Nussbaum et al. 1983) and widespread within the study watershed (Figures 15 and 18). Therefore, the associations of variables detected at multiple scales do not distinguish spatially distinct distributions within the watershed as was at least partly the case for the Cascade torrent salamander (Figures 11 and 14). Instead, they distinguish areas within the watershed-wide distribution of the salamander that were more or less likely to have Pacific giant salamanders. Because of the widespread occurrence of the species, and the likely confounding of certain variables with stream size (and concomitant increased search area), meaningful interpretation of associations of the odds of occurrence of Pacific giant salamander larvae with many of these variables was elusive.

Likely because of the widespread occurrence of the species, I could find no reference to preferred or tolerated temperatures of this species. Nussbaum (1969b) reported temperatures at two nest sites in the Coast Range of Benton County, Oregon: 10.3^{o}C (17 May), and 9.2^{o}C (31 May). These temperatures are only a few degrees cooler than the temperatures associated with highest odds of occurrence in the Blue River watershed (12-15^{o}C), but also were 1-2 months earlier in the season than my sampling, indicating that summer temperatures at these sites may have been comparable. The strong positive associations of presence with percent cobble and boulder observed in my study have been similarly reported for densities (Murphy 1979, Parker 1991). I have no convincing explanation for the negative association with percent litter, and find no indications in the literature. Pacific giant salamander larvae were frequently found in patches of litter that were coarse enough to provide interstitial space for the larvae. However, in sites with abundant fine, highly decomposed litter, which I did not distinguish from coarse litter, streambed interstitial space was very limited, and Pacific giant salamander larvae were not often found. Log cover is not often reported in stream amphibian studies. However, logs clearly influence channel morphology, particularly in small streams (Swanson and Lienkaemper 1978), and themselves provide cover for amphibians. Channel steps created by logs in small streams also may be sites of Pacific giant salamander nests (e.g. Nussbaum 1969b). The negative association of percent pebble with occurrence of Pacific giant salamander larvae seems to reflect the lack of interstitial space available in particles of that size, and merely compliments the positive associations already discussed with boulder and cobble. I cannot explain the positive associations with percent bedrock in the immediate context and local context models. The quadratic associations with cascades and positive associations with percent glide indicate the presence of step-pool formations along with adjacent moving water were important in determining presence of Pacific giant salamanders. Negative associations with stream gradient, and positive associations with average depth indicate a higher odds of occurrence in larger streams, as is illustrated in Figure 16. Negative associations with high-level cover and with conifer buffers in timber harvest units may reflect reduced productivity in streams with low light exposure (Murphy et al. 1981). Alternatively, as mentioned for Cascade torrent salamander, the presence of high canopy near the stream may indicate a difference in ground-level and below-ground habitat important to terrestrial forms of the Pacific giant salamander. An additional alternative explanation is that high canopy cover is negatively correlated with stream size, and the decreased odds of occurrence in streams with greater high-level cover may merely reflect the effect of decreased sample area in smaller streams (Figure 17). I cannot explain the apparent reduction in odds of occurrence in south-southwest flowing stream reaches. The inclusion of Julian Date in three of five Pacific giant salamander models indicates a potential need to randomize, stratify by or use Julian Date as a covariate in studies of this species. It is unknown if this result is an anomaly of the data set, a real change in presence of the species, or some sort of sampling bias. The dates of lowest probability of occurrence (first two weeks of August) correspond with the latter part of the period of highest water temperatures in Lookout Creek (Blue River Ranger District, in prep) and probably other streams in the watershed. Pacific giant salamanders may be taking refuge deeper in the substrate during the hot days to maintain cooler temperatures during this hottest period, and therefore were less likely to be detected.

Larval tailed frog

Most variables and estimated effects in models of tailed frog larvae occurrence are corroborated by other literature or seem to have a reasonable explanation. Second-year tadpoles studied by deVlaming and Bury (1970) selected temperatures >10°C. Most tadpoles observed in my study were >1 yr old. Temperature with the highest probability of occurrence of larvae were between 12°C and 13°C. The positive association with coarser substrates and negative association with finer substrates is commonly reported (Altig and Brodie 1972, Hawkins et al. 1988, Nussbaum et al. 1983). The stream depth and associated width-to-depth ratio indicate a perennial, flowing stream, with depth indicative of a cobble-dominated stream in this watershed. The negative effect of high canopy cover and quadratic effect of mid-level cover indicate a moderate-sized stream wide enough to produce its own canopy gap and allow growth of mid-level cover. The quadratic relationship of occurrence with distance from unharvested forest is an intriguing one. I first thought that this might merely be correlated with network position, but the relationship held strongly even after accounting for basin size. It is possible that tadpoles hatched in streams in forests move into stream sections in adjacent harvested areas if forage production is greater there, as was thought to be the case in streams studied near Mt. St. Helens (Hawkins et al. 1988). The quadratic log-linear association with watershed area indicates a high probability of occurrence in moderate-sized streams which is expected and supported in fact by many of the variables selected in previous models.

Metamorphosed tailed frog

While cold water is often mentioned as a requirement of tailed frogs in general (Nussbaum et al. 1983), the negative relationship with increasing water temperature observed in my study has been reported (but for density) from only one other study (Welsh 1990). Interestingly, though, in my study, water temperature appeared only in the instream model, indicating that other correlated variables either were more closely associated with presence of tailed frogs, or were perhaps equally associated in truth but more accurately measured. Percent boulder was consistently associated with presence of tailed frogs. Boulders not only provide excellent cover for tailed frogs, but also are likely sites for nests. Presence of boulders, cascades, and glides all indicate relatively high-gradient streams. Percent high cover entered only one model, and was subsequently replaced by distance to unharvested forest. The negative association of distance from unharvested forest was maintained in the large scale model in which elevation and slope context were added. The negative association of distance to unharvested forest is different than for tadpoles, and supported by reports that tailed frogs decline after timber harvest (Corn and Bury 1989). The positive association with elevation was highly significant, indicating that elevation may be correlated with one or more attributes important to tailed frogs. Mean slope context also was positively correlated with occurrence of tailed frogs. I speculate that streams in steeper topography have higher linear rates of occurrence of potential nest structures such as boulder steps and small log jams, than streams in more gentle topography.

INTERPRETING AND USING RESULTS IN THE BLUE RIVER WATERSHED

Some special explanation is required to ensure proper interpretation of model-building results and of the watershed network maps of the probability of occurrence of stream amphibians. First, the study design allows only correlative inferences to be made of the associations of explanatory variables and the probability of occurrence of stream amphibians. While the results are likely indicative of or related to causal factors, they cannot be used to infer causal relationships.

Second, my sampling resolution was a 5-m length of stream. Therefore all statistical analyses and model output refer to summertime searches of a 5-m length of stream, and not an entire segment of stream or tributary.

Third, the maps of probability of occurrence of stream amphibians in the Blue River watershed stream network (Figures 14, 18, 21, and 25) only display estimated means, given the explanatory variables used in the particular model. The maps illustrate rather smooth transitions along and between streams. However, there can be large variability within single stream reaches or segments. The maps should be viewed as the generalized distribution pattern of the amphibians within the watershed. The proper interpretation of the maps is as follows: If 100, 5-m lengths of stream were randomly selected from among those streams on the map labeled "40-50%", and were searched for amphibians, it is expected that the amphibian of interest would be found in 40-50 of them. To illustrate this I have prepared Figure 28. Note that while the overall average distribution of the organism in the stream network produces a clear trend of increasing probability of occurrence in smaller basins, the actual distribution, or even presence of the organism on any one stream segment can be quite different from others.

Another reason I do not recommend using the mapped estimates for single reaches or tributaries is that DEM-generated stream networks typically have mistakes that make little difference over a 2nd- or 3rd-order subbasin, but produce occasional inaccuracies in the configuration of, or joining of, the smallest 1st-order basins (pers. obs.). These problems are similar and perhaps greater in maps prepared by hand from aerial photos and topographic maps (pers. obs.). Further, the true stream network is under-represented by these maps. Nearly 20% of my sample sites were on stream extensions or tributaries not represented by the Blue River Ranger District stream layer, and 13% of my sites were on stream extensions or tributaries not mapped with a 9-ha channel initiation DEM stream network (Appendix). Some small streams simply are not detectable using either DEM flow accumulation models or aerial photos.

One region with many errors is in the upper 2-3 km of Lookout Creek. Here the original DEM was flawed, creating a few additional small tributaries off this portion of Lookout Creek. While the location and even the existence of some of those streams is incorrect, the estimated probability of occurrence for streams of that small size in that location in the watershed is correct.

The best and most proper use of the maps is for for strategic planning purposes at the watershed level. Managers may use maps to prioritize regions of the watershed for protection, restoration, or monitoring. If concerns for the amphibians arise during tactical planning of management activities in specific tributaries or locations on the landscape, field examination is necessary.

RELEVANCE TO OTHER WATERSHEDS

There is no statistical justification for application of these results outside of the Blue River watershed, and all considerations described for model application within the Blue River watershed apply outside as well. Nevertheless, one will wonder how representative these results are of other areas. I wish to discourage thoughtless application of the results of this study to basins other than the Blue River watershed, as well as to assist readers in considering what aspects of the results of this study might be similar in other basins. Some observations are likely consistent throughout most or all of the range of the species, while others are likely quite different in other areas. As Bury and Corn (1991) pointed out “Knowledge of local landscapes and the environmental setting of streams is essential to interpreting the population data of amphibians.” Swanson et al. (1988) demonstrated how landforms may affect many aspects of both terrestrial and aquatic ecosystems.

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Segment 1   =00==0=
Segment 2   0==000=
Segment 3   0=00===
Segment 4   =======
Segment 5   0=======
Segment 6   00==000=
Segment 7   ========
Segment 8   0==000===
Segment 9   ==00000===
Segment 10  0====00===
Segment 11  =000=======
Segment 12  ===========
Segment 13  0===00====0=0
Segment 14  0==00=========
Segment 15  0=======000====
Segment 16  =00000========00==
Segment 17  ==00====0====00=000
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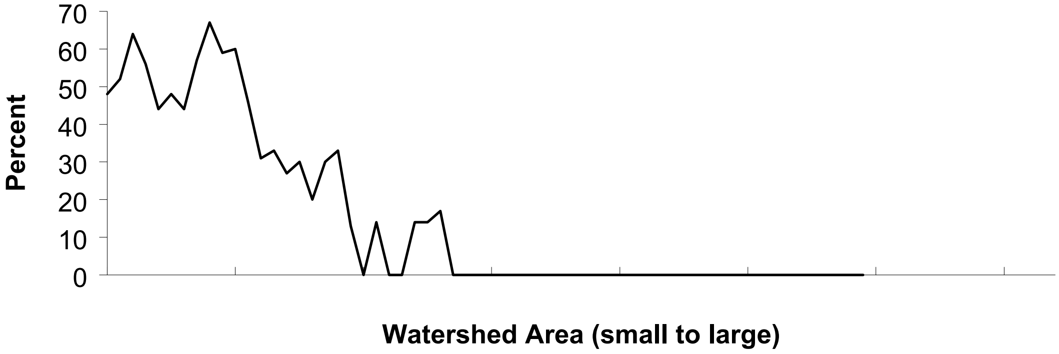

Figure 28. A hypothetical stream network consisting of 25 segments disassembled and stacked on top of each other such that basin sizes align vertically. Organism presence (0) and absence (=) are marked for each reach in each segment. The graph at the bottom displays the percent of reaches with the organism present in the stream network over the range of basin sizes.

In particular, geologic and hydrologic differences between basins may make distributions of torrent salamanders quite different in some basins. Torrent salamanders have been reported from a wide variety of habitat types, including small streams, waterfall splash zones, cliff seeps, cobbly and gravely seeps, and small side-channels in larger streams (Figure 29). In the Blue River watershed I rarely observed seeps that were not associated with or were not located at the headward extent of small streams. Some basins in the Pacific Northwest have more of some of these habitat types than others. In some basins or portions of basins these seeps are disjunct from any discernible stream channel. In other basins, seeps are common adjacent to large stream channels that would otherwise probably be uninhabited by torrent salamanders.

Observations made in my study are probably most similar to basins in the West Cascades physiographic province (Franklin and Dyrness 1973) of Oregon, in areas with a similar range of slopes, elevations, and soil types. Vegetation zones (Franklin and Dyrness 1973) and plant associations and series (Hemstrom et al. 1987) integrate numerous environmental factors over time and space and might be helpful indicators of similar conditions elsewhere.

It is likely that the broadest patterns and trends (without reference to the absolute physical measurements, such as stream size) occur elsewhere also. For example, the observations that torrent salamanders occur in small streams as demonstrated in this study, are widely reported (Nussbaum et al. 1983, Leonard et al. 1993, Applegarth 1994, Good and Wake 1992). The observation in this study of Cascade torrent salamander occurrence peaking in small streams between 850 and 900 m elevation lends support to Applegarth's (1994) hypothesis that Cascade torrent salamander “may be limited to the rather narrow zone of transient snowpack”. The pattern of Pacific giant salamander larvae size distribution being shifted to larger sizes was hypothesized by Corn and Bury (1991). These observations give me confidence that many of the landscape-level patterns are fairly consistent throughout the range of the species. The pattern of metamorphosed tailed frogs occurring farther upstream than tadpoles and tadpoles being more frequent in medium-sized streams is likely a consistent pattern.

Figure 29. Schematic representation of different habitat types occupied by torrent salamanders (*Rhyacotriton*) in a 4th-order watershed.

Nevertheless, it should be recognized that slightly different relationships are possible and likely in areas that are quite different from the area studied. For example, in this study, metamorphosed tailed frog showed a positive linear association with elevation, such as might have been observed in Study A (Figure 30). However, in a higher elevation basin, or perhaps at a higher latitude within the same elevation range, metamorphosed tailed frogs might show no relationship to elevation, or even a negative effect, as might be concluded from Study B or C, respectively (Figure 30).

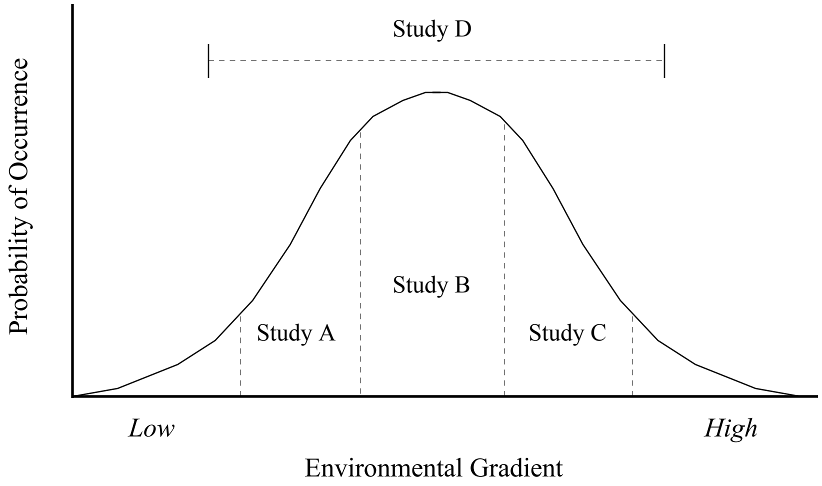

Figure 30. Conceptual display of a hypothetical relationship between the probability of occurrence of an amphibian and an environmental gradient, and the potential results that might be obtained from four studies.

RELEVANCE TO OTHER TIME PERIODS

Results of my study were obtained during the summer months, and refer only to individuals in the wetted channel during that period. Instream distributions during the winter months are unknown. They are expected to be similar for larvae, but movements may occur of which we are currently unaware, including both headward expansion concomitant with the winter expansion of the surface stream network, and downward expansion by dispersing or dislodged individuals.

Changes also are likely over time periods characterized by droughts and wet years and decades; 1995 was considered a dry year, while 1996 experienced a flood of significant magnitude just five months prior to the beginning of the 1996 summer sampling season. Changes in timing, amount, distribution, and form of precipitation may affect hydrologic regimes in streams over time. For example, the headward extent of perennial surface water may expand during wet years and retract during dry years. The possibility of these changes should be considered both within and outside the Blue River watershed.

LANDSCAPE-LEVEL ASPECTS OF LIFE-HISTORIES

Cascade torrent salamander

This study confirms the general observation that torrent salamanders occur primarily in small streams, and defines those sizes for the Blue River watershed. If all streams in the Blue River watershed with basin sizes less than 150 ha were considered potential habitat for Cascade torrent salamanders, the pattern of distribution would look something like what is depicted in Figure 31. These hypothetical habitat patches may represent subpopulations within a larger metapopulation of this species. It appears from this hypothetical maximum distribution that some parts of the stream network may provide a larger length of contiguous stream habitat for this species than others. Some streams of small size flow directly into larger, presumably uninhabited streams, while others are connected to several other streams of similar size. The implications to such things as genetic exchange depend somewhat on the avenues of exchange between populations, which is unknown. If genetic transfer is primarily through individuals traveling within the aquatic stream network, then patches of connected streams would seem to have a larger base of genetic material than individual, disjunct streams. If genetic exchange comes primarily from overland travel by this species, then the connnectedness of multiple tributaries may have little consequence.

Good and Wake (1992) stated “Because *Rhyacotriton* prefers rapidly-flowing, well aerated streams and springs, it is restricted to areas with considerable physical relief. These salamanders are absent from flat areas and areas with only low, gently sloping hills where such streams are lacking." While I believe their habitat description is a bit too narrow, it is interesting that their conclusion is similar to what I found in this study.

I frequently found Cascade torrent salamander larvae in habitats that were likely very dynamic during the winter flood, such as riffle areas just below plunge pools. This implies that Cascade torrent salamander larvae may have been taking cover within more stable locations, such as channel steps, during high flows, and later emerged to other locations after the water level dropped.

Pacific giant salamander

Why does the size distribution of Pacific giant salamander larvae shift toward larger sizes in larger streams? Why were hatchling-size larvae found in small streams but very few in larger streams? Several hypotheses might explain these observations.

1) Larger streams in the Blue River watershed are generally warmer streams with higher gross primary production, which may mean they are less energetically limiting.

2) Perhaps there is an upstream movement of neotenic Pacific giant salamanders to breeding sites. The few records of nests indicate that females guard the eggs. Perhaps male neotenes and non-breeding Pacific giant salamanders occupy larger streams while females are in smaller streams undetected with the eggs

3) Perhaps eggs laid and larvae hatched in larger streams are consumed rapidly by larger Pacific giant salamanders, fish, and crayfish, therefore resulting in low recruitment in larger streams.

4) Perhaps there is no substantial movement of neotenic adults within streams between breeding and non-breeding sites. Instead, reproduction takes place primarily by terrestrial adults in the small streams, and by neotenic adults in the larger streams.

It seems that any or all of the above hypotheses may contribute to the pattern observed. Increased growth rates in amphibians in warmer temperatures (within tolerance limits) is widely reported. However, the change in size distribution from small to larger streams is not merely a shift to larger sizes, but a change in shape

Figure 31. Hypothetical maximum distribution of Cascade torrent salamander larvae in stream channels of the Blue River watershed. Streams shown are those generated from a 30-m DEM and with basin sizes >7 ha. Stream segments delineated with a bold line are those considered small enough to contain potential larval-rearing habitat for Cascade torrent salamanders, while those delineated with a gray line are those considered too large to serve as larval-rearing habitat.

of the distribution, with relatively smaller individuals composing a smaller proportion of the population than in smaller streams (Figure 26). Therefore, while temperature certainly influences the size of individuals, it does not explain the change in shape of the distribution.

It seems quite likely that smaller streams host the bulk of Pacific giant salamander nests. Perhaps the peak in larval density in basins between about 20 and 100 ha (Figure 16) is indicative of the bulk of distribution of small larvae and nearby nest structures. Whether these young are progeny primarily of terrestrial adults or aquatic neotenes is unknown. Given the low numbers of very young larvae in larger streams, it seems likely that some neotenes from larger streams may travel upstream to breed. While there likely is increased predation on small larval salamanders in larger streams, it seems unlikely that this alone could account for the difference in size distribution among streams of different size.

Tailed frog

The most striking pattern for tailed frogs observed in my study was the apparent differential distribution of life stages in the stream network. At least two landscape-level life-history hypotheses might explain this pattern.

1) Adult tailed frogs breed primarily in small streams, including the smallest streams where larvae were not detected. Hatchling tailed frogs larvae were present but not detected deep in the substrate of the smallest streams. These larvae emerge in fall, winter, or spring during higher water levels and are transported downstream several hundred or thousand meters where they subsequently complete their growth and metamorphosis. After metamorphosis the juvenile frogs disperse during a period of wet weather, primarily upslope, and return to smaller streams at higher elevations where they complete their growth to maturity.

2) Metamorphosed tailed frogs do not breed in the smallest streams. Breeding occurs in moderate-sized streams, as indicated by the presence of tailed frog larvae. Metamorphosed individuals present in the smallest streams are either immature, pre-breeding, post-breeding, or non-breeding individuals. Presence of metamorphosed

individuals in the smallest streams represents a temporary movement by these frogs away from the breeding streams at lower elevations.

It would not be surprising that hatchling tailed frog larvae went undetected for the most part deep in substrate or channel steps in small streams. Hatchlings are rarely reported. In fact, Hawkins et al. (1988) reported seeing no hatchlings in three years of sampling, while finding large numbers of older larvae. Hawkins et al. (1988) speculated, as I will later, that larvae they found on lower reaches may have migrated from more headward reaches. Also, it makes sense that eggs would be laid and hatchlings start their life in stable, porous substrate where water is moving, but gently so. Locations such as this would be located deep in porous substrate, and most likely in accumulations of material through which water is flowing, such as channel steps formed by logs or boulders. Increased stream power in downstream reaches results in larger particles being moved during peak flows in larger streams. Therefore, substrate of a given size is generally expected to be more stable in smaller streams. Therefore, it seems that ideal tailed frog nest structures would be present in small streams that have reliable perennial flow.

Travel downstream during increasing or high flows seems reasonable. Increasing turbulence and turbidity of the water during these flows would seem to decrease the risk of predation enroute downstream, and high flows would ensure rapid transit downstream and an absence of dry patches of stream or slow water which would be encountered at other times of year. Hatchling tailed frog larvae survive on their yolk until emergence (Metter 1964, Brown 1975), at which time they must begin feeding or likely will die. In the west Cascades, bedload movement occurs frequently during winter peak flows, scouring and resetting plant communities in these streams (Gregory 1983). In the north Cascades of Washington it appears that tailed frog hatchlings may not emerge until winter or spring (Metter 1964). It seems that in the Blue River watershed it would be most efficient for hatchling tailed frog larvae to emerge and travel downstream in spring when the frequency of high-disturbance peak flows is reduced, turbidity of the water is lowering, and solar exposure is increasing, all of which contribute to increased periphyton production (Gregory 1980, Hawkins and Sedell 1981).

DeVlaming and Bury (1970) reported that first-year tadpoles prefer temperatures below 10^{o} C, while second-year tadpoles prefer temperatures from $10\text{-}22^{o}$ C. Water temperature had a strong negative correlation with elevation in the Blue River watershed, and a weaker positive correlation with basin size. These observations lend support for the hypothesis that tadpoles may move downstream to slightly warmer waters after emerging from their nest sites.

"The larvae are almost invariably seen in stretches of rapidly-moving water where there are smooth rock surfaces, with at least some water flowing over them.... They avoid moss-covered rocks and deposits of silt," (Nussbaum et al. 1983). My observations corroborate with those of others that tailed frog larvae prefer flowing water. It can be inferred from Figures 9 and 10 that reliable, rapidly-flowing perennial surface water in the Blue River watershed is found predominantly in streams with basin size equal to or greater than about 80-100 ha. Surface water in patchy distribution (Figure 10) often is moving rather slowly. Slow-moving water conditions appear unsuitable to tailed frog larvae after emergence from the substrate. In laboratory studies, tailed frog tadpoles preferred particles 55-96 mm diameter and 85-125 mm diameter over smaller particles 18-36 mm diameter and less than 4 mm diameter (Altig and Brodie 1972). Hawkins et al. (1988) reported greater abundances in streams with coarse substrates (>10 cm diameter). While rocks of this size are common throughout the watershed, smooth rocks of this size located in 10-15 cm (Table 6) of moving water, in are most common in riffle channel units in streams with basins from several hundred to several thousand hectares.

Scrapers are a guild of herbivorous invertebrates that forage by scraping periphyton off of instream substrates, most typically rocks. Tailed frogs feed in a similar fashion. In a study of invertebrates in four streams in the west Cascades (Hawkins and Sedell 1981) scraper abundance was greatest in the two midsize streams during summer and fall. The two mid-size streams were Mack Creek and Lookout Creek in the Blue River watershed, which also have populations of tailed frog tadpoles.

IMPLICATIONS FOR RESEARCH

The patterns of distribution observed in this study indicate that it would be important to interpret results of previous studies of stream amphibians within a context of potential watershed-level patterns. For example, the maximum of the range of basin sizes sampled by Corn and Bury (1989), 184 ha for forested sites, and 218 ha for logged sites, exceeds the maximum basin size of 142 ha in which Cascade torrent salamanders were detected in this study. Similarly, most studies of amphibians in PNW streams have loosely defined their sampled population as 1st- and 2nd-order streams (Bury et al. 1991, Diller and Wallace 1996), 1st- through 3rd-order streams (Corn and Bury 1989, Welsh and Lind 1996), or 2nd- and 3rd-order streams (Welsh and Lind 1991). In my study, large changes in occurrence and density were observed over this seemingly narrow zone of the stream network (Appendix). For example, Cascade torrent salamanders were primarily found in 1st- and 2nd-order streams, and small unmapped streams, rarely in 3rd-order streams. Tailed frog larvae were found in 1st- through 4th-order streams, but again, not in small unmapped streams and not commonly in 1st-order streams. It is unknown what basin sizes or stream orders were occupied by stream amphibians in these other study areas, but it indicates that these sampling schemes would not have been optimal in this watershed, and that results of previous studies might have been affected by similar patterns of occurrence and density in stream networks.

Bury and Corn (1988) recognized that the presence of small streams in their terrestrial sample areas likely influenced the capture of several species of amphibians in those stands. If patterns observed in the aquatic larvae population are reflected in the streamside terrestrial population, or vice versa, these patterns may give insight into interpretation of results from studies of streamside amphibians such as Vesely (1996), McComb et al. (1993), and Gomez and Anthony (1996), and perhaps many past and current terrestrial studies that have small streams in or near experimental plots such as Corn and Bury (1991), and Gilbert and Allwine (1991).

Corn and Bury (1989) noted that Pacific giant salamander sizes reported from electroshocking efforts were larger than that indicated by their data, which were from smaller streams. They questioned whether electro-shocking methods were biased to larger sizes or whether streams sampled by this method (typically fish-bearing streams) merely contained larger Pacific giant salamanders. My data indicate a clear increase in average size of Pacific giant salamanders from small to larger streams in the Blue River watershed. Therefore, at least part of the difference between Corn and Bury's data and the fish-shocking data is likely due to this downstream increase in average size of Pacific giant salamanders. This does not, however, eliminate the possibility that electroshocking methods introduce additional bias.

Given the above, I recommend that future investigations of associations of stream amphibians presence or abundance with environmental measurements either incorporate variables related to stream size or network position into study design and analysis, or more strictly control for these factors.

Still no studies are published that have examined instream populations of amphibians both before and after timber harvest. Such a study would be most useful if sampling was stratified by important watershed-level variables identified in this study.

Lastly, the patterns described and hypotheses put forth in the previous section on landscape-level life-histories highlight the importance and lack of understanding of landscape-level patterns and movements of these species. Further, the multi-scale model-building effort indicated that unmeasured environmental variables of aquatic and/or terrestrial stages of these amphibians may be important in determining instream distribution. I recommend that complete, temporally- and spatially-explicit, hypothetical life histories be developed for each species. These hypothetical life histories will highlight gaps in knowledge and foster hypothesis development.

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APPENDIX

AMPHIBIAN ASSOCIATIONS WITH STREAM CLASSIFICATIONS

Logistic regression was used to estimate means and confidence intervals for the probability of occurrence of each species within USFS Stream Class categories and two representations of stream order, by topographic region in the watershed. Estimated means for these categories are easily calculated by dividing the number of detections by the total number of samples in that category. However, the calculation of confidence intervals is much more complicated and was conducted with SAS.

Cascade torrent salamander larvae were found in USFS stream classes 4 and 3 (see Table 1 for definition of stream classes), as well as small, unmapped streams, but not in classes 2 or 1 (Table 10). Similarly, Cascade torrent salamander larvae were primarily found in 1st- and 2nd-order streams, including small unmapped streams, rarely in 3rd-order streams, and none in 4th-, 5th-, or 6th-order streams. Pacific giant salamander larvae were found in all stream classes and orders searched in the Blue River watershed including small unmapped reaches and tributaries (Table 11). Tailed frog larvae were found in class 4, 3, and 2 streams but not class 5 (small unmapped streams) or class 1 streams (Table 12). Tailed frog larvae were found in 1st- through 4th-order streams, but again, not in 0-order (unmapped) or 5th- or 6th-order streams (although sample sizes were small for the larger order streams). Tailed frog metamorphs were found in all but the largest streams: class 1, or 5th- and 6th-order (Table 13).

Stream classes are subjectively designated by one or more people based on some rather broad and sometimes indeterminable criteria. Therefore, while the occurrences listed in Tables 10-13 are relevant to the Blue River watershed, caution is recommended for application to other areas.

Table 10. Estimated mean occurrence of Cascade torrent salamander larvae in 5-m stream lengths within several stream classifications, in gentle and steep regions of the Blue River watershed, summers 1995 and 1996.

(a) USFS stream classes.

Region	5[1]	4	3	2	1	All
Steep	8/23[2] 35%[3] 18-56%[4]	20/71 28% 19-40%	13/44 30% 18-44%	0/35 0% n/a	0/7 0% n/a	41/180 23%
Gentle	6/29 21% 10-39%	2/24 8% 2-28%	3/26 12% 4-30%	0/12 0% n/a	0/2 0% n/a	11/93 12%
All	14/52 27%	22/95 23%	16/70 23%	0/47 0%	0/9 0%	52/273 19%

(b) Stream order, counted from Blue River Ranger District GIS stream layer.

Region	0[1]	1	2	3	4	5	6	All
Steep	8/23 35% 18-56%	20/79 25% 17-36%	10/46 22% 12-36%	3/23 13% 4-34%	0/2 0% n/a	0/5 0% n/a	0/2 0% n/a	41/180 23%
Gentle	6/29 21% 10-40%	3/30 10% 3-27%	2/20 10% 3-32%	0/8 0% n/a	0/6 0% n/a	none n/a n/a	none n/a n/a	11/93 12%
All	14/52 27%	23/109 21%	12/66 18%	3/31 10%	0/8 0%	0/5 0%	0/2 0%	52/273 19%

(c) Stream order, counted from DEM-derived stream network (9-ha channel initiation).

Region	0[1]	1	2	3	4	5	All
Steep	6/21 29% 13-51%	25/78 32% 23-43%	10/48 21% 12-35%	0/23 0% n/a	0/3 0% n/a	0/7 0% n/a	41/180 23%
Gentle	2/14 14% 4-43%	7/42 17% 8-31%	2/23 9% 2-29%	0/8 0% n/a	0/6 0% n/a	none n/a n/a	11/93 12%
All	8/35 23%	32/120 27%	12/71 17%	0/31 0%	0/9 0%	0/7 0%	52/273 19%

[1] Sites located on unmapped reaches or tributaries.

[2] Number of sites with detections / number of sites searched.

[3] Percent of sites searched that had detections.

[4] 95% confidence interval for the mean.

Table 11. Estimated mean occurrence of Pacific giant salamander larvae in 5-m stream lengths within several stream classifications, in gentle and steep regions of the Blue River watershed, summers 1995 and 1996.

(a) USFS stream classes.

Region	5[1]	4	3	2	1	All
Steep	10/23[2]	47/71	38/44	29/35	6/7	130/180
	43%[3]	66%	86%	83%	86%	72%
	25-64%[4]	54-76%	73-94%	67-92%	42-98%	
Gentle	15/29	18/24	17/26	12/12	2/2	64/93
	52%	75%	65%	100%	100%	69%
	34-69%	54-88%	46-81%	n/a	n/a	
All	25/52	65/95	55/70	41/47	8/9	194/273
	48%	68%	79%	87%	89%	71%

(b) Stream order, counted from Blue River Ranger District GIS stream layer.

Region	0[1]	1	2	3	4	5	6	All
Steep	10/23	55/79	36/46	21/23	2/2	4/5	2/2	130/180
	43%	70%	78%	91%	100%	80%	100%	72%
	25-64%	59-79%	64-88%	71-98%	n/a	31-97%	n/a	
Gentle	15/29	17/30	18/20	8/8	6/6	none	none	64/93
	52%	57%	90%	100%	100%	n/a	n/a	69%
	34-69%	39-73%	68-97%	n/a	n/a	n/a	n/a	
All	25/52	72/109	54/66	29/31	8/8	4/5	2/2	194/273
	48%	66%	82%	94%	100%	80%	100%	71%

(c) Stream order, counted from DEM-derived stream network (9-ha channel initiation).

Region	0[1]	1	2	3	4	5	All
Steep	6/21	56/78	41/48	18/23	3/3	6/7	130/180
	29%	72%	85%	78%	100%	86%	72%
	13-51%	61-81%	72-93%	57-91%	n/a	42-98%	
Gentle	3/14	27/42	20/23	8/8	6/6	none	64/93
	21%	64%	87%	100%	100%	n/a	69%
	7-49%	49-77%	66-96%	n/a	n/a	n/a	
All	9/35	83/120	61/71	26/31	9/9	6/7	194/273
	26%	69%	86%	84%	100%	86%	71%

[1] Sites located on unmapped reaches or tributaries.

[2] Number of sites with detections/number of sites searched.

[3] Percent of sites searched that had detections.

[4] 95% confidence interval for the mean.

Table 12. Estimated mean occurrence of tailed frog larvae in 5-m stream lengths within several stream classifications, in gentle and steep regions of the Blue River watershed, summers 1995 and 1996.

(a) USFS stream classes.

Region	5[1]	4	3	2	1	All
Steep	0/23[2] 0%[3] n/a[4]	5/71 7% 3-16%	5/44 11% 5-25%	8/35 23% 12-39%	0/7 0% n/a	18/180 10%
Gentle	0/29 0% n/a	0/24 0% n/a	2/26 8% 2-26%	1/12 8% 1-41%	0/2 0% n/a	3/93 3%
All	0/52 0%	5/95 5%	7/70 10%	9/47 19%	0/9 0%	21/273 8%

(b) Stream order, counted from Blue River Ranger District GIS stream layer.

Region	0[1]	1	2	3	4	5	6	All
Steep	0/23 0% n/a	6/79 8% 3-16%	5/46 11% 5-24%	6/23 26% 12-47%	1/2 50% 6-94%	0/5 0% n/a	0/2 0% n/a	18/180 10%
Gentle	0/29 0% n/a	0/30 0% n/a	2/20 10% 3-32%	1/8 13% 2-54%	0/6 0% n/a	none n/a n/a	none n/a n/a	3/93 3%
	0/52 0%	6/109 6%	7/66 11%	7/31 23%	1/8 13%	0/5 0%	0/2 0%	21/273 8%

(c) Stream order, counted from DEM-derived stream network (9-ha channel initiation).

Region	0[1]	1	2	3	4	5	All
Steep	0/21 0% n/a	4/78 5% 2-13%	4/48 8% 3-20%	9/23 39% 22-60%	1/3 33% 4-85%	0/7 0% n/a	18/180 10%
Gentle	0/14 0% n/a	0/42 0% n/a	2/23 9% 2-29%	1/8 13% 2-54%	0/6 0% n/a	none n/a n/a	3/93 3%
	0/35 0%	4/120 3%	6/71 8%	10/31 32%	1/9 11%	0/7 0%	21/273 8%

[1] Sites located on unmapped reaches or tributaries.

[2] Number of sites with detections/number of sites searched.

[3] Percent of sites searched that had detections.

[4] 95% confidence interval for the mean.

Table 13. Estimated mean occurrence of metamorphosed tailed frog in 5-m stream lengths within several stream classifications, in gentle and steep regions of the Blue River watershed, summers 1995 and 1996.

(a) USFS stream classes.

Region	5[1]	4	3	2	1	All
Steep	3/23[2]	20/71	12/44	7/35	0/7	42/180
	13%[3]	28%	27%	20%	0%	23%
	4-34%[4]	19-40%	16-42%	10-36%	n/a	
Gentle	5/29	5/24	7/26	3/12	0/2	20/93
	17%	21%	27%	25%	0%	22%
	7-35%	9-41%	13-47%	8-55%	n/a	
All	8/52	25/95	19/70	10/47	0/9	62/273
	15%	26%	27%	21%	0%	23%

(b) Stream order, counted from Blue River Ranger District GIS stream layer.

Region	0[1]	1	2	3	4	5	6	All
Steep	3/23	26/79	9/46	4/23	0/2	0/5	0/2	42/180
	13%	33%	20%	17%	0%	0%	0%	23%
	4-34%	23-44%	11-34	7-38%	n/a	n/a	n/a	
Gentle	5/29	6/30	5/20	3/8	1/6	none	none	20/93
	17%	20%	25%	38%	17%	n/a	n/a	22%
	7-35%	9-38%	11-48%	13-72%	2-63%	n/a	n/a	
All	8/52	32/109	14/66	7/31	1/8	0/5	0/2	62/273
	15%	29%	21%	23%	13%	0%	0%	23%

(c) Stream order, counted from DEM-derived stream network (9-ha channel initiation).

Region	0[1]	1	2	3	4	5	All
Steep	7/21	19/78	10/48	6/23	0/3	0/7	42/180
	33%	24%	21%	26%	0%	0%	23%
	17-55%	16-35%	12-35%	12-47%	n/a	n/a	
Gentle	4/14	5/42	7/23	3/8	1/6	none	20/93
	29%	12%	30%	38%	17%	n/a	22%
	11-56%	5-26%	15-52%	13-72%	2-63%	n/a	
All	11/35	24/120	17/71	9/31	1/9	0/7	62/273
	31%	20%	24%	29%	11%	0%	23%

[1] Sites located on unmapped reaches or tributaries.

[2] Number of sites with detections/number of sites searched.

[3] Percent of sites searched that had detections.

[4] 95% confidence interval for the mean.