AN ABSTRACT OF THE THESIS OF

Aimee P. McIntyre for the degree of Master of Science in Wildlife Science presented on November 18, 2003.
Title: Ecology of populations of Van Dyke's salamanders in the Cascade Range of Washington State

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The Van Dyke's salamander (*Plethodon vandykei*) is a rare species endemic to Washington State. It has been found in cool moist microhabitats along streams, splash zones of waterfalls, and headwater seeps. We explored the association of the Van Dyke's salamander with hydrologic condition, geomorphology, disturbance characteristics, and vegetation structure in first- and second-order streams, and headwater seeps in the Cascade Range of Washington. We conducted salamander surveys and measured habitat characteristics at 50 streams and 40 seeps May-October 2000-2002. We described Van Dyke's salamander occurrence in stream and seep sites at three spatial scales: between sites, within sites, and between microhabitat sites. Using presence and absence as the response, we fit logistic regression models predicting Van Dyke's salamander occurrence. To identify the model that best fit the data, we ranked *a priori* models using Bayesian Information Criterion (BIC). Results were consistent for both stream and seep sites, at all three spatial scales. Best approximating models indicated that Van Dyke's salamander occurrence at sites was related to geological and hydrological habitat characteristics that provided hydric and thermal stability.

The probability of Van Dyke's salamander occurrence along streams was associated with habitat characteristics that protected salamanders from exposure, provided a source cover, and stream habitat types providing splash zone areas. Between streams, Van Dyke's salamander occurrence was positively associated with the proportion of valley walls with canopy cover <5%, the proportion of the stream channel dominated by bedrock, boulder, or

soil substrates, and additional stream channels entering the main channel. Within streams, the probability of Van Dyke's salamander occurrence increased with the presence of non-forested areas, the presence of bedrock dominated stream habitat types, and the presence of vertical or V-shaped valley wall morphology. Between microhabitat sites, the probability of Van Dyke's salamander occurrence increased with an absence of trees, the presence of seeps, and the presence of small cobble sized substrates.

The probability of Van Dyke's salamander occurrence in seeps was associated with habitat characteristics that protected salamanders within the larger landscape, provided a moisture gradient from dry to saturated, and the presence of cover objects. Between seeps, Van Dyke's salamander occurrence was positively associated with seep faces having a dry and sheeting hydrology, and with seep faces >5 m high. Within seeps, the probability of Van Dyke's salamander occurrence was negatively associated with seeps that had proportionately more point measures of total overhead cover that were >25%. Between microhabitat sites, the probability of Van Dyke's salamander occurrence was positively associated with an increase in the percent cover of small cobble, small gravel, and bedrock substrates.

We conducted mark-recapture surveys of the Van Dyke's salamander at two high-gradient stream sites located within the Cascade Range of Washington State, June-November 2002. Sites known to support populations of the Van Dyke's salamander were chosen, and were ecologically different. One site, lacking significant overstory and located within the blast zone created by the 1980 eruption of Mount St. Helens, was surveyed 10 times. The other site, located in an old-growth coniferous stand, was surveyed 11 times. Abundance of salamanders at the blast zone site was estimated to be 458 (95% CI: 306-739). Abundance of salamanders at the old-growth site was estimated to be 100 individuals (95% CI: 61-209). Capture probabilities were extremely low ($\hat{p}$ = <0.10) for all trapping occasions at both sites, with an average capture probability for the two sites of 0.038 (range = 0.02-0.09). Analysis of movement patterns suggested that most individual salamanders had home ranges <2 m, at

least when moving on or near the surface. Individuals were recaptured under the same cover object as initial capture 36% of the time, and 89% of the recaptured individuals moved <2 m.

Our results indicated that populations of the Van Dyke's salamander were rare on the landscape, even within the species documented range. Van Dyke's salamander occurrence was associated with geological and hydrological habitat characteristics that created microhabitats favorable for a species that is especially sensitive to heat and drying due to physiological constraints. Animals were difficult to detect due to fossorial habits and low capture probabilities, and it is likely that the Van Dyke's salamander was not detected even at sites where it existed. Life history characteristics, such as lunglessness and fossorial habits, low capture probabilities, and low abundances make it difficult to manage for and protect the Van Dyke's salamander. However, habitat associations may be used to identify and protect habitats suitable for Van Dyke's salamander occurrence.

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Ecology of Populations of Van Dyke's Salamanders in the Cascade Range of Washington State

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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.

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Aimee P. McIntyre, Author

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CONTRIBUTION OF AUTHORS

Dr. Richard A. Schmitz and Charlie M. Crisafulli were involved in the design, analysis, and writing of each manuscript.

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Ecology of Populations of Van Dyke's Salamanders in the Cascade Range of Washington State

Chapter 1

Introduction

Distribution and life history information are particularly sparse for amphibians endemic to the Pacific Northwest (Nussbaum et al. 1983). The Van Dyke's salamander (*Plethodon vandykei*) is a terrestrial salamander endemic to Washington State. It has been documented along high gradient streams, in the splash zones of waterfalls, and in headwater seeps (Nussbaum et al. 1983, Leonard et al. 1993, Wilson 1993, Jones 1999). It has been reported in three disjunct locations: the southern and central Cascade Range, the Willapa Hills, and the Olympic Peninsula (Leonard et al. 1993). The distribution of the Van Dyke's salamander is more fragmented than those of other Pacific Northwest congeners (Brodie 1970, Nussbaum et al. 1983), with the three main population centers geographically separated by distances of up to 40 km (Wilson et al. 1995).

Plethodontid salamanders lack lungs (Noble 1931) and rely on their skin and buccopharynx to respire (Gatz et al. 1974). It is imperative that members of this family maintain moist permeable skin, making them susceptible to heat and drying (Feder 1983, Stebbins and Cohen 1995). *Plethodon* species have narrow physiological tolerance limits, and respiratory requirements appear to have an influence on their life history characteristics (Feder 1983).

Plethodontid salamanders are prone to enigmatic habits that insulate them from seasonal changes in climate (Houck 1977). They seek out cover refugia in microhabitats that maintain moisture levels that may act to diffuse harsh conditions by providing hydric and thermal stability (Hynes 1970, Huheey and Brandon 1973). Common refugia for plethodontid salamanders include the interstices of rocky substrates (Dumas 1956, Herrington 1988), logs, and woody debris (Aubry et al. 1988, Jones 1989). The microhabitats maintained under these

cover refugia allow *Plethodon* salamanders to take up water directly from the soil through their permeable skin (Spotila 1972). The availability of cover refugia can restrict the distribution and abundance of salamander species (Southerland 1986*a*, Grover 1998), and a lack of subterranean interstitial spaces may limit the occurrence of *Plethodon* salamanders by restricting distribution to the availability of rocky accumulations (Brodie and Storm 1970, Bury et al. 1991, Wilson et al. 1995).

The surface activity of *Plethodon* salamanders is largely restricted to periods of rain or high humidity (Spotila 1972, Feder 1983), and patterns of spacing and movement of plethodontid salamanders are strongly influenced by weather patterns (Grover 1998). Wilson et al. (1995) documented the distribution of Van Dyke's salamanders and compared occurrence with levels of precipitation, annual duration of cold weather and presence of rocky microhabitat. Bosakowski (1999) assessed the association of landscape-scale macrohabitat variables on amphibian communities, including Van Dyke's salamander, on private industrial forest. The unique life history characteristics and physiological requirements of *Plethodon* salamanders can make them extremely difficult to detect, even within their range and within habitats deemed likely for their occurrence. No previous study has assessed the habitat associations of the Van Dyke's salamander at multiple spatial scales, considering a variety of biotic and abiotic habitat characteristics.

Due to their ecological and physiological requirements, amphibians may be more sensitive to certain forms of habitat degradation than other taxa (deMaynadier and Hunter 1995). Species with low population densities, especially those that are extremely habitat specific, may be particularly sensitive to habitat loss and fragmentation (Gibbs 1998). Timber harvesting can negatively impact local amphibian populations, especially salamanders (Dupuis et al. 1995, Hyde and Simons 2001, Vesely 2002), with plethodontids often exhibiting greater population declines than other amphibian groups (deMaynadier and Hunter 1995).

It is important to develop species-specific conclusions regarding the relationship of amphibians to forest age (deMaynadier and Hunter 1995). The Van Dyke's salamander is considered an old-growth obligate protected under the measures of the Northwest Forest Plan

(USDA and USDI 1994). However, it is not necessarily forest age that determines species distributions, but rather associated microhabitats that tend to vary in relation to forest age (Aubry et al. 1988; Welsh 1990; Diller and Wallace 1994). Forest age may act as an indirect measure of the microhabitat characteristics that actually determine habitat suitability for a species (deMaynadier and Hunter 1995). We explored the possibility that Van Dyke's salamander occurrence is associated with microclimate conditions encountered in, but not limited to, late seral class forests.

We assessed the association of Van Dyke's salamander occurrence with hydrologic conditions, disturbance characteristics, geomorphology, and vegetation structure at first- and second-order streams, and headwater seeps located in the southern and central Cascade Range of Washington State. Data analysis led to the development of models that may be used to predict Van Dyke's salamander habitat and occurrence at three spatial scales: between sites, within sites, and between microhabitat sites. Mark-recapture efforts were used to estimate population characteristics and movement patterns for the Van Dyke's salamander at two stream locations.

This thesis contains an introduction, three chapters prepared as manuscripts for journal submission, and summary conclusions. In chapters 2 and 3 we examine habitat associations of the Van Dyke's salamander at streams and seeps, respectively. In Chapter 4 we use a mark-recapture study and a closed population estimator to calculate population abundances, capture probabilities, and movement patterns of the Van Dyke's salamander.

Chapter 2

Relationship between a western *Plethodon* salamander and geology and hydrology influenced habitat characteristics along stream channels

Aimee P. McIntyre, Richard A. Schmitz, Charlie M. Crisafulli

ABSTRACT

The Van Dyke's salamander (*Plethodon vandykei*) is a rare species endemic to Washington State that is encountered in cool, moist microhabitats along streams, splash zones of waterfalls, and headwater seeps. We investigated the association between Van Dyke's salamander occurrence and hydrologic condition, geomorphology, disturbance characteristics, and vegetation structure along first- and second-order stream channels located in the Cascade Range of Washington. We conducted salamander surveys and measured habitat characteristics at 50 stream sites May-October 2000 and 2001. We compared sites where the Van Dyke's salamander was detected to those where the Van Dyke's salamander was not detected, at three spatial scales: between streams, within streams, and between microhabitat sites. Using logistic regression, with presence and absence as the response, we developed models that predicted Van Dyke's salamander occurrence. To identify the best approximating resource selection model, we ranked *a priori* models using Bayesian Information Criterion (BIC). Between streams, increases in the proportion of boulders on the valley wall, in additional stream channels entering the main channel, and in the proportion of valley wall with a vertical morphology were positively associated with the probability of Van Dyke's salamander occurrence. Within streams, the probability of Van Dyke's salamander occurrence increased with the presence of non-forested areas on the valley wall, bedrock dominated stream habitats, and vertical or V-shaped valley wall morphology. Between microhabitat sites, the probability of Van Dyke's salamander occurrence increased with the absence of trees, the presence of seeps, and the presence of small cobble. The positive association between Van Dyke's salamander and non-forested areas is most likely due to the hydrological and geological characteristics associated with Van Dyke's salamander microhabitats that prevent woody vegetation from establishing. Thus, the likelihood of Van Dyke's salamander occurrence associated with streams in the Cascade Range was predicted by abiotic habitat characteristics.

INTRODUCTION

The Van Dyke's salamander (*Plethodon vandykei*) is endemic to Washington State. It is commonly encountered along high gradient streams, in the splash zones of waterfalls, and in headwater seeps (Nussbaum et al. 1983, Leonard et al. 1993, Wilson 1993, Jones 1999). It is often considered the most closely associated to water of all western *Plethodon* species (Brodie 1970, Petranka 1988), with the possible exception of Dunn's salamander (*P. dunni*) (Leonard et al. 1993, Gomez and Anthony 1996).

The Van Dyke's salamander lacks lungs entirely (Noble 1931), relying on its skin and buccopharynx to respire (Gatz et al. 1974). It is imperative that *Plethodon* maintain moist permeable skin (Grover 2000), making them susceptible to heat and drying (Feder 1983, Stebbins and Cohen 1995). *Plethodon* species appear to have narrow physiological tolerance limits due to their lunglessness, and respiratory requirements are presumed to influence the species life history characteristics (Feder 1983), including habitat requirements. The restricted occurrence of Van Dyke's salamander suggests that it has relatively sedentary habits or narrow ecological tolerances (Wilson et al. 1995).

Distribution and life history information is particularly sparse for amphibians endemic to the Pacific Northwest (Nussbaum et al. 1983, Aubry et al. 1988). Very little is known about habitat relationships for the Van Dyke's salamander (Blessing et al. 1999), whose distribution is more fragmented and patchy than those of other Pacific Northwest congeners (Brodie and Storm 1970, Nussbaum et al. 1983, Petranka 1988, Wilson 1993). It has been reported in three disjunct locations geographically separated by distances up to 40 km (Wilson et al. 1995): the southern and central Cascade Range, the Willapa Hills, and the Olympic Peninsula (Leonard et al. 1993).

The Van Dyke's salamander is commonly associated with areas that are affected by disturbances at multiple temporal and spatial scales. They appear to be associated with high gradient streams and seeps that maintain exposed bedrock due to their position in the landscape and steep valley walls. This exposed bedrock may be partially maintained by disturbance events including scouring along the stream channel and colluvial slumping on the

valley wall. Van Dyke's salamanders are also endemic to areas that have been affected by severe broad-scale disturbances such as volcanism, which can dramatically impact the biota of surrounding areas (del Moral and Wood 1988, Peterken 1996, Crisafulli and Hawkins 1998) and may have affected the distribution of Van Dyke's salamander in the Cascade Range (Wilson 1993).

We believe that the Van Dyke's salamander is highly adapted to habitat characteristics influenced by hydrology and geology features that are at least partially influenced by disturbance. Distributions of amphibian populations may be particularly influenced by small-scale habitat disturbances (deMaynadier and Hunter 1995) as a result of their relatively poor dispersal capabilities and restricted mobility (Sinsch 1990). It seems unlikely that a physiologically sensitive species such as the Van Dyke's salamander would be resistant to the major changes associated with frequent disturbances; rather, the species has likely adapted to microhabitats that remain relatively unchanged by disturbance events.

A species-specific understanding of habitat associations is required in order to develop conservation strategies for salamanders, especially those that are endemic or rare (Hyde and Simons 2001). This study was designed to assess whether hydrologic conditions, disturbance characteristics, geomorphology, and vegetation structure are associated with Van Dyke's salamanders in riparian zones of the southern and central Cascade Range, Washington. We suspect that habitat characteristics important for Van Dyke's salamander over a range of spatial scales may be linked to hydrological characteristics and geomorphology. In developing resource selection models for the Van Dyke's salamander along riparian habitats, our goal was to identify habitats utilized by the Van Dyke's salamander, so that the species may be more easily protected. Identifying and protecting habitats of the Van Dyke's salamander, a species currently listed under the Survey and Manage provision of the Northwest Forest Plan (USDA and USDI 1994), can help to ensure the species persistence in a landscape influenced by management activities. We assessed the influence of habitat characteristics on Van Dyke's salamander occurrence at multiple spatial scales: between streams, within streams, and between microhabitat sites.

STUDY AREA

We conducted this study along first- and second-order streams in the southern and central Washington Cascade Range, from the East Fork Lewis River in Skamania County, north to the Carbon River drainage in Mount Rainier National Park, Pierce County. The study area included lands administered by U. S. Forest Service (Gifford Pinchot National Forest), National Park Service (Mount Rainier National Park), and industry (West Fork Timber Company), and ranged in elevation from 140 m to 1480 m. Lands within the study area have been under different management objectives depending on ownership, including intensive timber management, multiple use, and preservation. Forest condition ranged from young plantations to old-growth forest, and included areas in the blast zone created by the 1980 eruption of Mount St. Helens. Areas adjacent to the three volcanic peaks (Mount Rainier, Mount Adams and Mount St. Helens) are generally mantled with pumice deposits of variable age, origin and thickness (Mullineaux 1996). The study area geology is dominated by andesite and basalt flows, and landforms are characterized by ridge crests separated by steep, deeply dissected valleys (Franklin and Dyrness 1973).

Much of the study area was covered with dense coniferous forest stands, punctuated by natural meadows, and young plantations created by clear-cut logging. Major tree species were Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), western red cedar (*Thuja plicata*), and western white pine (*Pinus monticola*). Also occurring with some frequency were non-forested talus slopes, often dominated by vine maple (*Acer circinatum*) and sitka alder (*Alnus crispa*) (Franklin and Dryness 1973).

The study area was located in the western hemlock and Pacific silver fir forest zones of the southern and central Cascade Range (Franklin and Dyrness 1973). Within the study area the western hemlock zone extends from 150-1,000 m in elevation and is typified by a wet, mild, maritime climate. Precipitation occurs mainly during the fall and winter and averages 1,500-3,000 mm per year. Summers are relatively dry with only 6-9 % of the total annual precipitation. Neither January nor July temperatures are extreme, with mean annual

temperatures averaging 8-9º Celsius. The Pacific silver fir zone occurs at elevations from 900-1,300 m on the western slopes of the southern Washington Cascade Range. This zone is wetter and cooler than the adjacent western hemlock zone. It receives considerably more precipitation, often in the form of snow, which may accumulate in winter snow packs as deep as 1-3 m. Mean annual temperatures average 5-6º Celsius.

METHODS

Site Selection

Our study focused on riparian habitats in the southern and central Cascade Range of Washington. Prior to our study, there were only about 25 locations where the Van Dyke's salamander had been documented in the Cascade Range (USDA and USDI Interagency ISMS data base), and exact information on the location of many of these sites was lacking. Those for which the original animal capture location could be identified, and at least one Van Dyke's salamander had been detected on more than one occasion or more than one individual had been detected on a single occasion, were included in this study. We also included newly discovered sites, for a total of 24 stream sites where Van Dyke's salamander had been recorded.

We chose 26 additional stream sites where there was no record of Van Dyke's salamander occurrence. Due to the rarity of the salamander, we wanted to be specific in our additional site selection. All additional sites had the same potential natural vegetation as currently known sites (Henderson 2001). Potential natural vegetation is the climax vegetation that will occupy a site in the absence of disturbance or climatic change (Kuchler and Zonneveld 1988). It expresses environmental factors such as topography, soils and climate across an area (Kuchler and Zonneveld 1988). In order to ensure that sites were representative of the entire known range of the Cascade Range populations, additional stream sites were in each of 4 elevation (0-610 m, 611-914 m, 915-1219 m, and >1219 m) and 3 latitudinal (45°45'00"-46°07'30", 46°07'30"-46°22'30", 46°22'30"-47°00'00") bands. All sites

were located along streams identified on U. S. Geological Survey 1:24,000 quadrangle maps and aerial photos as first- or second- order systems, and accessible.

Each site consisted of a 200-m reach running along the riparian corridor, and extending 8 m upslope on either side of the wetted stream channel for a total survey area of 3200 m^2. The area was divided into 4 parallel transects, 2 on either side of the wetted stream channel (Figure 2.1). The 2 transects adjacent to the stream, or streamside transects, included the area from the wetted channel upslope to 3 m. The 2 upslope transects were parallel to the streamside transects, and included an area that extended from the outer edge of the streamside transects upslope an additional 5 m. At 6 of the 50 streams we were unable to survey the entire 200 m due to impassable obstacles (e.g. waterfalls and steep terrain), but transects along streams were never <160 m.

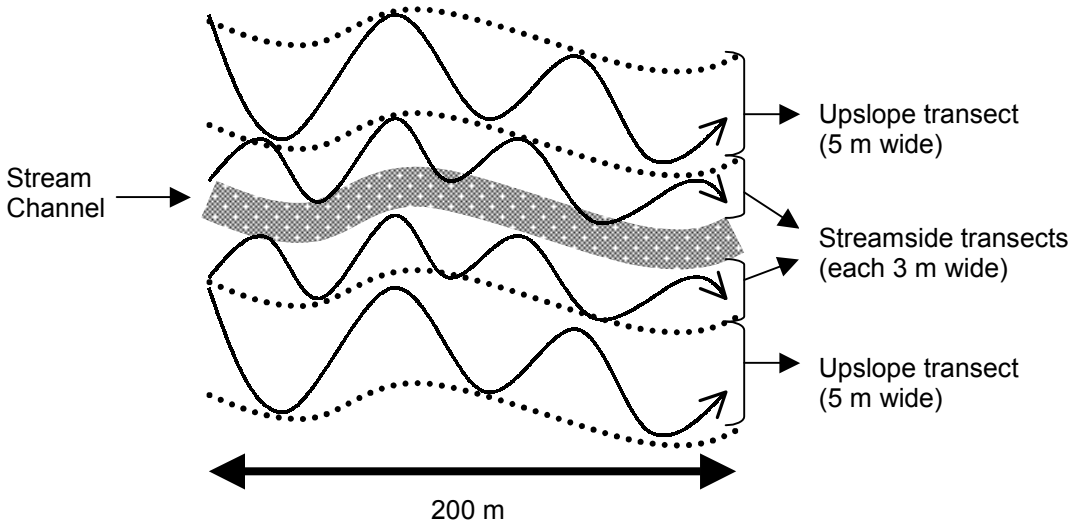

Figure 2.1. Transect layout and animal survey walk-and-turn method used for Van Dyke's salamander surveys at stream sites located in the Cascade Range, Washington, 2000-2001.

Salamander Surveys

Salamander surveys were conducted during the spring (May-July) and fall (September-October) 2000 and 2001, when spring snowmelt and fall rains provided conditions that were the most suitable for the detection of Van Dyke's salamanders (Jones 1999). Patterns of spacing and movement of plethodontid salamanders are strongly influenced by prevailing weather conditions (Grover 1998). Van Dyke's salamander may be surface active for periods longer than other Pacific Northwest *Plethodons*, especially when associated with riparian habitats (Jones 1999). Animal surveys were restricted to times when the substrates under the upper most layer of cover objects (e.g. litter, logs, and rocks) were moist, wet, or saturated, and ground temperatures had not dropped below freezing for at least 72 hours prior to the time of survey (Jones 1999). Crew members traveled within each transect following a zigzag path and searching under available cover objects using a walk-and-turn method (Figure 2.1) (Crisafulli 1999). The walk-and-turn method was selected to reduce the chances of sampling bias by preventing surveyors from forming search patterns for cover objects perceived as more likely to have Van Dyke's salamander under them, while still covering a large area in search of an animal that is often distributed in patches. Natural cover transects have been found to be more effective for sampling *Plethodon* salamanders than other amphibian sampling methods (Hyde and Simons 2001).

Habitat Measures

Habitat characteristics were measured a single time at each site July-October 2001. To evaluate the habitat associations of the Van Dyke's salamander at three distinct spatial scales (between stream or 200-m site level, within stream or 10-m segments, and microhabitat site or 4-m^2 quadrats), we measured specific habitat features indicative of current hydrologic conditions, disturbance characteristics, geomorphology, and vegetation structure.

Between Stream

The between stream analysis compared habitat characteristics for sites (200 m) where the Van Dyke's salamander was and was not detected. Several variables were recorded once for each site, including: elevation (m), an indicator of whether the site was located in or out of the 1980 blast zone of Mount St. Helens, the total number of side streams (or areas of actively flowing water) entering the study stream, and the frequency of each stream habitat along the 200 m stream reach. Fast water stream habitats were classified as waterfall, cascade, chute, run, high gradient riffle, and low gradient riffle; slow water stream habitats were classified as particular pool types: plunge, dammed, lateral-scour, and "other". The Van Dyke's salamander is considered an old-growth obligate protected under the Northwest Forest Plan (USDA and USDI 1994). We selected sites to ensure a balance between the numbers of sites located in and out of the 1980 blast zone of Mount St. Helens. We recorded the number of side streams as a possible source of available wetted habitat beyond the main stream channel. Finally, we predicted that the presence of specific stream habitat types, namely waterfalls, cascades and plunge pools, may provide splash zones associated with Van Dyke's salamander occurrence in riparian areas. Summaries of 10-m segment measures for each site were included in the between stream analysis.

Within Stream

The within stream analysis considered the difference between areas where the Van Dyke's salamander was and was not detected along a single stream channel. Therefore, only streams where the salamander had been detected were included in this analysis. Habitat characteristics were recorded for 20 contiguous 10-m segments along each 200-m study stream reach. Habitat characteristics recorded for each segment represented a systematic measure of available habitat along a 10-m stretch of the stream channel and associated valley walls. Valley wall measures were restricted to bands that included the area between the wetted stream channel out to 8 m. Measures were also recorded for 10-m segments centered on each Van Dyke's salamander animal capture location.

In each segment we measured both stream channel and valley wall habitats, resulting in the characterization of a stream and valley wall cross-section every 10 m. For a measure of hydrologic condition we identified a single systematically chosen stream habitat type within every 10-m segment. Measures of disturbance characteristics included the presence, type, and a cover estimate (%) of disturbance on the valley walls (colluvial slumping, mass wasting, or none) and within the stream channel (scouring, deposition, or none). Measures of geomorphology included stream channel and valley wall gradient (degrees), stream channel aspect (degrees azimuth), valley wall morphology (trough, U-shaped, V-shaped, or vertical), and dominant valley wall substrate (soil, sand, small gravel, large gravel, small cobble, large cobble, boulder, or bedrock). Measures of vegetation structure included dominant forest type (coniferous, deciduous, mixed, or non-forested), dominant seral class (non-vascular, grass-forb, forb-shrub, shrub-sapling, sapling-pole, young forest, mature forest, or old-growth forest), ocular estimates of over-story (only crown species) and total (crown and under-story species) canopy covers for both the stream channel and valley walls. Estimates of canopy cover were measured by holding arms up at a 45º angle, forming a circle with outspread arms, and recording the percent area of the circle filled by the canopy.

The microhabitat site analysis included only streams where the Van Dyke's salamander had been detected and focused on the difference between microhabitat sites where the salamander was detected and systematically chosen microhabitat sites along stream channels. Rectangular quadrats measuring 4 m^2 were systematically placed every 10 m along the 200-m site length, for a total of 21 quadrats per site. Quadrats characterizing microhabitat sites where salamanders were detected were centered at each animal capture location. Measures of hydrologic condition included the presence of a seep and distance from the center of the quadrat to the nearest water source. Disturbance was measured as the percent of the quadrat influenced by colluvial slumping, mass wasting, scouring, or deposition. Measures of geomorphology included the percent of the quadrat covered by soil, sand, small gravel, large gravel, small cobble, large cobble, boulder, and bedrock. Measures of vegetation structure included the percent cover of tree, shrub, forb, bryophyte, and graminoid.

All quadrat cover estimates and ocular canopy estimates were recorded using modified Daubenmire cover classes (0, >0-5, 6-25, 26-50, 51-75, and 76-100%) (Daubenmire 1959).

Statistical Analysis

Habitat characteristics at each of three spatial scales where Van Dyke's salamanders were detected were compared to habitat characteristics where they were not detected. Resource selection models (Manly et al. 1993) were developed for Van Dyke's salamander occurrence at three spatial scales. In these analyses, salamander detection was used as a surrogate measure for occurrence, knowing that there was the possibility salamanders were not detected at sites where they did occur. Van Dyke's salamander occurrence was a binary response of detected versus not detected, and modeled using logistic regression (PROC GENMOD, SAS Institute 2000). Logistic regression is suggested for retrospective studies with a binary response (Ramsey et al. 1994). The best approximating model for the odds of Van Dyke's salamander occurrence at each of the three spatial scales was selected from an *a priori* list of candidate models (Burnham and Anderson 1998). Results of logistic modeling after back-transformation from odds refer to the probability of Van Dyke's salamander occurrence.

Categorical Variable Selection

Many of the habitat characteristics measured were categorical variables (16 of the 37 measured), with some of the categorical factors having up to 9 categories (e.g. stream habitat type, where possible categories included: waterfall, cascade, chute, high-gradient riffle, low-gradient riffle, run, plunge pool, dammed pool, and other pool). When there were more than 2 possible categories for a single measure of habitat, categories were collapsed into a single binomial variable in a multiple logistic regression analysis that gave the greatest deviance reduction (Tables 2.1, 2.2, and 2.3) following Ramsey et al. (1994). For example, in the within stream analysis stream habitat type was collapsed into a single binomial variable representing waterfall, cascade, or chute versus all other stream habitat types (STREAM_WATERFALL_

CASCADE_CHUTE). In the between stream analysis, we used the same deviance reduction method, and summarized binomial independent variables into a proportion of all segment measures within a stream. For example, in the between stream analysis, STREAM_WATERFALL_CASCADE_CHUTE is the proportion of segments within a stream that have a waterfall, cascade, or chute stream habitat type.

Model Development

Candidate models describing Van Dyke's salamander occurrence for each of the three spatial scales was developed prior to analysis. The list of *a priori* models were hypotheses based on existing biological knowledge in conjunction with our own personal experience with the species (Burnham and Anderson 1998). To account for multicollinearity, variables with correlations >0.5 were not included in the same model. Models that consider the influence of hydrologic conditions on the odds of Van Dyke's salamander occurrence in riparian habitats focus on the type and frequency of different stream habitat types, the presence of side stream channels and seeps, and distance from microhabitat sites to the nearest water source. We hypothesized that the odds of Van Dyke's salamander occurrence at any one of the three spatial scales would increase with: an increase in the frequency of fast water habitat types such as waterfalls and cascades, and associated plunge pools; the presence of, or increase in, the number of side stream channels and seeps; and a decrease in the distance to nearest water source from microhabitat sites.

Models that considered a direct measure of disturbance focused on the potential influence of small-scale disturbances at the site level on the odds of Van Dyke's salamander occurrence in riparian habitats. We hypothesized that the presence of, or increased frequency of, disturbance within the stream channel or on the valley wall would increase the odds of Van Dyke's salamander occurrence. We also hypothesized that the location of a stream within the 1980 blast zone of Mount St. Helens would have no influence on the odds of occurrence. We felt that abiotic factors, rather than biotic factors such as seral class, would be more important in determining Van Dyke's salamander occurrence, but we wanted to account for the blast

zone to ensure that we did not have an overrepresentation of sites where Van Dyke's salamander had been detected within this zone.

Models that focused on the influence of geomorphology on the odds of Van Dyke's salamander occurrence between riparian habitats considered substrate types, gradient, aspect, morphology and elevation. We hypothesized that the odds of Van Dyke's salamander occurrence would increase with the presence of: bedrock and boulder substrates on the valley wall or in the stream channel, high gradient stream channels, steep valley walls as evidenced by measures of gradient, vertical or V-shaped valley wall morphology, stream channel aspects that may minimize sun exposure on the valley floor (north or south facing), or narrow, deeply incised stream channels as evidenced by a decrease in valley floor width. We hypothesized that there would be no evidence of an influence of elevation on the odds of Van Dyke's salamander occurrence, but we included this as a variable to ensure that our selection of additional sites was not biased.

Table 2.1. Nineteen variables used in the between stream analysis of Van Dyke's salamander occurrence at stream sites located in the Cascade Range, Washington, 2000-2001. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Hydrologic Condition	SIDE_STREAMS	C	Number of side streams running into the main channel surveyed (no.)
	STREAM_WATERFALL_ PLUNGE_POOL	C	Frequency of waterfall or plunge pool stream habitat types (%)
	STREAM_WATERFALL _CASCADE_CHUTE	C	Proportion of segments within a site that have a waterfall, cascade or chute stream habitat type
Disturbance Characteristics	BLAST_ZONE	B	Indicator of whether the site is located in or out of the 1980 blast zone of Mount St. Helens
	VALLEY_WALL_ DISTURBANCE	C	Proportion of segments within a site that have evidence of valley wall disturbance
	VALLEY_WALL_ DISTURBANCE_CLASS	C	Proportion of segments within a site that are >76% disturbed on the valley wall
Geomorphology	ELEVATION	C	Elevation of site (m)
	STREAM_GRADIENT	C	Average stream gradient within a site (degrees), as measured with a clinometer
	STREAM_ASPECT	C	Proportion of segments within a site that have a west flowing stream (225-314 degrees)
	STREAM_BEDROCK_ BOULDER_SOIL	C	Proportion of segments within a site that have a bedrock, boulder, or soil dominated stream habitat type
	VALLEY_WALL_ GRADIENT	C	Average valley wall gradient within a site (degrees), as measured with a clinometer

Table 2.1. Nineteen variables used in the between stream analysis of Van Dyke's salamander occurrence at stream sites located in the Cascade Range, Washington, 2000-2001. Continued. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Geomorphology	VERTICAL_VALLEY_ WALL	C	Proportion of segments within a site that have a vertical shaped valley wall morphology
	VALLEY_WALL_ BEDROCK_BOULDER	C	Proportion of segments within a site that have bedrock or boulder dominated valley walls
	VALLEY_FLOOR_ WIDTH	C	Average valley floor width within a site (m)
Vegetation Structure	OVER-STORY_ STREAM_CANOPY	C	Proportion of segments within a site that have <50% stream over-story canopy cover
	TOTAL_STREAM_ CANOPY	C	Proportion of segments within a site that have a <5% total stream canopy cover estimate (includes crown and under-story species)
	TOTAL_VALLEY_WALL_ CANOPY	C	Proportion of segments within a site that have a >0-5% total valley wall canopy cover estimate (includes crown and under-story species)
	YOUNG_FOREST	C	Proportion of segments within a site that have a young forest dominated valley wall seral class
	NON-FORESTED	C	Proportion of segments within a site that have non-forested valley walls

Table 2.2. Twenty-two variables used in the within stream analysis of Van Dyke's salamander occurrence at stream sites located in the Cascade Range, Washington, 2000-2001. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Hydrologic Condition	STREAM_WATERFALL_ CASCADE_CHUTE	B	Indicator of segments with a waterfall, cascade or chute stream habitat type versus all other stream habitat types
Disturbance Characteristics	STREAM_DISTURBANCE _CLASS	C	Proportion of stream channel in a segment with evidence of disturbance
	VALLEY_WALL_1 _DISTURBANCE	B	Indicator of segments with evidence of disturbance on valley wall 1, versus no evidence of disturbance
	VALLEY_WALL_2 _DISTURBANCE	B	Indicator of segments with evidence of disturbance on valley wall 2, versus no evidence of disturbance
	VALLEY_WALL_1_ DISTURBANCE_ CLASS	C	Proportion of valley wall 1 in a segment with evidence of disturbance
	VALLEY_WALL_2_ DISTURBANCE_ CLASS	C	Proportion of valley wall 2 in a segment with evidence of disturbance
Geomorphology	STREAM_GRADIENT	C	Stream gradient within an segment (degrees), as measured with a clinometer
	STREAM_ASPECT	B	Indicator of segments with a west or north versus east or south facing stream aspect (west = 225-314°, north = 315-44°)
	STREAM_BEDROCK	B	Indicator of segments with a bedrock dominated stream habitat type versus all other substrate types
	VALLEY_WALL_1_ GRADIENT	C	Valley wall 1 gradient within a segment (degrees), as measured with a clinometer
	VALLEY_WALL_2_ GRADIENT	C	Valley wall 2 gradient within a segment (degrees), as measured with a clinometer

Table 2.2. Twenty-two variables used in the within stream analysis of Van Dyke's salamander occurrence at stream sites located in the Cascade Range, Washington, 2000-2001. Continued. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Geomorphology	VERTICAL_V-SHAPED _VALLEY_WALL_1	B	Indicator of segments with a vertical or V-shaped versus trough or U-shaped valley wall 1 morphology
	VERTICAL_V-SHAPED _VALLEY_WALL_2	B	Indicator of segments with a vertical or V- shaped versus trough or U-shaped valley wall 2 morphology
	VALLEY_WALL_1_ BEDROCK_LARGE_COBBLE	B	Indicator of segments with a bedrock or large cobble dominated valley wall 1, versus all other substrate types
	VALLEY_WALL_2_ BEDROCK	B	Indicator of segments with a bedrock dominated valley wall 2 versus all other substrate types
Vegetation Structure	OVER-STORY_STREAM_ CANOPY	B	Indicator of segments with a stream over-story canopy cover >0-50% versus 0% or >50%
	TOTAL_VALLEY_WALL_1_ CANOPY	B	Indicator of segments with a total canopy cover estimate of 0% on valley wall 1 (includes crown and under-story species) versus >0%
	TOTAL_VALLEY_WALL_2_ CANOPY	B	Indicator of segments with a total canopy cover estimate of 0% on valley wall 2 (includes crown and under-story species) versus >0%
	GRASS-FORB_FORB-SHRUB_ VALLEY_WALL_1	B	Indicator of segments with a grass-forb or forb-shrub dominated valley wall 1, versus all other seral stages
	GRASS-FORB_FORB-SHRUB_ VALLEY_WALL_2	B	Indicator of segments with a grass-forb or forb-shrub dominated valley wall 2, versus all other seral stages
	NON-FORESTED _VALLEY_WALL_1	B	Indicator of segments with a non-forested valley wall 1, versus coniferous, deciduous, or mixed forest
	NON-FORESTED _VALLEY_WALL_2	B	Indicator of segments with a non-forested valley wall 2, versus coniferous, deciduous, or mixed forest

Table 2.3. Sixteen variables used in the microhabitat site analysis of Van Dyke's salamander occurrence at stream sites located in the Cascade Range, Washington, 2000-2001. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Hydrologic Condition	SEEP	B	Indicator of the presence versus absence of a seep within a quadrat
	DISTANCE_TO_WATER	C	Distance from the middle of quadrat to the nearest source of water (cm)
Disturbance Characteristics	DISTURBANCE	C	Percent area of a quadrat with evidence of disturbance
Geomorphology	SAND	B	Indicator of quadrats with sand (substrate <2 mm in diameter, excluding soil) cover >0-25% versus 0 or 26-100%
	SMALL_GRAVEL	B	Indicator of quadrats small gravel (substrate 2-32 mm in diameter) present versus absent
	LARGE_GRAVEL	B	Indicator of quadrats with large gravel (substrate 33-64 mm in diameter) cover >0-50% versus 0 or 51-100%
	SMALL_COBBLE	B	Indicator of quadrats with small cobble (substrate 65-128 mm in diameter) present versus absent
	LARGE_COBBLE	B	Indicator of quadrats with large cobble (substrate 129-256 mm in diameter) present versus absent
	BOULDER	B	Indicator of quadrats with boulder (substrate >256 mm in diameter) present versus absent
	BEDROCK	B	Indicator of quadrats with bedrock (solid surface) present versus absent

Table 2.3. Sixteen variables used in the microhabitat site analysis of Van Dyke's salamander occurrence at stream sites located in the Cascade Range, Washington, 2000-2001. Continued. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Vegetation Structure	TREE	B	Indicator of quadrats with trees absent versus present
	SHRUB	B	Indicator of quadrats with shrub cover <25% versus >26%
	FORB	B	Indicator of quadrats with forb cover 26-50% versus 0-25% or 51-100%
	BRYOPHYTE	B	Indicator of quadrats with bryophyte cover 51-75% versus 0-50% or 76-100%
	GRAMINOID	B	Indicator of quadrats with graminoid present versus absent
	LITTER	C	Percent area of a quadrat covered with litter (e.g. leaves, pine needles, twigs <30 mm in diameter)

Models that explored the relationship of vegetation structure with the odds of Van Dyke's salamander occurrence between riparian habitats included: ocular estimates of over-story and total canopy covers on both the stream channel and valley walls; dominant seral class and forest type within segments; and the presence of specific vegetation life forms at microhabitat sites. We hypothesized that the influence of abiotic factors, such as dominant substrate and morphology, would outweigh the importance of biotic factors, such as vegetation, in predicting the odds of Van Dyke's salamander occurrence.

We identified measures of hydrologic conditions, disturbance characteristics, geomorphology and vegetation structure that we felt were the most important in predicting Van Dyke's salamander occurrence at each of the three spatial scales. In the between stream analysis we identified 3 measures of hydrologic condition, 3 measures of disturbance characteristics, 8 measures of geomorphology, and 5 measures of vegetation structure (Table 2.1). In the within stream analysis we identified 1 measure of hydrologic condition, 5 measures of disturbance characteristics, 9 measures of geomorphology, and 7 measures of vegetation structure (Table 2.2). In the microhabitat site analysis we identified 2 measures of hydrologic condition, 1 measure of disturbance characteristic, 7 measures of geomorphology, and 6 measures of vegetation structure (Table 2.3).

A priori candidate models were limited to one, two, or three variables to maintain parsimony, to ensure biological interpretations, and to easily predict the odds of Van Dyke's salamander occurrence. Models involving habitat measures from more than one group (e.g. hydrologic conditions and disturbance characteristics) explored the possibility that one or more type of habitat measure may concurrently predict Van Dyke's salamander occurrence. We developed a total of 130 candidate models for the between stream analysis (n = 47), 290 for the within stream analysis (n = 462), and 285 for the microhabitat site analysis (n = 742). The best approximating model was identified for each of the three spatial scales.

Model Selection

We used an information theoretic approach to rank *a priori* candidate models at each spatial scale (Burnham and Anderson 1998). We used a Bayesian Information Criterion (BIC), which tends to favor lower-dimensional models more than Akaike's Information Criterion (Schwartz 1978), and decreases the chances of having a non-significant variable coefficient in best approximating models:

$BIC = -2\ln(L) + K \cdot \ln(n)$

Where $\ln(L)$ denotes the maximum value of the natural logarithm of the likelihood function; K is the number of estimable parameters in a given model; and n is the number of valid observations.

The best approximating model for each of three spatial scales was identified as the model with the minimum BIC value. We considered competing models to be those with a delta (Δ) BIC value of <2.0. Delta BIC is a measure of the difference in BIC rank between the top and current models. Competing models were considered to be equally useful at describing the data as the best approximating model. Models with a ΔBIC >2.0 and <4.0 were considered meaningful but not as descriptive as those with ΔBIC <2.0 (Burnham and Anderson 1998). We presented all models with some reasonable level of support within ΔBIC 10.0 (Anderson et al. 2001). We assessed model selection uncertainty among competing models by calculating posterior probabilities, or the probability of a model given the data. In the absence of a reason to believe that any single candidate model may be better than another, all prior probabilities were considered to be equal (Ramsey and Schafer 2002). We report maximum rescaled adjusted generalized coefficients of determination ($\overline{R}^2$) as an evaluation of the proportion of the response variation explained by each model (Nagelkerke 1991).

$R^2 = 1 - \{ L(0) / L(\hat{\beta}) \}^{2/n}$ and $\overline{R}^2 = R^2 / \max(R^2)$,

Where $L(\hat{\beta})$ and $L(0)$ denote the log likelihood of the fitted and null models, respectively.

RESULTS

During the spring and summer of 2001 crew members surveyed 50 stream sites and recorded the presence of 350 individual Van Dyke's salamanders. Van Dyke's salamanders were detected at 26 streams, and were not detected at 24 streams (Figure 2.2). The Van Dyke's salamander was detected at only 2 of the 26 sites chosen in addition to those previously known to have the salamander. Our results emphasize the rarity of the Van Dyke's salamander in the landscape. The total number of Van Dyke's salamander detected at any one site ranged from 1-49 individuals. The mean number of Van Dyke's salamander detected at the 26 sites at which they were encountered was 13 individuals (S.E.=2.7), with a median of 6 individuals.

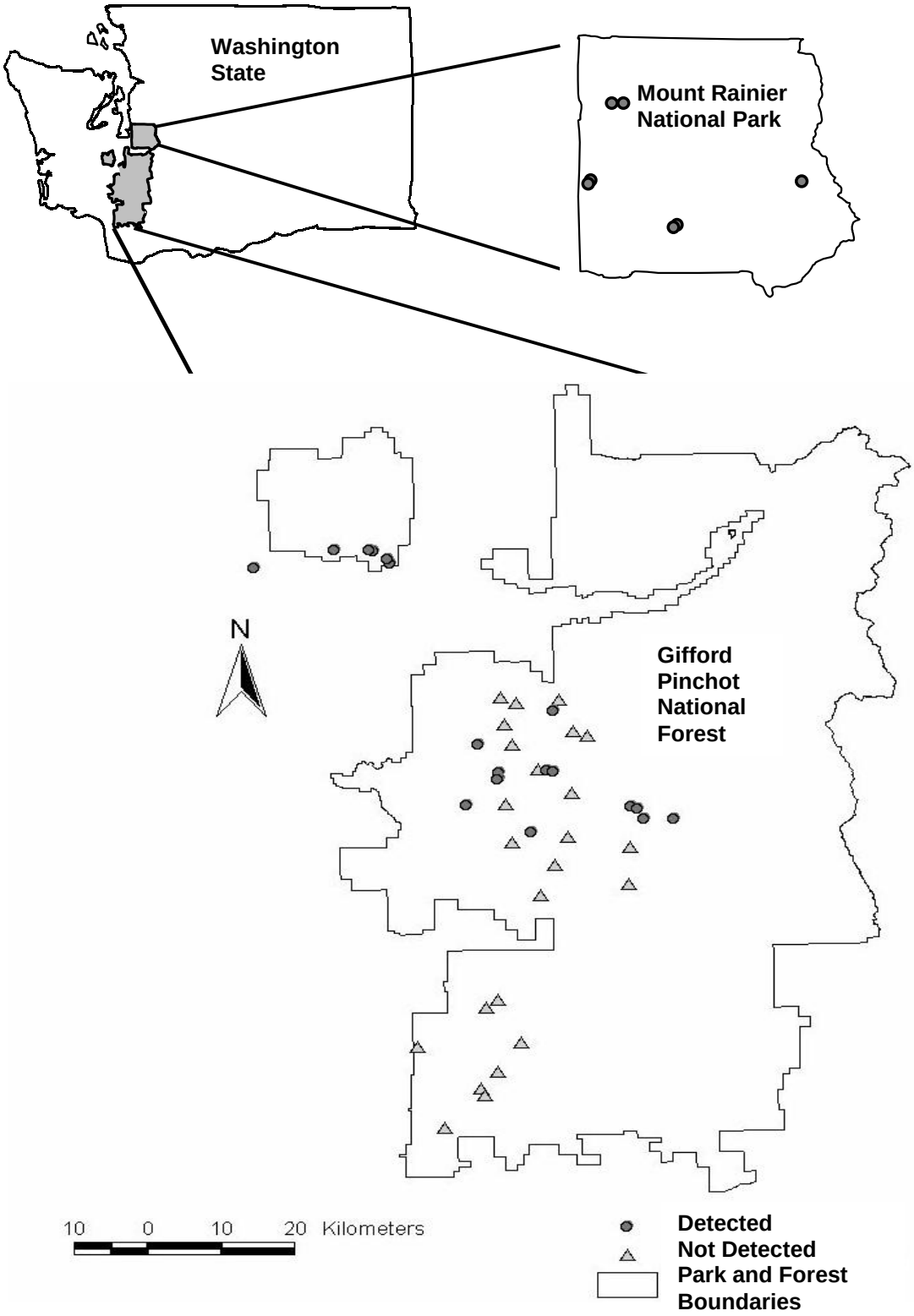

Figure 2.2. Location of 50 stream sites surveyed for the Van Dyke's salamander in the Gifford Pinchot National Forest and Mount Rainier National Park, Cascade Range, Washington, 2000-2001. Van Dyke's salamanders were detected at 26 streams and not detected at 24 streams.

Van Dyke's salamanders more often occurred closer to flowing water. The mean distance from Van Dyke's salamander animal capture locations to the nearest source of water (including the wetted stream channel, side streams, and valley wall seeps) was 143 cm (S.E. = 9.1), with a median of 76 cm. Van Dyke's salamanders were encountered within 300 cm of the nearest source of water 81.4% of the time, and within 100 cm of the nearest water source 52.2% of the time (Figure 2.3).

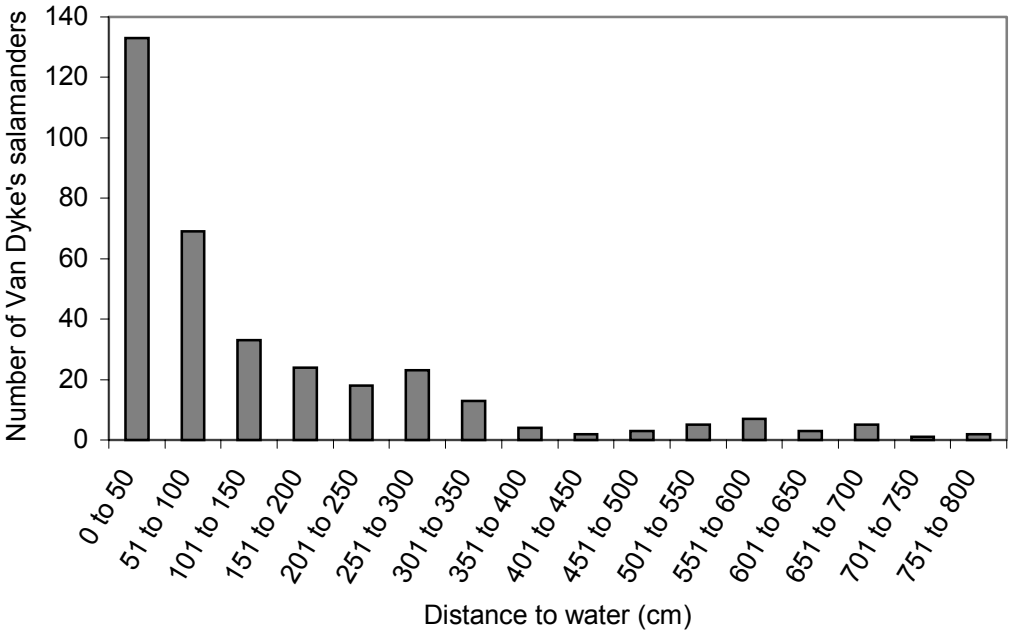

Figure 2.3. Distribution of Van Dyke's salamander animal capture locations in riparian areas and the distance to the nearest water source (cm). Cascade Range, Washington, 2000-2001.

Between Stream

In the between stream analysis we used 47 of the 50 sites surveyed, 25 sites with Van Dyke's salamander detected and 22 sites with Van Dyke's salamander not detected. Three of the stream sites were excluded from the between stream analysis because they were dry either entirely or along portions of the stream channel during habitat data collection. Nineteen measures of habitat were used in this analysis (Table 2.1).

The best approximating model relating Van Dyke's salamander occurrence to habitat characteristics in the between stream analysis included three measures of habitat (Model {TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + STREAM_BEDROCK_BOULDER_SOIL}) (Table 2.4). The probability of Van Dyke's salamander occurrence increased with an increase in: the proportion of segments within a site having a valley wall total canopy cover estimate <5% (including crown and under-story species), the number of side streams flowing into the main stream channel, and the proportion of stream channel habitats within a site having a dominant substrate type of bedrock, boulder, or soil (Figure 2.4). There were no competing models based on a cutoff of ΔBIC 2.0 (Table 2.5).

To explore the possibility that there may be more variables than can be represented by three variable models important in predicting Van Dyke's salamander occurrence, forward selection using habitat characteristics was performed from the best approximating model at all three spatial scales. Habitat characteristics chosen with forward selection, in addition to those already represented in the best approximating model, would be considered important for predicting Van Dyke's salamander occurrence. There were no additional habitat characteristics suggested by forward selection from the best approximating model in the between streams analysis. This suggests that the variables in the best approximating model best explain the variability in the data.

Within Stream

We used 25 sites where Van Dyke's salamander was detected in the within stream analysis, excluding one stream that was entirely dry at the time of habitat data collection. There were a total of 462 segment measures used in the analysis, 263 representing segments where Van Dyke's salamander was not detected, and 199 where the salamander was detected. Twenty-two measures of habitat were used in this analysis (Table 2.2). When systematic segments overlapped with those centered on animal capture locations, the

systematic measures were excluded from analysis so that results would reflect the difference in used versus unused habitats.

Table 2.4. Coefficients for best approximating models of Van Dyke's salamander occurrence in riparian habitats at three spatial scales. Cascade Range, Washington, 2001. Models were fitted by logistic regression. Parameter estimates are log-odds ratios of occurrence.

Variable	Parameter Estimate	S.E.	95% C.I.
Between Stream			
TOTAL_VALLEY_WALL_CANOPY	46.03	19.73	16.44, 92.45
SIDE_STREAMS	0.37	0.19	0.09, 0.85
STREAM_BEDROCK_BOULDER_SOIL	6.22	2.33	2.27, 11.56
Within Stream			
NON-FORESTED_VALLEY_WALL_1	2.1977	0.2672	1.69, 2.74
STREAM_BEDROCK	0.8717	0.2355	0.41, 1.34
VERTICAL_V-SHAPED_VALLEY_WALL_1	2.3172	0.6127	1.22, 3.66
Microhabitat Sites			
TREE	1.10	0.2085	0.70, 1.52
SMALL_COBBLE	1.51	0.1863	1.15, 1.88
SEEP	1.79	0.3721	1.09, 2.56

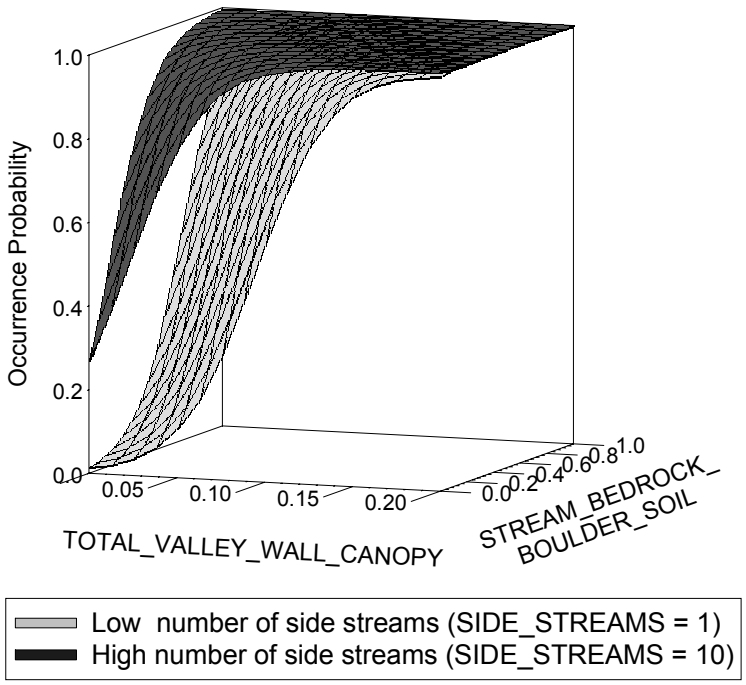

Figure 2.4. Probability of Van Dyke's salamander occurrence and three measures of habitat indicated by the best approximating model in the between stream analysis. Cascade Range, Washington, 2001. TOTAL_VALLEY_WALL_CANOPY is the proportion of segments within a site that have >0-5% total valley wall canopy cover estimates (includes crown and under-story species). STREAM_BEDROCK_BOULDER_SOIL is the proportion of segments within a site that have a bedrock, boulder, or soil dominated stream habitat type. SIDE_STREAMS is the number of side streams or areas of actively running water flowing into the main stream channel surveyed. The two surfaces show maximum and minimum values for SIDE_STREAMS.

Table 2.5. Rankings based on BIC for *a priori* models used in the between stream analysis relating the occurrence of Van Dyke's salamander to habitat features in riparian areas. Cascade Range, Washington, 2001. (ΔBIC <10.0 and null model shown).

Rank	Model	ln(L)	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
1	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + STREAM_BEDROCK_BOULDER_SOIL	40.95	4	56.35	0.00	0.957	0.534
2	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + VERTICAL_VALLEY_WALL	45.05	4	60.45	4.41	0.016	0.461
3	TOTAL_VALLEY_WALL_CANOPY + STREAM_BEDROCK_BOULDER_SOIL	49.59	3	61.14	4.79	0.008	0.373
4	SIDE_STREAMS + STREAM_WATERFALL_PLUNGE_POOL + OVER-STORY_STREAM_CANOPY	46.59	4	61.99	5.64	0.003	0.432
5	TOTAL_VALLEY_WALL_CANOPY + VERTICAL_VALLEY_WALL + VALLEY_WALL_DISTURBANCE_CLASS	46.71	4	62.11	5.76	0.003	0.430
6	TOTAL_VALLEY_WALL_CANOPY + VERTICAL_VALLEY_WALL	50.85	3	62.40	6.05	0.002	0.346
7	TOTAL_VALLEY_WALL_CANOPY + STREAM_BEDROCK_BOULDER_SOIL + VALLEY_WALL_DISTURBANCE_CLASS	47.34	4	62.74	6.39	0.002	0.417
8	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + STREAM_WATERFALL_CASCADE_CHUTE	47.48	4	62.88	6.53	0.001	0.415
9	TOTAL_VALLEY_WALL_CANOPY + VERTICAL_VALLEY_WALL + STREAM_WATERFALL_PLUNGE_POOL	47.59	4	62.99	6.64	0.001	0.413
10	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + STREAM_WATERFALL_PLUNGE_POOL	47.79	4	63.19	6.84	0.001	0.409
11	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS	52.09	3	63.64	7.29	<0.001	0.320

Table 2.5. Rankings based on BIC for *a priori* models used in the between stream analysis relating the occurrence of Van Dyke's salamander to habitat features in riparian areas. Cascade Range, Washington, 2001. (ΔBIC <10.0 and null model shown). Continued.

Rank	Model	ln(L)	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
12	SIDE_STREAMS + STREAM_BEDROCK_BOULDER_SOIL + OVER-STORY_STREAM_CANOPY	48.49	4	63.89	7.54	<0.001	0.395
13	TOTAL_VALLEY_WALL_CANOPY + VERTICAL_VALLEY_WALL + STREAM_WATERFALL_CASCADE_CHUTE	48.60	4	64.00	7.65	<0.001	0.393
14	STREAM_WATERFALL_PLUNGE_POOL + OVER-STORY_STREAM_CANOPY	52.51	3	64.06	7.71	<0.001	0.311
15	TOTAL_VALLEY_WALL_CANOPY	56.43	2	64.13	7.78	<0.001	0.222
16	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + VALLEY_WALL_BEDROCK_BOULDER	48.80	4	64.20	7.85	<0.001	0.389
17	TOTAL_VALLEY_WALL_CANOPY + VALLEY_WALL_DISTURBANCE_CLASS	52.88	3	64.43	8.08	<0.001	0.303
18	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS + VALLEY_WALL_DISTURBANCE_CLASS	49.10	4	64.50	8.15	<0.001	0.382
19	TOTAL_VALLEY_WALL_CANOPY + STREAM_BEDROCK_BOULDER_SOIL + STREAM_WATERFALL_PLUNGE_POOL	49.16	4	64.56	8.21	<0.001	0.381
20	TOTAL_VALLEY_WALL_CANOPY + STREAM_BEDROCK_BOULDER_SOIL + STREAM_WATERFALL_CASCADE_CHUTE	49.58	4	64.98	8.63	<0.001	0.373
21	TOTAL_VALLEY_WALL_CANOPY + STREAM_WATERFALL_PLUNGE_POOL	53.44	3	64.99	8.64	<0.001	0.290
22	TOTAL_VALLEY_WALL_CANOPY + SIDE_STREAMS	53.52	3	65.07	8.72	<0.001	0.289

Table 2.5. Rankings based on BIC for *a priori* models used in the between stream analysis relating the occurrence of Van Dyke's salamander to habitat features in riparian areas. Cascade Range, Washington, 2001. (ΔBIC <10.0 and null model shown). Continued.

Rank	Model	ln(L)	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
23	VERTICAL_VALLEY_WALL + STREAM_WATERFALL_PLUNGE_POOL + OVER-STORY_STREAM_CANOPY	49.79	4	65.19	8.84	<0.001	0.368
24	TOTAL_VALLEY_WALL_CANOPY + VALLEY_WALL_BEDROCK_BOULDER	53.97	3	65.52	9.17	<0.001	0.278
25	STREAM_BEDROCK_BOULDER_SOIL + OVER-STORY_STREAM_CANOPY	54.04	3	65.59	9.24	<0.001	0.277
26	SIDE_STREAMS + VERTICAL_VALLEY_WALL + STREAM_WATERFALL_PLUNGE_POOL	50.21	4	65.61	9.26	<0.001	0.360
27	VALLEY_WALL_DISTURBANCE_CLASS + STREAM_ASPECT	54.19	3	65.74	9.39	<0.001	0.274
28	STREAM_ASPECT	58.19	2	65.90	9.55	<0.001	0.179
29	STREAM_GRADIENT	50.66	4	66.06	9.71	<0.001	0.350
30	TOTAL_VALLEY_WALL_CANOPY + VALLEY_WALL_DISTURBANCE_CLASS + VALLEY_WALL_BEDROCK_BOULDER	50.68	4	66.08	9.73	<0.001	0.350
31	TOTAL_VALLEY_WALL_CANOPY + VALLEY_WALL_DISTURBANCE_CLASS + STREAM_WATERFALL_CASCADE_CHUTE	50.79	4	66.19	9.84	<0.001	0.348
32	SIDE_STREAMS + STREAM_WATERFALL_PLUNGE_POOL + VALLEY_WALL_BEDROCK_BOULDER	50.93	4	66.33	9.98	<0.001	0.345
70	Null model	64.96	1	68.81	12.46	<0.001	0.000

The best approximating model relating occurrence of Van Dyke's salamander to habitat characteristics in the within stream analysis included 3 measures of habitat (Model {NON-FORESTED_VALLEY_WALL_1 + STREAM_BEDROCK + VERTICAL_V-SHAPED_VALLEY_WALL_1}) (Table 2.4). The probability of Van Dyke's salamander occurrence increased with the presence of non-forested segments, bedrock dominated stream habitats, and vertical or V-shaped valley wall morphology (Figure 2.5). Model {NON-FORESTED_VALLEY_WALL_1 + STREAM_BEDROCK + VALLEY_WALL_1_GRADIENT} was a competing model with ΔBIC of 1.24 and a posterior probability of 0.23 (Table 2.6). In the competing model, valley wall morphology is replaced with valley wall gradient, where the odds of Van Dyke's salamander occurrence increases with an increase in valley wall gradient. This model is consistent with the best approximating model, in which Van Dyke's salamander occurrence increases with the presence of vertical and V-shaped valley walls (the two steepest valley wall categories). In order to make sure that results were not biased due to the allocation of valley walls as "VALLEY_WALL_1" or "VALLEY_WALL_2" we randomly assigned the valley walls as 1 or 2 and re-ran the analysis 20 times. We found that the results were consistent between reiterations.

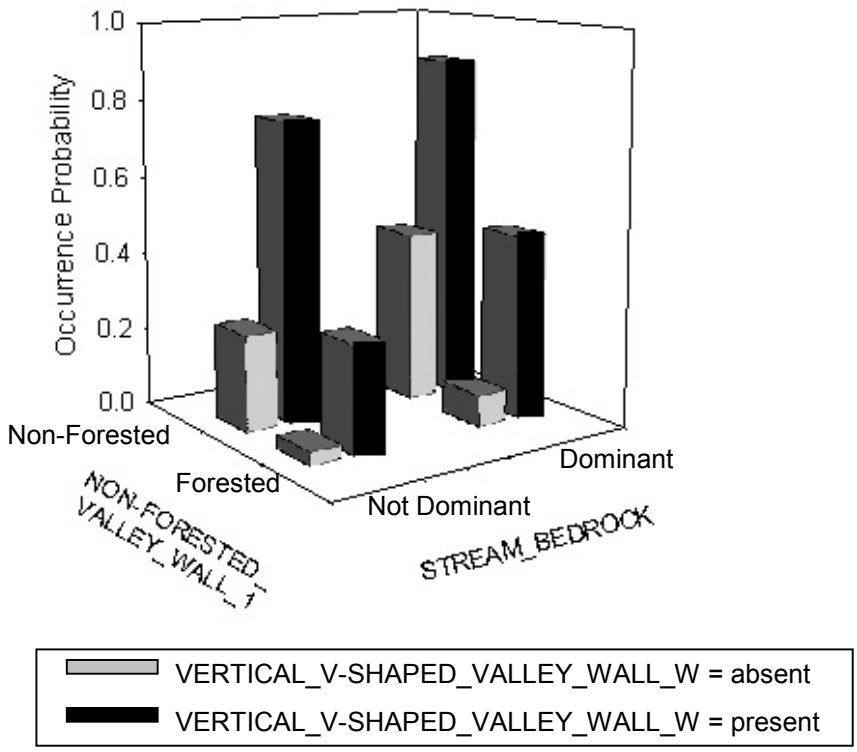

Figure 2.5. Probability of Van Dyke's salamander occurrence and the three measures of habitat indicated by the best approximating model in the within stream analysis. Cascade Range, Washington, 2001. STREAM_BEDROCK is an indicator of segments with a bedrock dominated habitat type. NON-FORESTED_VALLEY_WALL_1 is an indicator of segments with a non-forested valley wall 1. VERTICAL_V-SHAPED_VALLEY_WALL_1 is an indicator of segments with a vertical or V-shaped valley wall 1 morphology.

Table 2.6. Rankings based on BIC for *a priori* models used in the within stream analysis relating the occurrence of Van Dyke's salamander to habitat features in riparian areas. Cascade Range, Washington, 2001. (ΔBIC <10.0 and null model shown).

Rank	Model	ln(L)	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
1	NON-FORESTED_VALLEY_WALL_1 + STREAM_BEDROCK + VERTICAL_V-SHAPED_VALLEY_WALL_1	507.21	4	531.75	0.00	0.773	0.317
2	NON-FORESTED_VALLEY_WALL_1 + STREAM_BEDROCK + VALLEY_WALL_1_GRADIENT	508.44	4	532.99	1.24	0.225	0.314
3	NON-FORESTED_VALLEY_WALL_1 + VERTICAL_V-SHAPED_VALLEY_WALL_1 + STREAM_DISTURBANCE _CLASS	513.92	4	538.46	6.71	0.001	0.302
4	NON-FORESTED_VALLEY_WALL_1 + VALLEY_WALL_1_GRADIENT + OVER-STORY_STREAM_ CANOPY	513.92	4	539.38	7.63	<0.001	0.300
5	NON-FORESTED_VALLEY_WALL_1 + VERTICAL_V-SHAPED_VALLEY_WALL_1	513.92	3	539.43	7.68	<0.001	0.286
6	NON-FORESTED_VALLEY_WALL_1 + VALLEY_WALL_1_GRADIENT + STREAM_DISTURBANCE _CLASS	513.92	4	540.00	8.25	<0.001	0.298
7	NON-FORESTED_VALLEY_WALL_1 + VERTICAL_V-SHAPED_VALLEY_WALL_1 + OVER-STORY_STREAM_ CANOPY	513.92	4	540.20	8.45	<0.001	0.298
8	NON-FORESTED_VALLEY_WALL_1 + VALLEY_WALL_1_GRADIENT	513.92	3	540.53	8.78	<0.001	0.283
289	Null model	631.57	1	637.71	105.96	<0.001	0.000

Forward selection from the best approximating model in the within stream analysis resulted in the addition of 5 habitat characteristics that met a significance level for entry of α = 0.05 (Table 2.7). In addition to the habitat characteristics in the best approximating model, the presence of grass-forb or forb-shrub seral class on valley wall 2, an increase in the valley wall gradient (which was also indicated by its inclusion in the top competing model), and an increase in disturbance within the stream channel and on valley wall 1, were all positively associated with the odds of Van Dyke's salamander occurrence in riparian habitats. Alternatively, the odds of Van Dyke's salamander occurrence within riparian habitats decreased when stream channel over-story canopy cover was >0-50%.

Table 2.7. Parameter estimates for additionally selected habitat characteristics when forward selection was performed from the best approximating model for Van Dyke's salamander occurrence in the within stream analysis. Cascade Range, Washington, 2001. Parameter estimates are log-odds ratios of occurrence.

Variable	Parameter Estimate	S.E.	Chi-Square	Pr > ChiSq
NON-FORESTED_VALLEY_WALL_1	1.3794	0.3074	20.1401	<.0001
STREAM_BEDROCK	0.9098	0.2500	13.2475	0.0003
VERTICAL_V-SHAPED_VALLEY_WALL_1	1.5670	0.6450	5.9014	0.0151
GRASS-FORB_FORB-SHRUB_VALLEY_WALL_2	0.9691	0.2668	13.1895	0.0003
VALLEY_WALL_1_ GRADIENT	0.0229	0.0084	7.3955	0.0065
STREAM_DISTURBANCE _CLASS	1.3459	0.5003	7.2367	0.0071
OVER-STORY_STREAM_ CANOPY	-0.6403	0.2455	6.8044	0.0091
VALLEY_WALL_1 _DISTURBANCE	0.4757	0.2327	4.1770	0.0410

Microhabitat Site

Microhabitat site analysis of the 26 stream sites where the Van Dyke's salamander was detected included 742 quadrats, 508 representing microhabitat sites where the Van Dyke's salamander was not detected, and 234 where the Van Dyke's salamander was detected. Sixteen measures of habitat were used in the analysis. When systematic quadrats overlapped with those centered on animal capture locations, the systematic measures were excluded from analysis so that results would reflect the difference between microhabitat sites utilized by the Van Dyke's salamander and unused microhabitat sites.

The best approximating model relating occurrence of the Van Dyke's salamander to habitat characteristics in the microhabitat site analysis included 3 measures of habitat (Model {TREE + SEEP + SMALL_COBBLE}) (Table 2.4). The probability of Van Dyke's salamander occurrence increased with the absence of trees in a quadrat, and the presence of a seep and the small cobble (Figure 2.6). There were no competing models based on a cutoff of ΔBIC = 2.0 (Table 2.8).

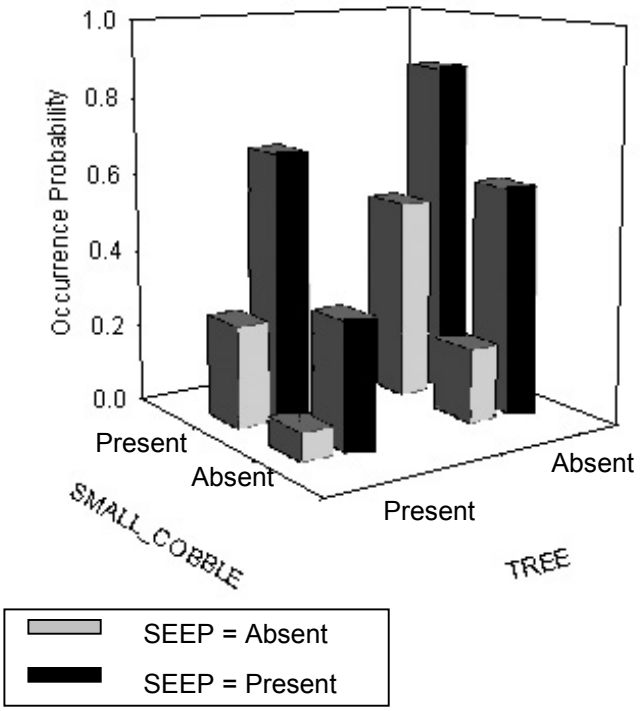

Figure 2.6. Probability of Van Dyke's salamander occurrence and three measures of habitat indicated by the best approximating model in the microhabitat site analysis. Cascade Range, Washington, 2001. TREE is an indicator of quadrats with trees absent versus present. SMALL_COBBLE is an indicator of quadrats with small cobble present versus absent. SEEP is an indicator of quadrats with a seep present versus absent.

Table 2.8. Rankings based on BIC for *a priori* models used to relate the occurrence of Van Dyke's salamander to habitat features in riparian habitats in the microhabitat site analysis. Cascade Range, Washington, 2001. (ΔBIC <10.0 and null model shown).

Rank	Model	ln(L)	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
1	TREE + SEEP + SMALL_COBBLE	763.55	4	789.99	0.00	0.996	0.274
2	TREE + SEEP + LARGE_COBBLE	769.21	4	795.65	5.66	0.003	0.266
3	TREE + SMALL_COBBLE + BEDROCK	772.46	4	798.90	8.91	<0.001	0.261
283	Null model	925.02	1	931.62	141.63	<0.001	0.000

Forward selection from the best approximating model in the microhabitat site analysis resulted in the addition of 3 habitat characteristics that met a significance level for entry of α = 0.05 (Table 2.9). In addition to the habitat characteristics previously discussed for the best approximating model, the presence of large cobble, bedrock, and small gravel all have a positive association with the odds of Van Dyke's salamander occurrence between microhabitat sites.

Table 2.9. Parameter estimates for additionally selected habitat characteristics when forward selection was performed from the best approximating model for Van Dyke's salamander occurrence in the microhabitat site analysis. Cascade Range, Washington, 2001. Parameter estimates are log-odds ratios of occurrence.

Variable	Parameter Estimate	S.E.	Chi-Square	Pr > ChiSq
TREE	0.9749	0.2150	20.5661	<.0001
SMALL_COBBLE	0.8591	0.2311	13.8154	0.0002
SEEP	1.7218	0.3855	19.9476	<.0001
SMALL_GRAVEL	0.5996	0.2198	7.4438	0.0064
LARGE_COBBLE	0.8246	0.2234	13.6178	0.0002
BEDROCK	0.7416	0.1994	13.8357	0.0002

DISCUSSION

We found the Van Dyke's salamander to be associated with grass, herb and shrub dominated vegetation communities maintained by hydrologic conditions, geomorphology and disturbances along the stream channel and associated steep valley walls. Models that best fit the data were consistent between the three spatial scales. Total canopy of >0-5%, non-forested valley walls, and tree absence at the between stream, within stream, and microhabitat site analyses are indicators of grass, herbaceous or shrub dominated vegetation, and show up in all competing models at every spatial scale. Other habitat measures in the best fitting models included: running water (side streams and seeps); exposed bedrock, boulders and soil; steep valley walls; and rocky accumulations (small cobble).

We found Van Dyke's salamanders associated with non-forested valley walls and the absence of trees. Steep valley walls are disturbed frequently, probably preventing plants from colonizing and resulting in valley walls without trees. Dominant hydrology, geology and disturbance processes can affect riparian zones and alter succession and spatial patterns of riparian vegetation. Steep valley walls and areas of exposed bedrock probably limit the

amount of woody vegetation in areas where the Van Dyke's salamander occurs. Riparian zones such as those where Van Dyke's salamander are commonly encountered are extremely dynamic, and seasonal flooding may be aiding in the maintenance of a complex and heterogeneous habitat (Gregory 1991) through scouring along the stream channel and colluvial slumping on the valley wall. Disturbance along the stream channel, along with hydrology and geomorphology, may be limiting the amount of canopy cover and tree species, by preventing colonization through periodic inundation (Gregory 1991) and by exposing substrates such as bedrock. In our study, canopy cover generally decreased near stream channels, particularly where there were seeps and steep valley walls. We do not believe that there is a causal relationship between Van Dyke's salamander occurrence and the absence of tree species, but rather that the relationship between salamander occurrence and grass, herb and shrub dominated vegetation is directly linked to hydrology, geology, and disturbances that limit the ability of tree species to colonize.

Several plethodontid salamanders endemic to the Pacific Northwest have been positively correlated with late seral class forests and closed canopy covers, including the Van Dyke's salamander (Bosakowski 1999), Larch Mountain salamander (*P. larselli*) (Herrington and Larsen 1985) and the Del Norte salamander (*P. elongatus*) (Welsh and Lind 1995). Corn and Bury (1991) found a positive correlation between stand age and estimated numbers of clouded salamander (*Aneides ferreus*) and Western redback salamander (*P. vehiculum*), however they attribute this association to a correlation between the volumes of downed wood and stand age. Others have attributed the association between plethodontid salamander abundance and stand age to structural features and microhabitats maintained by, or often occurring in, late seral class forests (Bury et al. 1991), including disturbance history (Welsh 1990). Heatwole (1962) suggested that local distributions of salamanders are indirectly influenced by plant cover through its effect on temperature and moisture content of substrates. Our study demonstrates that the Van Dyke's salamander can exploit microhabitats that ameliorate the effects of heat and drying, even in the absence of over-story canopy. Though a

few studies found no correlation between forest age and occurrence of plethodontid salamanders endemic to the Pacific Northwest (Diller and Wallace 1994, Aubry 2000), ours is the first study finding a positive association between a Pacific Northwest plethodontid salamander and the absence of canopy concomitant with presence of grass, herb and shrub dominated vegetation. However, we are not the first to suggest that seral class may be merely an indicator of underlying habitat characteristics that are actually more important in predicting salamander occurrence.

Best approximating models predicting Van Dyke's salamander occurrence included availability of alternative flowing water sources in both the between site and microhabitat site analyses. Between sites, an increase in the number of side streams resulted in an increase in the probability of Van Dyke's salamander occurrence. In the microhabitat site analysis, the presence of seeps within quadrats was positively associated with Van Dyke's salamander occurrence. These hydrological conditions provide a source of moisture beyond the active stream channel. *Plethodon* salamanders appear to have no physiological mechanisms to control dehydration rates (Spotila 1972), and appear to select microhabitats providing conditions that do not exceed their physiological tolerance limits (Spotila 1972), thus preventing desiccation. A closely related salamander, the Coeur d'Alene salamander (*P. idahoensis*), has been shown to diffuse the effects of severe environments by occupying wet microhabitats (Wilson 1988), which provide hydric and thermal stability (Hynes 1970, Huheey and Brandon 1973). Seeps along the valley wall are most likely partially maintained by disturbance events; they can occur where soils become thin over impermeable bedrock (Ziemer and Lisle 1998) as scouring by flooding events and colluvial slumping exposes areas of bedrock where subsurface flows are forced above ground. Thus, geomorphology plays an important role in structuring potential seep sites as salamander habitat

Van Dyke's salamander occurrence was positively associated with the presence of bedrock stream channels in both the between and within stream analyses, in addition to boulder and soil in the between stream analysis. The presence of bedrock and boulder

substrates in stream channels may be indicative of certain stream habitat types, namely waterfalls, cascades, chutes, and associated plunge pools. Past observations have associated the Van Dyke's salamander with waterfalls and splash zones (Nussbaum et al. 1983, Leonard et al. 1993, Wilson et al. 1995, Jones 1999). *Plethodons* have exhibited a strong preference for moist substrates (Taub 1961, Sugalski and Claussen 1997), while avoiding standing water altogether (Taub 1961). However, the Coeur d'Alene salamander has been observed partly submerged in standing water (Wilson and Larsen 1988). It may be that waterfalls and associated plunge pools, along with chutes and cascades provide splash zone areas that allow salamanders to remain moist without becoming inundated with water.

Van Dyke's salamander occurrence was associated with the presence of steep, deeply incised vertical and V-shaped valley walls in the within stream analysis. Vertical and V-shaped valley walls are constrained, composed of exposed bedrock or large substrates such as boulders, and are maintained by high gradient channels and flooding events down the stream channel. The impacts of disturbance may be greater in constrained stream reaches due to their incised nature, and valley walls composed of immovable substrates such as bedrock. Deeply incised valley walls may insulate salamanders from seasonal differences by sheltering them within the larger landscape (Moore et al. 2001). Steep valley wall morphology may provide a more thermally stable environment, protecting Van Dyke's salamanders from sun and wind exposure.

The presence of small cobble sized substrates (65-128 mm in diameter) increased the probability of Van Dyke's salamander occurrence in the microhabitat site analysis. Substrates of this size have been positively associated with other amphibians (Welsh and Ollivier 1998), including the Del Norte salamander (*P. elongatus*) (Welsh and Lind 1995). It may be that small cobbles provide a source of coarse cover objects; increasing the amount of interstitial space and providing additional cover (Welsh and Ollivier 1998). The presence and amount of cover objects can restrict the distribution and abundance of salamander species (Southerland 1986*a,b*). Salamanders probably select larger, cooler cover object types (Mathis 1990,

Grover 2000), especially under an open forest canopy (Gabor 1995). Doing so provides them with an environment that is more moderate than under smaller, warmer items (Moore et al. 2001).

The Van Dyke's salamander is encountered in habitats that enable the species to remain in moist areas while exploiting specific microhabitats that stay unchanged during small-scale disturbances, such as increased water volumes during spring snowmelt. Thus, the species can exist in a landscape frequented by disturbance, by choosing microhabitats that are the most resistant to disturbances. Species interact with disturbance regimes and ultimately mitigate the impacts of disturbance either through resistance or by exploiting it to their own advantage (Peterken 1996). Our results indicate that the Van Dyke's salamander is able to do the latter, occupying areas that are resistant to disturbance.

Landscapes contain a range of sites from those that are prone to disturbance to those that are somewhat protected (White 1979). The occurrence of protected sites within a landscape can be particularly important for the survival of certain species (Peterken 1996). We believe that the Van Dyke's salamander is associated with riparian habitats that experience disturbances associated with stream channel disturbances, but are more specifically associated with microhabitats within the broader riparian corridor that are not necessarily the most protected, but are perhaps the most resistant to disturbance. Bedrock channels tend to occur on steeper slopes than alluvial channels of comparable drainage area (Montgomery et al. 1996). Due to high transport capacity, steep, high-energy channels recover quickly from disturbance and the changes caused by deposition and scouring (Montgomery et al. 1996, Montgomery and Buffington 1998). Substrates in streams and along riparian areas are heterogeneous in their distributions. Different substrates are disturbed at different frequencies. Large rocky substrate types, such as the bedrock and boulders associated with Van Dyke's salamanders, are the hardest to mobilize (Reice 1994), and are only moved during more extreme flooding events (Wolman and Miller 1960, Grant 1990, Ziemer and Lisle 1998).

Due to their ecological and physiological requirements, amphibians may be more sensitive than some other taxa to certain forms of habitat alteration, or anthropogenic disturbances created by activities such as timber harvesting and road building (deMaynadier and Hunter 1995). Species with low population sizes, especially those that are habitat specialists, may be particularly sensitive to fragmentation (Gibbs 1998). Amphibians often exhibit strong site fidelity (Sinsch 1990), and territoriality (Petranka 1994), showing reluctance to remove themselves from an area during or after human disturbances or handling (Nishikawa 1990). Timber harvesting has been indicated in negatively impacting local amphibian populations, especially salamanders (Dupuis et al. 1995, Hyde and Simons 2001, Vesely 2002), often with plethodontids exhibiting even greater population declines than other amphibian groups (deMaynadier and Hunter 1995).

Plethodon salamanders have low vagility (Herrington and Larsen 1985, Welsh and Lind 1992, Marvin 1998) and fecundity (Stebbins and Cohen1995). Life history characteristics of the Van Dyke's salamander may inhibit the ability of individuals to survive in or colonize disturbed habitats (Wilson 1993), and plethodontid salamanders may be particularly prone to local extinctions in managed forests (Welsh 1990). Riparian areas may act as dispersal corridors between suitable habitats (Noss 1983, Dupuis et al. 1995) including stream channels utilized by Van Dyke's salamanders. However, studies have shown that simply retaining a buffer zone of forested habitats may not be sufficient to maintain conditions supporting high salamander abundance in small stream ecosystems (Willson and Dorcas 2003). Connectivity of populations may buffer salamanders from the effects of logging or other stream-scale disturbances (Lowe and Bolger 2001). However, logging activities may act to fragment the landscape and limit the dispersal capabilities of salamander species that already have restricted dispersal (Johnston and Frid 2002).

It is important to develop species-specific conclusions regarding the relationship of amphibians to forest age (deMaynadier and Hunter 1995). Even though best approximating models show an increase in the probability of Van Dyke's salamander occurrence with the

absence of tree species, the unnatural removal of trees from the landscape may negatively impact Van Dyke's salamander populations. Forest seral class is an indirect measure of the actual microhabitat elements that ultimately determine whether a site is suitable for a given species (deMaynadier and Hunter 1995). It is not necessarily forest age that determines species distributions but rather the associated microhabitats that may vary in relation to forest age during succession (Aubry et al. 1988; Welsh 1990; Diller and Wallace 1994). Our data suggest that Van Dyke's salamanders are not necessarily dependent on late seral class trees, but rather particular microhabitats and disturbance characteristics characteristically associated with old-growth forests, or landscapes unaltered by human disturbances.

A lack of information for salamanders, including long-term data, habitat requirements, and the precision and accuracy of sampling methods, have hindered efforts to create monitoring and conservation programs for salamanders (Hyde and Simons 2001). Bury and Pearl (1999) note that headwater streams are important habitat for many of the amphibian species endemic to the Pacific Northwest and recommend a conservation strategy that includes preservation of headwater stream habitats. The unique habitat preferences of endemic or rare species should be considered when selecting methods for long-term population monitoring (Hyde and Simons 2001).

The Van Dyke's salamander appears to be relatively rare on the landscape. The salamander has been historically difficult to find, and we found Van Dyke's salamanders at only 2 of 26 additionally chosen streams. We hypothesize that the rarity of the Van Dyke's salamander is largely due to a limit in suitable habitat within its range, and that low mobility of the Van Dyke's salamander (McIntyre 2003) may further lead to rarity. Considering the unique habitat requirements of the Van Dyke's salamander and its relative rarity on the landscape, conservation efforts that focus on headwater streams could greatly aid in conservation efforts for this endemic species.

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Chapter 3

Habitat Associations of the Van Dyke's Salamander (*Plethodon vandykei*) with Geomorphic Conditions in Headwater Seeps of the Cascade Range, Washington State.

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ABSTRACT

We explored the association between Van Dyke's salamander and hydrologic condition, geomorphology, and vegetation structure in headwater seeps in the Cascade Range of Washington State. After conducting salamander surveys and measuring habitat characteristics at 40 seep sites from July-August of 2002, we modeled Van Dyke's salamander occurrence at three spatial scales: between seeps, within seeps, and between microhabitat sites. We ranked *a priori* models using Bayesian Information Criterion (BIC). Using logistic regression, with presence and absence as the response, we found best approximating models of Van Dyke's salamander occurrence at the three spatial scales is predicted by hydrological and geological habitat characteristics. Between seeps, the probability of Van Dyke's salamander occurrence increased with increasing proportions of seep face with a dry or sheeting hydrology, and increasing proportions of seep face >5 m high. Within seeps, the probability of Van Dyke's salamander occurrence was negatively associated with seeps where total overhead cover was >25%. Between microhabitat sites, the probability of Van Dyke's salamander occurrence was positively associated with increases in the percent cover of small cobble, small gravel, and bedrock substrates. The Van Dyke's salamander appears to be associated with habitats that can aid in the maintenance of thermal and hydric conditions favorable for a species that is sensitive to heat and desiccation due to physiological constraints.

INTRODUCTION

The Van Dyke's salamander (*Plethodon vandykei*), endemic to Washington State, is often considered more closely associated with water than any other western *Plethodon* species (Brodie 1970), with the possible exception of the Dunn's salamander (*P. dunni*) (Leonard et al. 1993). It has been documented along high gradient streams, in the splash zones of waterfalls, and in headwater seeps (Nussbaum et al. 1983, Leonard et al. 1993, Wilson 1993, Jones 1999). Zones of saturated overland flow occur where soils thin over impermeable bedrock (Ziemer and Lisle 1998); they can occur when the soil becomes fully saturated and subsurface flow emerges on the surface (Ziemer and Lisle 1998), forming what are referred to as headwater seeps. While habitat associations have been explored for the Van Dyke's salamander along high gradient streams in the southern and central Cascade Range of Washington State (McIntyre 2003), no studies have explored the relationship of the Van Dyke's salamander with headwater seep habitats.

The Van Dyke's salamander is found in three disjunct population centers in Washington State: the southern and central Cascades (the area included in this study), the Willapa Hills, and the Olympic Peninsula (Leonard et al. 1993). The restricted range of the Van Dyke's salamander suggests that it has relatively sedentary habits or narrow ecological tolerances (Wilson et al. 1995). Respiratory requirements may influence life history characteristics of *Plethodon* salamanders (Feder 1983), which lack lungs (Noble 1931) and rely on moist permeable skin to respire (Gatz et al. 1974). *Plethodon* species appear to have narrow physiological tolerance limits due to their lunglessness, making them susceptible to heat and drying (Feder 1983, Stebbins and Cohen 1995).

McIntyre (2003) found that habitat characteristics influenced by geomorphic processes were indicators of Van Dyke's salamander occurrence at stream sites in the Cascade Range. The probability of Van Dyke's salamander occurrence along streams was positively associated with steep, vertical and V-shaped valley walls that were unable to support woody vegetation, high gradient stream channel habitats as evidenced by bedrock

and boulder substrates within the stream channel, availability of suitable cover objects, and hydrologic conditions such as the presence of valley wall seeps. We designed this study to assess whether the habitat characteristics that are predictive of Van Dyke's salamander occurrence at stream sites were similar to the habitat characteristics associated with Van Dyke's salamander occurrence at seep sites in the Cascade Range. We developed resource selection models for the Van Dyke's salamander in headwater seeps and assessed the influence of habitat characteristics on Van Dyke's salamander occurrence at multiple spatial scales: between seeps, within seeps, and microhabitat sites. The Van Dyke's salamander is rare even within its range, and exploring the importance of quantifiable habitat characteristics in headwater seeps may enable us to gain a better understanding of the underlying ecological processes that limit the occurrence of Van Dyke's salamanders.

STUDY AREA

Our study area included lands in the southern and central Washington Cascade Range, from the Muddy River drainage in Skamania County, north to the Carbon River drainage in Mount Rainier National Park, Pierce County. Sample sites were headwater seeps located in the Gifford Pinchot National Forest (administered by U. S. Forest Service) and Mount Rainier National Park (administered by National Park Service). The area has been subjected to a range of land management practices including timber harvest, protection for fish and wildlife habitat, and management for educational and recreational purposes. These lands have been affected by a variety of natural disturbances, and ranged from intact old-growth forest to areas impacted by the 1980 eruption of Mount St. Helens. Headwater seep locations ranged in elevation from 450 m to 1550 m.

The area included dense coniferous forest stands dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), western red cedar (*Thuja plicata*), and western white pine (*Pinus monticola*). Dominant shrubs included salmonberry (*Rubus spectabilis*), swamp gooseberry (*Ribes*

lacustre), stink currant (*Ribes bracteosum*), vine maple (*Acer circinatum*), sitka alder (*Alnus crispa*), and devil's club (*Oplopanax horridus*). Dominant herbaceous plants present at seeps were those primarily associated with wet habitats and included wood saxifrage (*Saxifraga mertensiana*), heart-leaved saxifrage (*S. punctata*), Alaska saxifrage (*S. ferruginea*), smooth alumroot (*Heuchera glabra*), goat's beard (*Aruncus dioicus*), tall bluebells (*Mertensia paniculata*), red columbine (*Aquilegia formosa*), Pacific bleeding heart (*Dicentra formosa*), and maidenhair fern (*Adiantum pedatum*), along with various grasses and bryophytes.

Seeps were located in the western hemlock and Pacific silver fir forest zones of the southern and central Cascade Range (Franklin and Dyrness 1973). The western hemlock zone of the southern Cascade extends from 150-1,000 m in elevation and is typified by a wet, mild, maritime climate. Precipitation occurs mainly during the winter and averages 1,500-3,000 mm per year. Summers are relatively dry with only 6-9 % of the total annual precipitation. Neither January nor July temperatures are extreme, with mean annual temperatures averaging 8-9º Celsius. The Pacific silver fir zone occurs at elevations from 900-1,300 m on the western slopes of the southern Washington Cascade Range. This zone is wetter and cooler than the adjacent western hemlock zone. It receives considerably more precipitation, often in the form of snow, which may accumulate in winter snowpacks as deep as 1-3 m. Mean annual temperatures average 5-6º Celsius. Our study included naturally occurring headwater seeps. Roadcut sites were not included due to the difficulty with assessing habitats that are highly altered by the presence of a road, which often truncate seeps unnaturally.

METHODS

Site Selection

Five naturally occurring seeps at which the salamander was known to occur prior to our study were included. It was necessary to identify additional seeps at which Van Dyke's salamander had not previously been documented. Topographic maps could not be used to

pinpoint seep locations, so we relied on local experts within the Gifford Pinchot National Forest, Mount St. Helens National Volcanic Monument and Mount Rainier National Park areas to help us locate seeps. We also used topographic maps to find relatively high gradient areas that we considered potential seep sites. Using the information from these sources, we identified possible seep locations within the range of the Van Dyke's salamander in the Cascade Range, and visited the sites to determine if they were suitable for use in our study. Suitable sites were those areas where subsurface waters were forced to the surface creating a seepage that was moist to saturated. Seep faces were often composed of bedrock, with rocky accumulation along the seep base.

Plethodon salamanders rely on moist conditions, so we focused our efforts on the wetted area of the seep. Consequently, the total area sampled between seeps varied. We placed transects along the base of the seep and parallel to the seep face. Transects were 1 m wide, and ran the entire length of the wetted area. When the wetted area of the seep extended down from the seep base >1 m, additional downslope transects were placed paralleling the original transect until the entire wetted area was covered (Figure 3.1). Subsequent down-slope transects were often not the same length as the first transect. Each transect was divided into 2 m long sampling units, where animal surveys were conducted. Habitat characteristics were measured at equidistant points along the seep face. When seeps measured 30 m or less in total length, measures were taken at 3 equidistant points along the seep face (i.e. at a seep measuring 20m in length, equidistant point measures would be recorded at 5, 10 and 15 m along the seep base). Seeps >30 m long had additional equidistant point measures proportional to the total seep length.

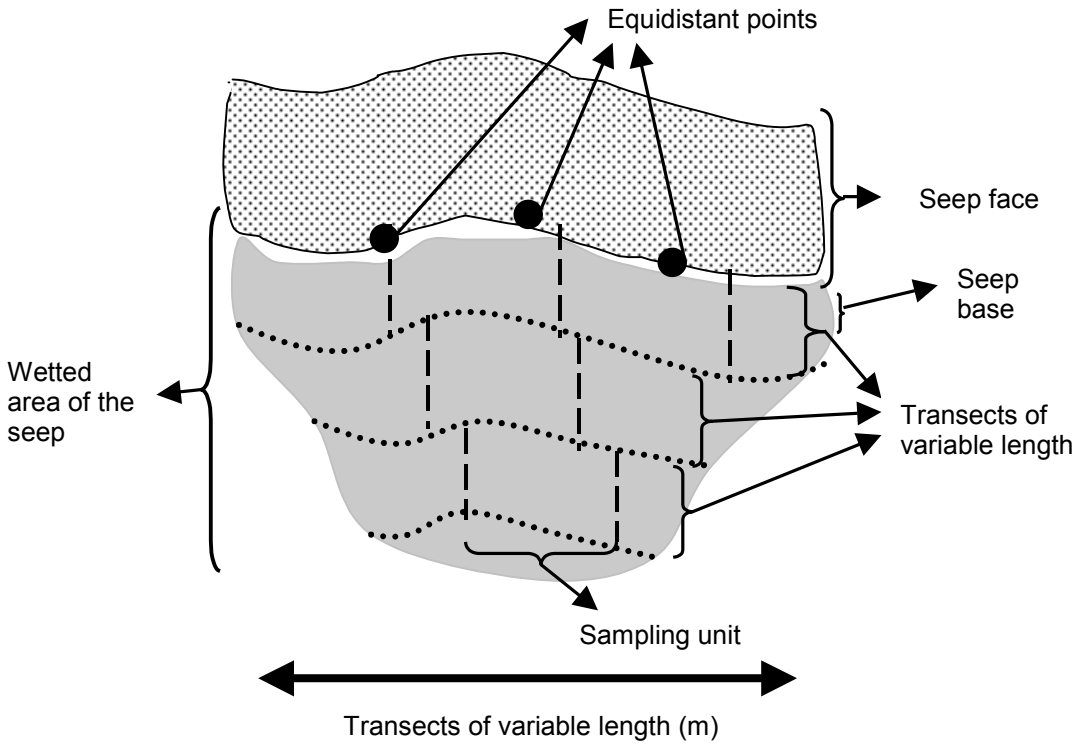

Figure 3.1. Transect design at a headwater seep surveyed for the Van Dyke's salamander. Cascade Range, Washington, 2002.

Salamander Surveys

Salamander surveys were conducted at each seep in July and August 2002. Sites were surveyed after snowmelt and rains, when conditions were favorable for the detection of Van Dyke's salamanders (Jones 1999). Animal surveys were conducted only when substrates were moist, wet, or saturated and ground temperatures had not dropped below freezing for at least the 72-hour period prior to sampling (Jones 1999). Crew members surveyed a single 1 by 2 m sampling unit at a time, turning over all available surface cover objects (e.g. rocks, wood, and bryophytes) and documenting the presence of any salamanders before moving onto the next sampling unit.

Habitat Measures

Habitat measures were recorded concurrently with animal surveys during July and August 2002. Animal surveys were conducted first, with care taken to replace all cover objects to their original position. We evaluated the habitat associations of the Van Dyke's salamander with headwall seeps at three distinct spatial scales: between seeps, within seeps, and between microhabitat sites. We recorded measures of current hydrologic condition, geomorphology, and vegetation structure.

The between seep analysis, comparing habitat characteristics for seeps where the Van Dyke's salamander was and was not detected, included several variables that were recorded once for each seep. Measures of hydrologic condition included the presence or evidence of any stream channel(s) associated with the seep (located within 10 m of the wetted area of the seep), the current hydrologic condition of those streams (dry, moist, wet, trickling, sheeting, or rushing), and the length (cm) of the seep face dominated by each hydrologic condition (same categories as above). A measure of geomorphology was the total length of the seep (m) (the length of the transect placed along the seep base) (Figure 3.1). A measure of vegetation structure was the dominant seral class in the vicinity of the seep (non-vascular, grass-forb, forb-shrub, shrub-sapling, sapling-pole, young forest, mature forest, or old-growth forest). Measures of current hydrologic conditions allowed us to assess the species association with moisture conditions. We were interested in the total length of the seep because we posit that Van Dyke's salamanders might be associated with longer seeps that provided more suitable habitat. We included a measure of vegetation structure to evaluate association with seral class. The Van Dyke's salamander is currently considered an old-growth obligate, included as a survey and manage species under the Northwest Forest Plan (USDA and USDI 1994). This provision was designed to protect species that were believed to be associated with old-growth forests, but did not receive adequate protection under the general guidelines for the Northern Spotted Owl (*Strix occidentalis caurina*). The Van Dyke's

salamander may rely on microhabitat conditions maintained by the dense over-story vegetation of old-growth forests.

The within seep analysis examined the differences between areas where the salamander did and did not occur within seeps. Habitat characteristics were measured at equidistant points along the seep face. The same measures taken at equidistant points were also recorded at points positioned at the seep base directly above each Van Dyke's salamander animal capture location. Summaries of equidistant point measures at each site were also included in the between stream analysis.

At each equidistant point we measured seep face and seep base characteristics including: total overhead cover (%), height of the seep face (m), slope of the seep face (degrees), and slope of the seep base (degrees). The total overhead cover was an ocular estimate including the cover contributed by over- and under-story canopy, and the seep face. Estimates of total overhead cover were measured by holding arms up at a 45° angle, forming a circle with outspread arms. The percentage of the circle covered was recorded. Ocular overhead cover estimates were recorded using modified Daubenmire cover classes of 0, >0-5, 6-25, 26-50, 51-75, and 76-100% (Daubenmire 1959). The height of the seep face was estimated as one of 4 classes (0-5.0, 5.1-10.0, 10.1-20.0, and >20.0 m). Seep face slope was an ocular estimate recorded as one of four classes (20-40, 41-60, 61-80, and >80 degrees). Seep base slope was measured using a clinometer, recorded to the nearest degree. We predicted that Van Dyke's salamanders would be positively associated with seep face and base characters that minimized sun and wind exposure, such as an increase in overhead cover, taller seep face, and steeper seep face.

The microhabitat site analysis focused on the difference between locations where the salamander did and did not occur and included only seeps where the Van Dyke's salamander had been detected. Square quadrats measuring 0.5 m^2 were systematically placed in the center of every 1 by 2 m sampling unit. We alternated the position of the quadrat between flush with the upslope or the downslope edge of the transect. The total number of

systematically placed quadrats varied between sites. Quadrats representing microhabitat sites in which the salamander was detected were centered on each capture location. When systematic quadrats overlapped with those centered on animal capture locations, only those around animal capture locations were included in the analysis. A single measure of hydrologic condition was the dominant hydrology within the quadrat (dry, moist, wet, trickling, sheeting, or rushing). Measures of geomorphology included the percent of the quadrat covered by substrate types (soil, sand, small gravel, large gravel, small cobble, large cobble, boulder, and bedrock). We measured vegetation structure as the percent cover of vegetation (tree, shrub, forb, bryophyte, graminoid, wood, branch, logs, and litter). We predicted that Van Dyke's salamander occurrence would be positively associated with large substrates (bedrock, boulder, large cobble, and small cobble), sheeting hydrology, and early succession vegetation.

Statistical Analysis

Resource selection models (Manly et al. 1993) compared habitat characteristics of seeps for Van Dyke's salamander occurrence at each of three spatial scales. Occurrence of Van Dyke's salamander was a binary response of detected versus not detected, and modeled using logistic regression (PROC GENMOD, SAS Institute 2000). Salamander detection was used as a surrogate measure of occurrence, with the recognition that salamanders may not have been detected at sites where they did occur. An *a priori* list of candidate models was developed at each of the three spatial scales and best approximating models for the odds of Van Dyke's salamander occurrence were selected (Burnham and Anderson 1998). Results of logistic modeling after back-transformation from odds refer to the probability of Van Dyke's salamander occurrence.

Categorical Variable Selection

Seven of the 27 habitat characteristics measured were categorical variables (e.g. measure of seep face height, where possible categories were 0-5.0, 5.1-10.0, 10.1-20.0, and >20.0 m), with some of the categorical factors having up to 8 categories. When there were more than 2 possible categories for a single measure of habitat, categories were collapsed into a single binomial independent variable in a multiple logistic regression analysis that gave the greatest deviance reduction (Tables 3.1, 3.2, and 3.3) following Ramsey et al. (1994). For example, seep face height (SEEP_FACE_HEIGHT) in the within seep analysis was collapsed into a single binomial independent variable representing seep faces that were either ≤10 or >10 m high. In the between seep analysis, we used the same deviance reduction method, except we further summarized binomial independent variables into a proportion of all equi-distant point measures within a seep. For example, SEEP_FACE_SLOPE in the between seep analysis is the proportion of equidistant point measures within a seep that have a seep face slope >60 degrees.

Table 3.1. Nine variables used in the between seep analysis of Van Dyke's salamander occurrence at seep sites located in the Cascade Range, Washington, 2002. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Hydrologic Condition	STREAM_PRESENCE	B	Presence or absence of a stream associated with them within 10 m of the seep face, where presence was an incised stream channel or evidence of scouring and/or deposition.
	STREAM_HYDROLOGY	B	Indicator of seeps that have a stream channel with a current hydrology of rushing or moist versus dry, wet, trickling, or sheeting. Moist is defined as substrate that contain water but lack beaded water on surfaces or filling small depressions; rushing as water flow that is significant and rapid; dry as substrate surfaces that lack water; wet as surfaces with water pooled in small surface depressions; trickling as visible water flowing over uneven rocky surfaces, where the unevenness of the rock causes turbulence in the flow of water; sheeting as water flow over smooth rock surfaces.
	SEEP_HYDROLOGY	C	Proportion of seep face with a dry or sheeting flow.
Geomorphology	SEEP_LENGTH	C	Total length of the wetted area along the seep base (m).
	SEEP_FACE_SLOPE	C	Proportion of equidistant point measures within a seep that have a seep face slope >60 degrees.
	SEEP_BASE_SLOPE	C	Average seep base slope within a seep (degrees).
	SEEP_FACE_HEIGHT	C	Proportion of equidistant point measures within a seep that have a seep face height of >5 m.
	TOTAL_OVERHEAD_ COVER	C	Proportion of equidistant point measures within a seep that have a total overhead cover of 0-5% (includes crown and under-story species as well as cover contributed by the seep face).
Vegetation Structure	SERAL_CLASS	B	Indicator of seeps that have a forb-shrub or mature forest seral class versus non-vascular, grass-forb, shrub-sapling, young forest, or old growth forest.

Table 3.2. Four variables used in the within seep analysis of Van Dyke's salamander occurrence at seep sites located in the Cascade Range, Washington, 2002. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Geomorphology	SEEP_FACE_SLOPE	C	Proportion of equidistant point measures within a seep that have a seep face slope >80 degrees.
	SEEP_BASE_SLOPE	C	Seep base slope (degrees).
	SEEP_FACE_HEIGHT	B	Indicator of equidistant point measures that have a seep face height >10 m versus <10m.
	TOTAL_OVERHEAD_ COVER_>25%	B	Indicator of equidistant point measures that have a total overhead cover >25% versus <25%(includes crown and under-story species as well as cover contributed by the seep face).

Table 3.3. Eighteen variables used in the microhabitat site analysis of Van Dyke's salamander occurrence at seep sites located in the Cascade Range, Washington, 2002. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Hydrologic Condition	HYDROLOGY	B	Indicator of a sheeting hydrology present within a quadrat, versus dry, moist, wet, trickling, or rushing hydrology. Hydrology categories as defined in Table 3.1.
Geomorphology	SOIL	C	Percent (%) quadrat covered with soil (e.g. mineral soil, volcanic ash, and organic soil).
	SAND	C	Percent (%) quadrat covered with sand (<2 mm in diameter, excluding soil).
	SMALL_GRAVEL	C	Percent (%) quadrat covered with small gravel (2-32 mm in diameter).
	LARGE_GRAVEL	C	Percent (%) quadrat covered with large gravel (33-64 mm in diameter).
	SMALL_COBBLE	C	Percent (%) quadrat covered with small cobble (65-128 mm in diameter).
	LARGE_COBBLE	C	Percent (%) quadrat covered with large cobble (129-256 mm in diameter).
	BOULDER	C	Percent (%) quadrat covered with boulder (>256 mm in diameter).
	BEDROCK	C	Percent (%) quadrat covered with bedrock.

Table 3.3. Eighteen variables used in the microhabitat site analysis of Van Dyke's salamander occurrence at seep sites located in the Cascade Range, Washington, 2002. Continued. Independent variables are either continuous (C) or binomial (B).

Habitat Characteristic Type	Variable	Variable Type	Definition
Vegetation Structure	SHRUB	C	Percent (%) quadrat covered with shrubs (woody plant species, non-tree).
	FORB	C	Percent (%) quadrat covered with forbs (herbaceous plant species).
	BRYOPHYTE	C	Percent (%) quadrat covered with bryophytes (moss and lichen species).
	GRAMINOID	C	Percent (%) quadrat covered with graminoids (grass species).
	LITTER	C	Percent (%) quadrat covered with litter (e.g. leaves, small twigs <30 mm in diameter, and conifer needles).
	WOOD	C	Percent (%) quadrat covered with wood (all non-round wood including bark, slabs and course woody debris).
	BRANCH	C	Percent (%) quadrat covered with branches (round wood 30-101 mm in diameter).
	LOG_1	C	Percent (%) quadrat covered with logs, size class 1 (round wood 101-500 mm in diameter).
	LOG_2	C	Percent (%) quadrat covered with logs, size class 2 (round wood >501 mm in diameter).

Model Development

Prior to analysis we developed a suite of candidate models describing Van Dyke's salamander occurrence at each of three spatial scales. Our lists of *a priori* models represent hypotheses (Burnham and Anderson, 1998) that are based on known biology of plethodontid salamanders, along with personal experience with the Van Dyke's salamander. To account for multicollinearity, variables with correlations >0.5 were not included in the same model.

We identified measures of hydrologic condition, geomorphology and vegetation structure that we felt were the most important in determining Van Dyke's salamander occurrence at each of the three spatial scales. In the between seep analysis we identified 3 measures of hydrologic condition, 3 measures of geomorphology, and a single measure of vegetation structure (Table 3.1). In the within seep analysis we identified 4 measures of geomorphology (Table 3.2). In the microhabitat site analysis we identified 1 measure of hydrologic condition, 8 measures of geomorphology, and 9 measures of vegetation structure (Table 3.3).

In the between stream analysis of hydrologic condition, we hypothesized that the odds of Van Dyke's salamander occurrence would increase with the presence of stream channels associated with seeps, streams with a currently moist or rushing hydrology, and seeps that had a greater proportion of sheeting and dry seep face hydrology. In the microhabitat site analysis, we hypothesized that the presence of sheeting hydrology within a quadrat would increase the odds of Van Dyke's occurrence.

Models that consider the influence of geomorphology on the odds of Van Dyke's salamander occurrence included seep length, seep face and base slopes, seep face height, the total overhead cover, and substrate types. We hypothesized that the odds of Van Dyke's salamander occurrence in the between and within seep analyses would increase with longer seeps, steeper seep faces, taller seep faces, and greater overhead cover. In the microhabitat site analysis, we hypothesized that an increase in the amount of large rocky substrates

(bedrock, boulder, large cobble, and small cobble) would increase the odds of Van Dyke's salamander occurrence.

The importance of vegetation structure, assessed as dominant seral class, was explored in the between seep and microhabitat site analyses. We hypothesized that abiotic factors such as dominant substrate and seep morphology would have a greater influence on the odds of Van Dyke's salamander occurrence between seeps, than biotic factors such as vegetation. In the microhabitat site analysis, models evaluated the importance of vegetation type and vegetation litter (e.g. wood, branch). We hypothesized that Van Dyke's salamander occurrence would be positively associated with the presence of early seral class vegetation (bryophytes and graminoids), and negatively associated with the presence of vegetation litter.

A priori candidate models were limited to those with no more than three variables to maintain parsimony, and to ensure biologically interpretable models. We included models involving habitat measures from more than one group (e.g. hydrologic condition and geomorphology) to explore the possibility that one or more type of habitat measure may concurrently predict Van Dyke's salamander occurrence. We developed a total of 57 candidate models for the between seep analysis (n = 39), 16 for the within seep analysis (n = 81), and 86 for the microhabitat site analysis (n = 274).

Model Selection

We used an information theoretic approach to rank *a priori* candidate models at each spatial scale. We used Bayesian Information Criterion (BIC), which tends to favor lower-dimensional models more than Akaike's Information Criterion (Schwartz 1978) and decreases the chances of non-significant variable coefficients in top models.

$$BIC = -2\ln(L) + K \cdot \ln(n)$$

Where $\ln(L)$ denotes the maximum value of the natural logarithm of the likelihood function; K is the number of estimable parameters in a given model; and n is the number of valid observations.

The best approximating model at each of the three spatial scales was the model with the minimum BIC value. Delta (Δ) BIC values were used to identify competing models. Delta BIC is a measure of the difference in BIC rank between the top and current models. Competing models with a ΔBIC <2.0 were likely to describe the given data equally as well as the top model. Models with a ΔBIC <4.0 were considered meaningful but not as descriptive as those within ΔBIC 2.0 (Burnham and Anderson 1998). We assessed model selection uncertainty among competing models by calculating posterior probabilities, or the probability of a model given the data. In the absence of a reason to believe that any single candidate model may be better than another, all prior probabilities were considered to be equal (Ramsey and Schafer, 2002). We report maximum rescaled adjusted generalized coefficients of determination ($\overline{R}^2$) as an evaluation of the proportion of the response variation explained by each model (Nagelkerke 1991).

$R^2 = 1 - \{ L(0)/ L(\hat{\beta})\}^{2/n}$, max ($R^2$) = $1 - L(0)^{2/n}$, and $\overline{R}^2 = R^2 / \max(R^2)$,

Where $L(\hat{\beta})$ and $L(0)$ denote the log likelihood of the fitted and null models, respectively.

RESULTS

During July and August 2002 we recorded Van Dyke's salamanders at 15 of 40 seeps surveyed (Figure 3.2). Thirty-two Van Dyke's salamanders were captured, with the total number detected at a seep ranging from 1 to 3 individuals. The mean number of Van Dyke's salamanders captured within the 15 seeps was 2 individuals (S.E.=0.59), and the median was 1.

Between Seep

We used 39 seeps in the between seep analysis, 14 seeps with Van Dyke's salamander detected and 25 seeps with Van Dyke's salamander not detected. One seep where Van Dyke's salamander had been previously recorded was excluded from this analysis because at the time of animal surveys and habitat characterization the seep face had dried

completely and no longer resembled a seep as defined for the purpose of this study. Nine measures of habitat were included in this analysis (Table 3.1).

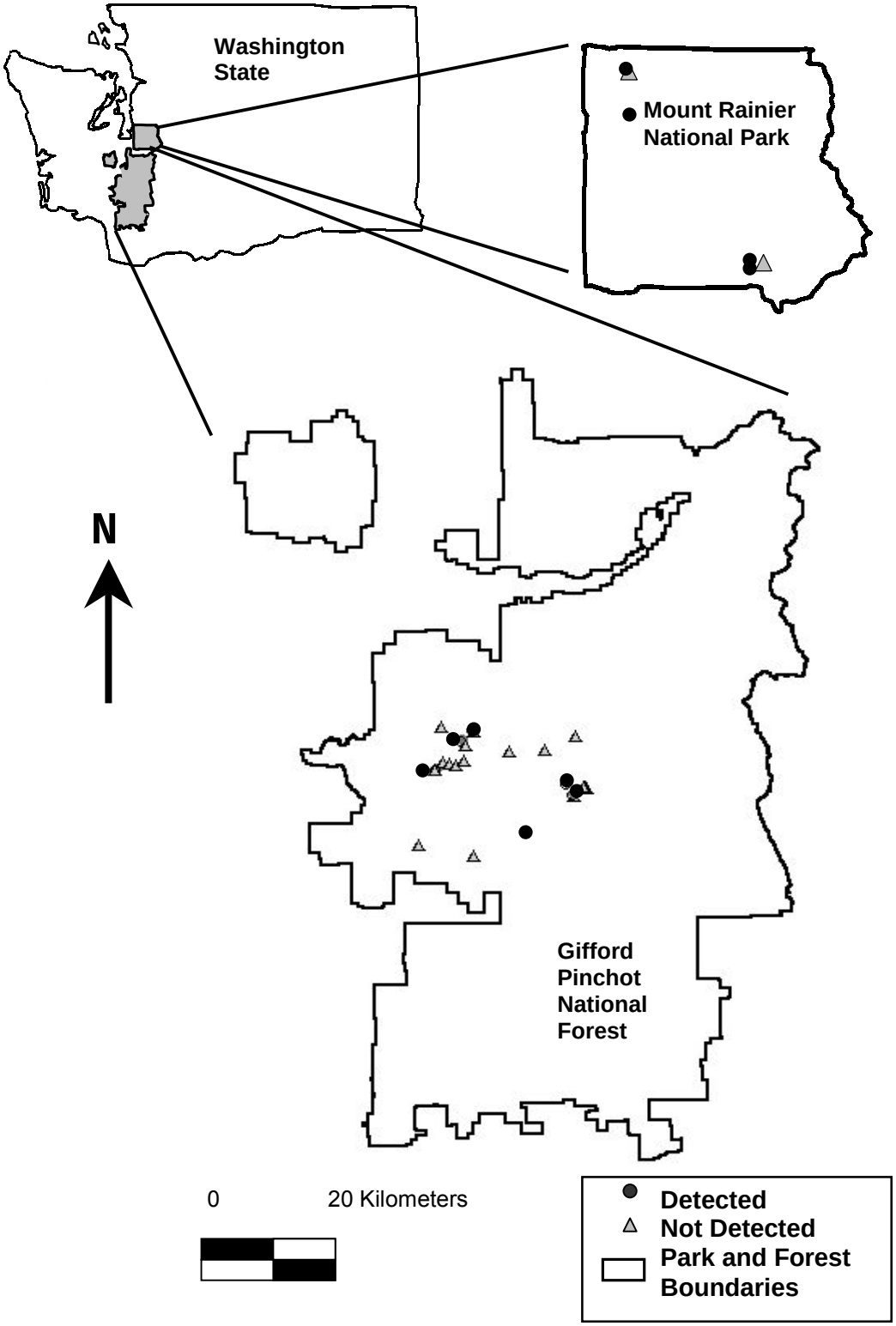

Figure 3.2. Location of seeps surveyed for the Van Dyke's salamander in the Gifford Pinchot National Forest and Mount Rainier National Park, Cascade Range, Washington, 2002. Some sites were located close enough that a single symbol represents more than one site.

The best approximating model selected using BIC and relating detection of the Van Dyke's salamander to habitat characteristics in the between seep analysis included two measures of habitat (Model {SEEP_HYDROLOGY + SEEP_FACE_HEIGHT}) (Table 3.4). The probability of Van Dyke's salamander occurrence increased as the proportion of the seep face with a dry or sheeting flow increased, and with an increase in the proportion of equidistant point measures of seep face height >5 m (Figure 3.3). A single variable model (Model {SEEP_HYDROLOGY}) was a competing model with ΔBIC 1.48 (Table 3.5). However, the top ranked model had a posterior probability of 0.621 versus 0.142 for the competing model, suggesting that the top model is more than 4 times as likely to explain the variability in the data. There were 33 models with some reasonable level of support within ΔBIC 10.0 (Burnham and Anderson 1998). We only present models within ΔBIC 4.0 (Table 3.5). Models within ΔBIC 10.0 contained only the 8 measures of seep habitat indicated by models within ΔBIC 4.0.

Table 3.4. Coefficients in best approximating models selected using BIC and fitted by logistic regression for the detection of Van Dyke's salamander in seep habitats at three spatial scales. Cascade Range, Washington, 2002. Parameter estimates are log-odds ratios of occurrence.

Variable	Parameter Estimate	S.E.	95% C.I.
Between Seep			
SEEP_HYDROLOGY	7.32	2.76	2.60, 13.61
SEEP_FACE_HEIGHT	2.64	1.41	0.32, 6.16
Within Seep			
TOTAL_OVERHEAD_COVER_>25%	-1.25	0.49	0.31, 2.23
Microhabitat Site			
SMALL_COBBLE	0.11	0.03	0.06, 0.17
SMALL_GRAVEL	0.06	0.02	0.02, 0.09
BEDROCK	0.05	0.01	0.02, 0.08

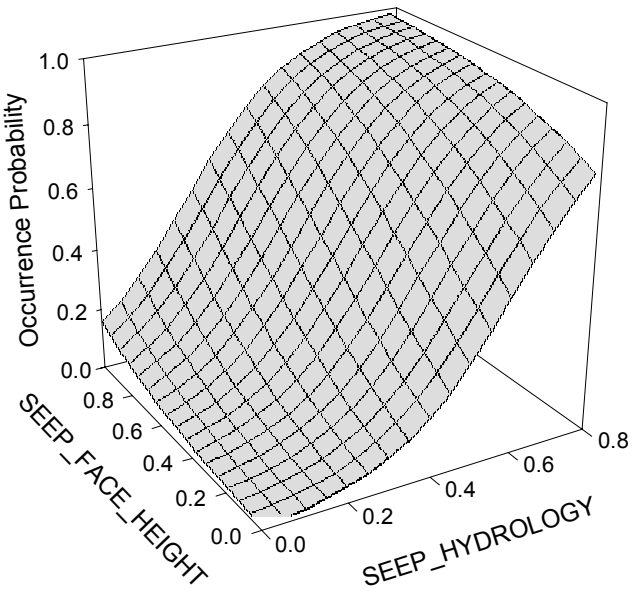

Figure 3.3. Probability of Van Dyke's salamander occurrence and two measures of habitat indicated by the best approximating model in the between seep analysis. Cascade Range, Washington, 2002. SEEP_FACE_HEIGHT is the proportion of equidistant point measures within a seep that have a seep face height >5m. SEEP_HYDROLOGY is the proportion of the seep face with a hydrology of dry or sheeting.

Table 3.5. Rankings based on BIC for *a priori* models used in the between seep analysis relating Van Dyke's salamander occurrence to habitat features in seeps. Cascade Range, Washington, 2002. (ΔBIC <4.0 and null model shown).

Rank	Model	$\ln(L)$	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
1	SEEP_HYDROLOGY + SEEP_FACE_HEIGHT	34.54	3	45.53	0.00	0.621	0.470
2	SEEP_HYDROLOGY	39.68	2	47.01	1.48	0.142	0.344
3	SEEP_HYDROLOGY + STREAM_HYDROLOGY	36.88	3	47.87	2.34	0.060	0.415
4	SEEP_HYDROLOGY + SERAL_CLASS	34.13	3	47.87	2.34	0.060	0.415
5	SEEP_HYDROLOGY + SEEP_FACE_HEIGHT + SEEP_BASE_SLOPE	34.39	4	48.79	3.25	0.024	0.480
6	SEEP_HYDROLOGY + SEEP_FACE_HEIGHT + SEEP_FACE_SLOPE	38.27	4	49.05	3.51	0.018	0.474
7	SEEP_HYDROLOGY + STREAM_PRESENCE	38.40	3	49.26	3.73	0.015	0.380
8	SEEP_HYDROLOGY + TOTAL_OVERHEAD_COVER	34.80	3	49.39	3.86	0.013	0.377
9	SEEP_HYDROLOGY + STREAM_HYDROLOGY + TOTAL_OVERHEAD_COVER	39.00	4	49.45	3.92	0.012	0.464
29	Null	50.92	1	54.58	9.05	<0.001	0.000

Within Seep

We conducted the within seep analysis using the 15 seeps at which Van Dyke's salamander occurred. There were a total of 81 equidistant point measures included in the analysis, 29 representing Van Dyke's salamander capture locations, and 52 representing systematic measures of unused habitat. Four measures of habitat were included in this analysis (Table 3.2).

The top model selected using BIC and relating the detection of Van Dyke's salamander to habitat characteristics in the within seep analysis included one measure of habitat (Model {TOTAL_OVERHEAD_COVER_>25%}) (Table 3.4). The probability of Van Dyke's salamander occurrence decreased as total overhead cover >25% increased (Figure 3.4). There were no competing models within ΔBIC 2.0 (Table 3.6).

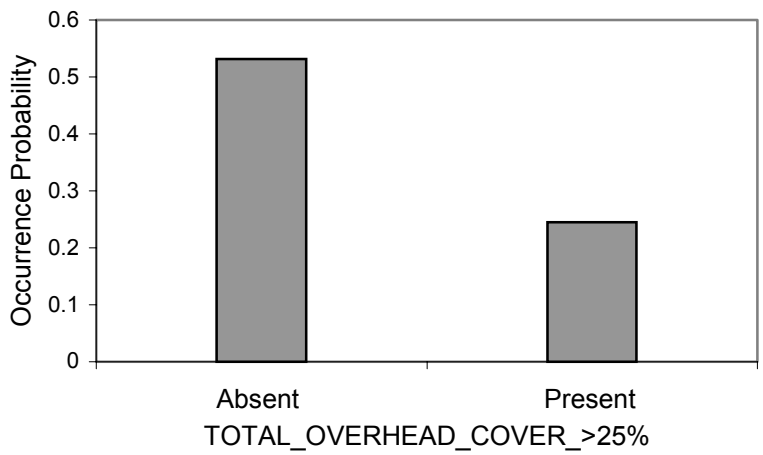

Figure 3.4. Probability of Van Dyke's salamander occurrence and the single measure of habitat indicated by the best approximating model in the within seep analysis. Cascade Range, Washington, 2002. TOTAL_OVERHEAD_COVER_>25% is a binomial indicator of equidistant point measures that have a total overhead cover >25% (includes crown and under-story species as well as cover contributed by the seep face) versus <25%.

Table 3.6. Rankings based on BIC for *a priori* models used in the within seep analysis relating Van Dyke's salamander occurrence to habitat features in seeps. Cascade Range, Washington, 2002. (ΔBIC <10.0 and null model shown).

Rank	Model	ln(L)	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
1	TOTAL_OVERHEAD_COVER_>25%	98.79	2	107.58	0.00	0.844	0.116
2	Null Model	105.67	1	110.06	2.49	0.070	0.000
3	SEEP_BASE_SLOPE	102.41	2	111.20	3.62	0.023	0.056
4	TOTAL_OVERHEAD_COVER_>25% + SEEP_FACE_SLOPE	98.14	3	111.33	3.75	0.020	0.126
5	TOTAL_OVERHEAD_COVER_>25% + SEEP_BASE_SLOPE	98.43	3	111.62	4.04	0.015	0.121
6	SEEP_FACE_HEIGHT	102.91	2	111.70	4.12	0.014	0.048
7	TOTAL_OVERHEAD_COVER_>25% + SEEP_FACE_HEIGHT	98.78	3	111.97	4.39	0.010	0.116
8	SEEP_FACE_SLOPE	104.84	2	113.63	6.05	0.002	0.015
9	SEEP_BASE_SLOPE + SEEP_FACE_HEIGHT	101.12	3	114.30	6.72	0.001	0.078
10	TOTAL_OVERHEAD_COVER_>25% + SEEP_BASE_SLOPE + SEEP_FACE_SLOPE	97.77	4	115.35	7.77	< 0.001	0.132
11	SEEP_BASE_SLOPE + SEEP_FACE_SLOPE	102.24	3	115.42	7.85	< 0.001	0.056
12	TOTAL_OVERHEAD_COVER_>25% + SEEP_FACE_SLOPE + SEEP_FACE_HEIGHT	98.14	4	115.72	8.14	< 0.001	0.126
13	SEEP_FACE_SLOPE + SEEP_FACE_HEIGHT	102.65	3	115.72	8.25	< 0.001	0.052
14	TOTAL_OVERHEAD_COVER_>25% + SEEP_BASE_SLOPE + SEEP_FACE_HEIGHT	98.43	4	116.01	8.43	< 0.001	0.121

Microhabitat Site

For the 15 seeps where the Van Dyke's salamander occurred there were a total of 274 quadrats, 28 representing microhabitat sites where the Van Dyke's salamander was detected and 246 representing microhabitat sites where the Van Dyke's salamander was not detected. Eighteen measures of habitat were included in the analysis (Table 3.3).

The top model selected using BIC and relating Van Dyke's salamander occurrence to habitat characteristics in the microhabitat site analysis included 3 measures of habitat (Model {SMALL_COBBLE + SMALL_GRAVEL + BEDROCK}) (Table 3.4). The probability of Van Dyke's salamander occurrence increased with an increase in small cobble, small gravel, and bedrock substrates (Figure 3.5). There were no competing models within ΔBIC 2.00 (Table 3.7).

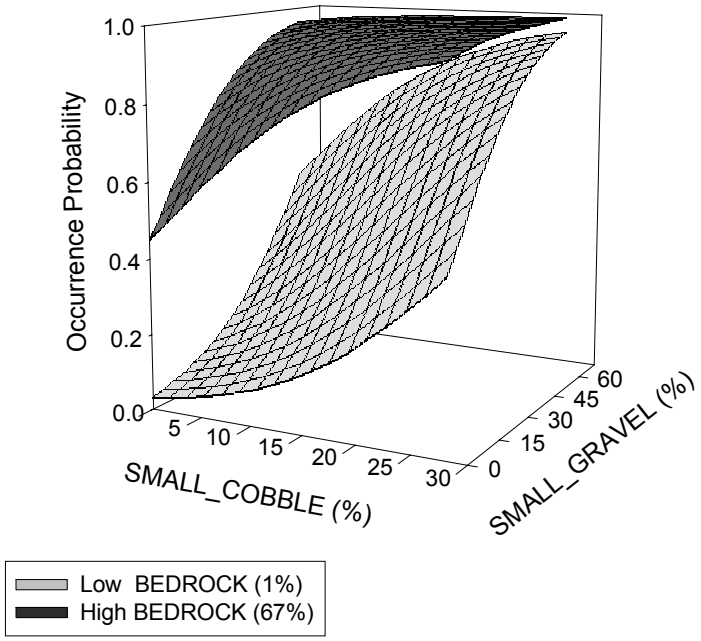

Figure 3.5. Probability of Van Dyke's salamander occurrence and three measures of habitat indicated by the best approximating model in the microhabitat site analysis. Cascade Range, Washington, 2002. SMALL_COBBLE is the percent area of a 0.5 m^2 quadrat covered by small cobble substrate (65-128 mm in diameter). SMALL_GRAVEL is the percent area of a 0.5 m^2 quadrat covered by small gravel substrate (2-32 mm in diameter). The two surfaces show maximum and minimum values of BEDROCK, which is the percent area of a 0.5 m^2 quadrat covered with bedrock (solid rock surface).

Table 3.7. Rankings based on BIC for *a priori* models used in the microhabitat site analysis relating Van Dyke's salamander occurrence to habitat features in seeps. Cascade Range, Washington, 2002. (ΔBIC <10.0 and null model shown).

Rank	Model	$\ln(L)$	K	BIC	ΔBIC	Posterior Probability	$\overline{R}^2$
1	SMALL_COBBLE + SMALL_GRAVEL + BEDROCK	151.02	4	173.48	0.00	0.969	0.213
2	SMALL_COBBLE + SMALL_GRAVEL	160.67	3	177.51	4.03	0.017	0.146
3	SMALL_COBBLE + BEDROCK	161.02	3	177.86	4.39	0.012	0.144
4	SMALL_COBBLE	169.10	2	180.32	6.85	0.001	0.086
5	SMALL_GRAVEL + BEDROCK	164.90	3	181.74	8.26	< 0.001	0.117
6	SMALL_COBBLE + SMALL_GRAVEL + HYDROLOGY	159.69	4	182.15	8.67	< 0.001	0.153
7	SMALL_COBBLE + SMALL_GRAVEL + BRYOPHYTE	160.13	4	182.58	9.10	< 0.001	0.150
8	SMALL_GRAVEL + BEDROCK + LARGE_GRAVEL	160.88	4	183.33	9.86	< 0.001	0.145
9	SMALL_COBBLE + BEDROCK + HYRDROLOGY	160.93	4	183.39	9.91	< 0.001	0.145
10	BEDROCK + LARGE_GRAVEL	166.58	3	183.42	9.94	< 0.001	0.104
23	Null Model	180.77	1	186.38	12.90	< 0.001	0.000

Since the top model in the microhabitat site analysis included three variables, we explored the possibility that there may be more variables than can be represented by a three variable model important in predicting Van Dyke's salamander occurrence at this spatial scale. Post priori forward selection was performed from the top model to see if any additional variables would be identified. Habitat characteristics chosen with forward selection, in addition to those already represented in the top model, would be considered important for predicting Van Dyke's salamander detection. Because forward selection from the top model in microhabitat site analysis did not yield additional variables, variables in the top model best explain the variability in the data.

DISCUSSION

The Van Dyke's salamander is well adapted to the unique habitat characteristics provided by seep habitats. We documented the salamander at 10 of 35 seep sites at which the salamander had never been recorded. The salamander was always found in low abundance, with no more than 3 individuals captured at a seep. We hypothesize that the rarity of the Van Dyke's salamander is largely due to a limit in suitable habitat within its range. Although we did not quantify seep density, we found that suitable seep habitats for the Van Dyke's salamander were rare on the landscape. The low mobility of the Van Dyke's salamander (McIntyre 2003) may further the rarity of this species.

Our results indicate that geomorphology and hydrology are indicative of, and possibly help to maintain, habitat conditions that predict Van Dyke's salamander occurrence at seep sites in the Cascade Range, Washington. Van Dyke's salamander occurrence was positively associated with specific hydrologic conditions in the between seep analysis. It was not the presence of dry or sheeting hydrology alone, but the combination of the two that was an indicator of Van Dyke's salamander occurrence. These conditions along the seep face and seep base are most likely indicative of a moisture gradient along the seep from driest to wettest. Sheeting hydrology probably indicates seeps that are more likely to maintain wet,

favorable conditions for plethodontid salamanders during dry summer months. Most *Plethodons* have been shown to exhibit a strong preference for moist substrates (Taub 1961, Sugalski and Claussen 1997, Moore et al. 2001), while avoiding standing water altogether (Taub 1961). However, the Coeur d'Alene salamander has been observed partially submerged in water (Wilson and Larsen 1988). A moisture gradient along the seep allows salamanders to move into areas that are wet, but not inundated with water, as seeps expand during wet periods and contract during dry periods (Ziemer and Lisle 1998).

Our results are consistent with those found in our concurrent study (McIntyre 2003), in which hydrologic conditions influenced Van Dyke's salamander occurrence along high-gradient streams in the same systems. An increase in the number of side streams, or areas of actively flowing water entering the stream channel, resulted in an increase in the probability of Van Dyke's salamander occurrence. In the same study seeps along the stream valley wall was positively associated with Van Dyke's salamander occurrence. The presence of actively flowing water provides a source of moisture for salamanders that rely on moist permeable skin in order to respire (Gatz et al. 1974). The microhabitats created by these hydrological characteristics allow *Plethodon* salamanders to absorb water directly from substrates through their permeable skin (Spotila 1972), thus preventing desiccation.

In our related study (McIntyre 2003), Van Dyke's salamander occurrence was positively associated with seep face heights >5 m. In the within stream analysis conducted by McIntyre (2003), vertical or V-shaped valley walls were important in predicting the probability of Van Dyke's salamander occurrence within streams. Just as deeply incised stream channels may insulate salamanders from seasonal differences by sheltering them within the larger landscape (Moore et al., 2001), taller seep faces may provide a more thermally stable environment, protecting Van Dyke's salamanders from sun and wind exposure. These tall seep faces may also protect salamanders from seasonal disturbances associated with increased water flows experienced during spring snowmelt and fall rains.

In the within seep analysis, Van Dyke's salamander occurrence was negatively associated with total overhead cover >25%. We hypothesized that salamanders would be associated with seeps that provide a greater protection from wind and sun exposure, and thought this would be reflected in more overhead cover. In our study of Van Dyke's salamander along streams, the correlation between salamanders and a lack of over-story tree species was attributed to geomorphology (bedrock substrates and steep valley walls) and hydrology that prevented woody vegetation from establishing. We believe that geology and hydrology characteristics that maintain exposed bedrock and steep seep faces may be responsible for a lack of over-story canopy at seep sites where Van Dyke's salamanders occur, as evidenced by a lack of soil substrates and the presence of rock accumulations that are saturated with water.

Specific substrates were important to Van Dyke's salamander occurrence in the microhabitat site analysis, specifically an increase in small cobble, small gravel, and bedrock. Similar associations were observed at larger scales among Van Dyke's salamanders in streams. McIntyre (2003) found small cobble to be important in predicting Van Dyke's salamander occurrence between capture locations along high gradient streams, and bedrock was positively associated with this species between and within streams. Small cobble and small gravel probably provide good cover objects. Exposed bedrock areas can occur where soils become thin over impermeable bedrock (Ziemer and Lisle 1998), acting as a conduit between ground and surface waters, often forming areas of the seep that remain saturated (Ziemer and Lisle 1998).

Our results indicate that geomorphology and hydrology may form the habitat characteristics on which the Van Dyke's salamander relies. The habitat characteristics that are the most important are similar in both stream and headwall seep habitats. Hydrologic conditions that allow the Van Dyke's salamander to remain moist, exposed bedrock, small cobble, and early seral class vegetation are indicative of conditions suitable for Van Dyke's salamander habitation.

Seeps may act to diffuse harsh conditions by providing hydric and thermal stability (Hynes 1970, Huheey and Brandon 1973) necessary for Van Dyke's salamander survival. Huheey and Brandon (1973) attributed use of seep habitats by the Allegheny mountain dusky salamander (*Desmognathus ochrophaeus*) to the stability of moisture and temperature that seep habitats provide. Coeur d'Alene salamanders (*P. idahoensis*) are tolerant to more severe environments where they occupy wet seep microhabitats (Wilson and Larsen 1988). Tumlison and Cline (1997) propose that seep habitats provide underground corridors to isolated sites, facilitating passage of the Oklahoma salamander (*Eurycea tynerensis*) among habitat patches through areas that would otherwise be unsuitable.

The Van Dyke's salamander is using seep habitats, as evidenced by their occupancy in seeps located within the Cascade Range of Washington. Although seeps appear to be relatively rare on the landscape, as compared to streams, it may be that they often provide the conditions necessary for Van dyke's salamander occurrence. We suggest that these seep environments are providing thermal and hydric stability, in addition to adequate amounts of cover objects. Seeps may also be a source of connectivity for the Van Dyke's salamander, facilitating movement between stream habitats. This connectivity may be important for dispersing individuals, especially over landscapes with relatively low canopy cover.

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Chapter 4

Population and Movement Estimates of the Van Dyke's Salamander (*Plethodon vandykei*) using Mark-recapture Techniques

Aimee P. McIntyre, Richard A. Schmitz, Charlie M. Crisafulli

ABSTRACT

Population parameters are particularly difficult to estimate for plethodontid salamanders as they often have extremely low capture and recapture probabilities due to their fossorial nature. Only a small number of land salamanders may be on or near the surface at any given time, resulting in heterogeneous capture probabilities among individuals. Patterns of spacing and movement of plethodontid salamanders are strongly influenced by prevailing weather conditions, and capture probabilities may be sensitive to prevailing weather patterns. The Van Dyke's salamander (*Plethodon vandykei*) is a rare land salamander endemic to Washington State. To estimate population abundances and capture probabilities of the Van Dyke's salamander, we conducted mark-recapture surveys at two high gradient streams located within the Cascade Range of Washington State, June-November 2002. One stream was located within old-growth forest and the other within the blast zone created by the 1980 eruption of Mount St. Helens. There were 10 trapping occasions at the stream within the blast zone, and 11 at the stream within old-growth forest. To estimate population size and capture probabilities of Van Dyke's salamander populations at the two sites we used the M_{th}-Chao estimator for closed populations with varying capture probabilities due to time effects and individual heterogeneity. Abundance of salamanders at the site located within the blast zone was estimated to be 458 (95% CI: 306-739), whereas abundance of salamanders at the old-growth forest site was estimated to be 100 individuals (95% CI: 61-209). Capture probabilities were extremely low ($\hat{p}$ = <0.10) for all capture occasions at both sites, with an average capture probability at the blast zone site of 0.033 (range = 0.02-0.05), and of 0.043 (range = 0.02-0.09) at the old-growth site. Most salamanders (89%) moved <2.0 m between capture events at both sites. Only 3 salamanders moved distances >2 m, the longest move equaling 33 m. Analysis of movement patterns suggested that most salamanders have small home ranges when moving on or near the surface. Individuals were recaptured under the same cover object as their initial capture 36% of the time. Our estimates of population abundances and capture probabilities for the Van Dyke's salamander at both sites suggest

that these salamanders are difficult to detect and often may not be observed at sites where they occur.

INTRODUCTION

Accurate estimates of amphibians, in particular terrestrial salamanders, may be especially difficult to obtain due to their fossorial habits and low capture probabilities. *Plethodon* salamanders lack lungs (Noble 1931) and primarily respire through their skin (Gatz et al. 1974). They have narrow physiological tolerance limits due to their respiratory requirements (Feder 1983) and must maintain moist permeable skin in order to carry out respiratory processes (Spotila 1972, Grover 2000). Plethodontid lunglessness makes them extremely sensitive to heat and desiccation (Feder 1983, Stebbins and Cohen 1995). They have relatively poor dispersal capabilities (Herrington and Larsen 1985, Sinsch 1990, Welsh and Lind 1992, Marvin 1998) and low fecundity (Stebbins and Cohen1995).

Plethodons appear to have no physiological mechanisms for controlling dehydration rates (Spotila 1972), and are only surface active during times when environmental conditions, or conditions maintained by microhabitats, are favorable. Spacing and movement patterns of plethodontid salamanders are strongly influenced by prevailing weather conditions and the availability of surface cover objects (Grover 1998). In the Pacific Northwest, they are most readily detected during spring and fall rains and spring snow melt, when humidity and soil moisture are high (Heatwole 1962, Spotila 1972, Feder 1983). The unique life history characteristics and physiological requirements of *Plethodon* salamanders may make some difficult to detect, even within suitable habitats.

The Van Dyke's salamander (*Plethodon vandykei*) is a terrestrial species endemic to Washington State. It is currently listed under the Survey and Manage provision of the Northwest Forest Plan (USDA and USDI 1994), designed to protect species believed to be associated with old-growth forests. Because it is rare and a species of concern, it is important to improve our understanding of capture probability estimates. Accurate estimations of

abundance are imperative to evaluate the status of populations, especially when we focus on species that are rare or endangered. Ultimately managers require a clear understanding of whether individual populations are increasing, stable, or possibly in decline.

The purpose of our study was to estimate population abundances of the Van Dyke's salamander over two vastly different habitats, compare capture probabilities for salamanders at the two sites, and to assess movement patterns for the Van Dyke's salamander. The Van Dyke's salamander has been documented along high gradient streams, in the splash zones of waterfalls, and in headwater seeps (Nussbaum et al. 1983, Leonard et al. 1993, Wilson et al. 1995, Jones 1999). We conducted mark-recapture surveys of the Van Dyke's salamander at two high gradient streams located within the Cascade Range of Washington State. One stream was located within an old-growth coniferous stand and the other within the blowdown zone created during the1980 eruption of Mount St. Helens. We also evaluated the ability of closed population methods in estimating population parameters for the Van Dyke's salamander, and in a more general sense, for other rare plethodontid salamanders.

STUDY AREA

We studied the Van Dyke's salamander in the southern Washington Cascade Range, on lands within the Gifford Pinchot National Forest (administered by U.S. Forest Service). Two sites that were ecologically very different were selected. They included stream sections along each of two second-order channels: Bean Creek and Clearwater Creek. The study sites are in the vicinity of Mount St. Helens and are mantled with pumice deposits of variable age, origin and thickness (Mullineaux 1996). Andesite and basalt flows dominate the area, which is characterized by ridge crests separated by steep, deeply dissected valleys (Franklin and Dyrness 1973).

Bean Creek was at an elevation of 1122 m, located within the blowdown zone created by the 1980 eruption of Mount St. Helens (Mullineaux 1996). Overstory trees present pre-eruption were either blown down or snapped off during the eruption, and understory species

were buried under a thick layer of ash (Crisafulli and Hawkins 1998). At the time of this study, the area was forb-shrub dominated. Some were noble fir (*Abies procera*) and Douglas-fir (*Pseudotsuga menziesii*) saplings were planted post eruption, and <3 m tall. Dominant shrub species were myrtle boxwood (*Pachistima myrsinites*), black huckleberry (*Vaccinium membranaceum*), swamp gooseberry (*Ribes lacustre*), sitka alder (*Alnus crispa*), and willow species (*Salix* spp.). Herbaceous plants included pearly everlasting (*Anaphalis margaritacea*), fireweed (*Epilobium angustifolium*), and broadleaf lupine (*Lupinus latifolius*).

The study site at Clearwater Creek was at an elevation of 1061 m, located within an old-growth coniferous stand, within the high tephra-fall zone of the 1980 eruption of Mount St. Helens (Mullineaux 1996). Major tree species were western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabilis*), with some western red cedar (*Thuja plicata*). The shrub species in the area included black huckleberry (*V. membranaceum*), oval-leaved blueberry (*V. ovalifolium*), Alaskan blueberry (*V. alaskaense*), and fool's huckleberry (*Menziesia ferruginea*). Major herbaceous species were sweet coltsfoot (*Petasites frigidus*) and bunchberry (*Cornus canadensis*).

METHODS

The 2 streams were selected because Van Dyke's salamanders were encountered in high enough numbers to mark a sufficient population of animals. Each site consisted of a 200-m area along the riparian corridor. In our study of Van Dyke's salamander distributions (McIntyre 2003) 81% of the Van Dyke's salamanders encountered along high-gradient streams in the Cascade Range were within 3 m of the wetted stream channel. Two transects parallel to the stream, or streamside transects, included the area from the wetted channel upslope to 3 m wide (Figure 4.1), for a total area surveyed of 1200 m^2 per site.

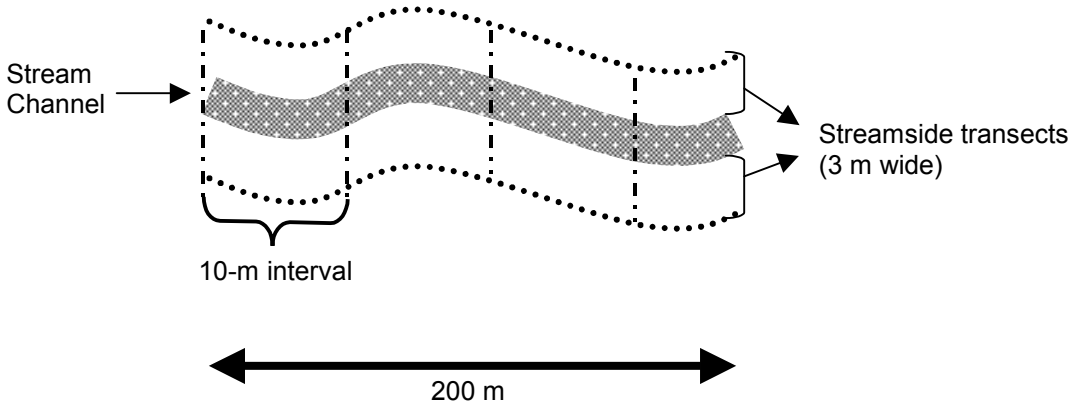


Figure 4.1. Transect layout used for Van Dyke's salamander mark-recapture study at Bean and Clearwater Creeks, Cascade Range, Washington, 2002.

Salamander Surveys

We conducted this study June-November 2002. Surveys began in the spring soon after snowmelt allowed access to the sites. Once temperatures were above freezing and surface substrates were saturated, salamanders were likely to be surface active (Jones 1999). Surveys continued into the fall until salamanders were no longer active on the surface (once temperatures began to fall below freezing) (Taub 1961, Jones 1999). On each side of the stream, the 200-m streamside transects were divided into 20 10-m segments. Crew members had a maximum of 8 minutes to completely search each 10-m segment turning cover objects such as rocks, wood, and bryophytes. Natural cover searches have been found to have lower spatial and temporal variation in capture rates for *Plethodon* salamanders than other amphibian sampling methods (Hyde and Simons 2001). When Van Dyke's salamanders were captured, we marked the exact animal capture location with a numbered flag. Each animal was given an identifying mark by clipping a unique toe or combination of toes, with no more than one toe clipped per foot. Toe regeneration was too slow to obscure marks during the 5 month duration of the study. We processed animals in <15 minutes to minimize stress and the chances of a behavioral response to capture. All animals were released at the point of

capture. Movement of recaptured individuals was calculated as the distance (cm) between capture locations. This project was approved by the Oregon State University Institutional Animal Care and Use Committee.

Estimation of Population Parameters

We used estimation methods for closed populations (Program CAPTURE, Otis et al. 1978) to analyze mark-recapture data. The basic assumptions inherent in models used to estimate abundances and capture probabilities (Otis et al. 1978) are: (1) the population is geographically and demographically closed (with no recruitments due to birth or immigration, and no losses due to death or emigration), (2) animals do not lose their marks during the course of the study, (3) all marks are correctly noted and recorded on each trapping occasion, and (4) each animal has a constant and equal probability of capture on each trapping occasion (equal catchability). Several models allow for the relaxation of the last assumption (4) allowing for variation due to time (or trapping occasion), behavioral responses to capture (where individuals may be more or less likely to be recapture after initial capture), and heterogeneity (where capture probabilities vary by individual animal) (Otis et al. 1978, White 1982).

Our strategy for analyzing mark-recapture data for the Van Dyke's salamander was as follows: (1) we ran the MODEL SELECTION procedure (in Program CAPTURE, herein referred to as model selection) to select the model that best fit the variability of the data, (2) we evaluated the chosen model to see if it was appropriate to use model selection given the estimated population parameters of the Van Dyke's salamander, and deciding that it was not, we (3) ran simulations using the SIMULATION procedure (in Program CAPTURE, herein referred to as simulations) for each model and selected the model that appeared to perform the best for populations of Van Dyke's salamanders at our sites, (4) we assessed whether the chosen model was biologically relevant considering the known biology of plethodontid salamanders, and deciding that it was not we (5) reassessed the biological relevance of each

model, and reran simulations using only those models that we considered biologically appropriate.

Model selection tests appropriateness of closed population models comparing absolute and relative fits to the data for the various models, and selects the model that most closely approximates the variability observed in capture probabilities (White et al. 1982). The use of an inappropriate model leads to biased estimates of population size, with unreasonably large or unrealistically small estimates of standard error (Otis et al. 1978, White et al. 1982, Menkens and Anderson 1988).

We used initial output from the POPULATION ESTIMATE procedure (in Program CAPTURE, herein referred to as population estimates) as a general reference for establishing hypothesized estimates of population abundances, as well as time, heterogeneity, and behavioral effects on capture probabilities, for each site. We used these estimates in simulations to assess the performance of each estimator (null, M_t-Darroch, M_t-Chao, M_b-Zippin, M_h-Jackknife, M_h-Chao, M_{tb}-Burnham, M_{th}-Chao, M_{bh}-Removal and M_{bh}-Pollock). Simulations allowed us to evaluate the relative performance of a given estimator under conditions that we specified. We specified population parameters that were representative of the preliminary results obtained with the population estimates, and assessed model performance under varying capture probabilities due to time, heterogeneity, and behavioral responses.

Each estimator was evaluated based on the percent relative bias and the percent confidence interval coverage of 1000 replications. The bias of an estimator is defined as the difference between the expected value of the estimator ($E(\hat{N})$) and the true parameter specified for the simulation (N):

Bias (B) is calculated as:

$$B = E(\hat{N}) - N$$

Percent relative bias (RB) is calculated as:

$$RB = 100\{[E(\hat{N}) - N]/N\}$$

Percent confidence interval coverage is the percent of estimated confidence intervals that include the true parameter being estimated (N).

Analysis of Movement

In the analysis of individual movements, we eliminated repeated measurements by including only the first two captures of each individual. We calculated summary statistics using S-Plus 2000 (1999) and compared movement patterns between sites.

RESULTS

Population Estimates

More than three times the number of individual animals were encountered at Bean Creek than at Clearwater Creek (Table 4.1)

Table 4.1. Van Dyke's salamander animal capture histories for mark-recapture surveys conducted at Bean and Clearwater Creeks. Cascade Range, Washington, 2002.

	No. trapping occasions (t)	No. distinct individuals (M_{t+1})	Total no. of captures (n.)	No. of recaptured individuals
Bean Creek	10	125	148	20
Clearwater Creek	11	37	47	8

Output from model selection indicated that the null model (M_o) was the most appropriate model for estimating population abundances of the Van Dyke's salamander at both Bean and Clearwater Creeks (Table 4.2).

Table 4.2. Model selection criteria results for Bean Creek and Clearwater Creek populations of Van Dyke's salamander using Program CAPTURE. Cascade Range, Washington, 2002. [M = model, and o = null, h = heterogeneity, b = behavior, and t = time. A selection criteria value of 1.00 corresponds to the most likely model].

Model	Bean Creek	Clearwater Creek
M_o	1.00	1.00
M_h	0.86	0.78
M_b	0.28	0.25
M_{bh}	0.50	0.56
M_t	0.00	0.00
M_{th}	0.50	0.15
M_{tb}	0.27	0.35
M_{tbh}	0.67	0.61

We assessed whether the use of model selection was appropriate given the estimated population parameters of the Van Dyke's salamander, by estimating population parameters for the null model (M_o) and all other models available. The M_{tb}-Burnham estimator did not estimate population parameters successfully. The numbers of animals captured or recaptured on each trapping occasion (Figures 4.2 and 4.3), and capture ($\hat{p}$) and recapture ($\hat{c}$) probabilities estimated for both sites (Table 4.3), were relatively low. The performance of the model selection decreases for populations with small capture probabilities ($\hat{p} \leq 0.10$) and population sizes ($N \leq 100$) (Otis et al. 1978, Menkens and Anderson 1988). However, closed population estimators appear to be robust to small population sizes (Menkens and Anderson 1988). So, if the correct model, or the model which most closely approximates the variability in the data, can be identified, it should provide relatively accurate estimates of population parameters for Van Dyke's salamanders at these sites. Based off of small capture probabilities and population size estimates for Van Dyke's salamanders at our sites, we decided that the use of the model selection was not appropriate.

Figure 4.2: Number of Van Dyke's salamanders captured and recaptured on each trapping occasion, for mark-recapture surveys conducted at Bean Creek. Cascade Range, Washington, 2002.

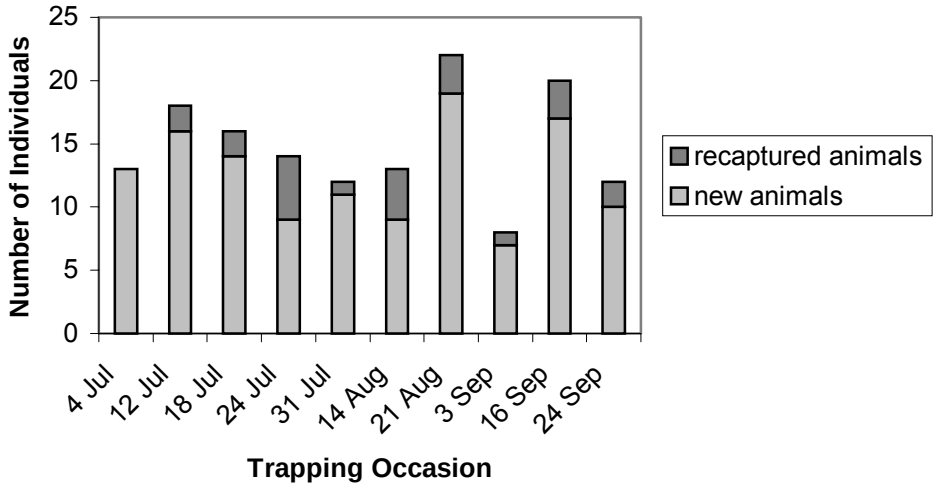


Figure 4.3. Number of Van Dyke's salamanders captured and recaptured on each trapping occasion, for mark-recapture surveys conducted at Clearwater Creek. Cascade Range, Washington, 2002.

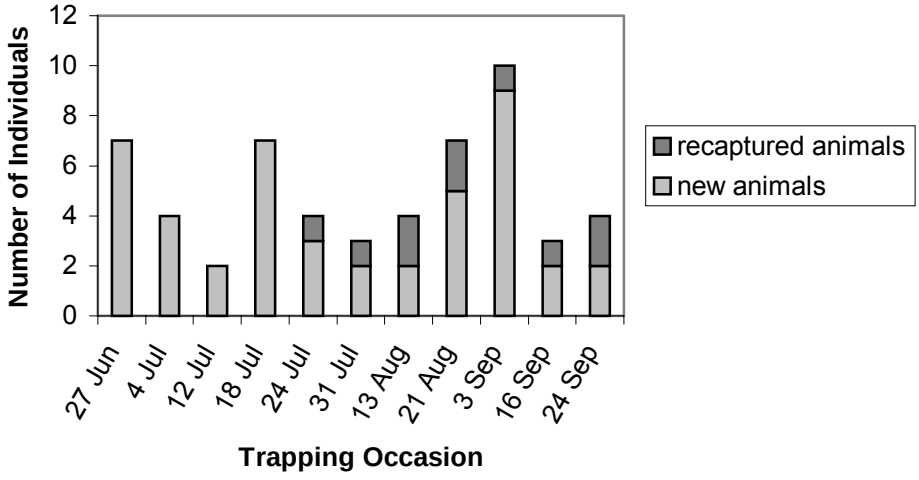
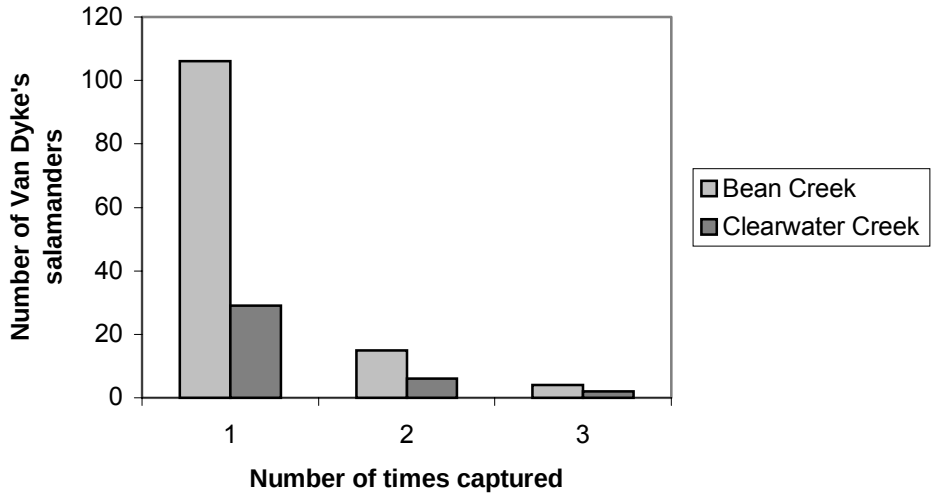


Table 4.3. Summary of output from the population estimates in Program CAPTURE for Van Dyke's salamander mark-recapture surveys at Bean and Clearwater Creeks. Cascade Range, Washington, 2002. ($\hat{p}$ = capture probability, $\hat{c}$ = recapture probability; $\hat{p}$ under M_t is the capture probability for individuals on each trapping occasion)

	Bean Creek	Clearwater Creek
$\hat{p}$ under M_o:	0.04	0.05
$\hat{p}$ under M_t:	0.03, 0.04, 0.04, 0.03, 0.03, 0.03, 0.05, 0.02, 0.05, 0.03	0.08, 0.05, 0.02, 0.08, 0.03, 0.02, 0.02, 0.06, 0.10, 0.02, 0.05
$\hat{p}$ / $\hat{c}$ under M_b:	0.02 / 0.04	0.09 / 0.05

Output from a model including time effects (M_t) suggested that there were slight variations in capture probabilities between trapping occasions at both sites (Table 4.3). The numbers of capture-recapture animals on each trapping occasion (Figures 4.2 and 4.3) and recapture frequency distributions (Figure 4.4) suggest that a small amount of heterogeneity in capture probabilities may be present in the populations at both sites, but if present is most likely minimal. There did not appear to be a distinctive seasonal trend in capture probabilities at either site. Estimated $\hat{p}$ and $\hat{c}$ from a model including behavior effects (M_b) suggested the possibility of a behavioral response to capture at both sites (Table 4.3). At Bean Creek this response appeared to be a positive response to capture (similar to the "trap-happy" response in Otis et al. 1978) where individuals were more likely to be recaptured after initial capture, while at Clearwater Creek it appeared to be a negative response (similar to the "trap-shy" response in Otis et al. 1978) where individuals were less likely to be recaptured after initial capture.

Figure 4.4. Capture frequency distribution for the Van Dyke's salamander at Bean and Clearwater Creeks. Cascade Range, Washington, 2002.



We ran a series of computer simulations using model output (M_t, M_b, and M_h) for initial conditions (Tables 4.4 and 4.5). The simulations helped us to assess the relative performance of closed population estimators for estimating population parameters similar to those exhibited by Van Dyke's salamander populations. For the simulation input, we included slight variations in capture probabilities over time, but with this time variation held constant over all trials. We assessed the performance of estimators when a population exhibited a slight heterogeneity in capture probabilities between individuals as overall capture probabilities decreased, and as the overall behavioral response increased. We used the mean $\hat{N}$ for each site in simulation inputs ($\hat{N}$ = 481 (SE = 59) for Bean Creek, $\hat{N}$ = 83 (SE = 7) for Clearwater Creek). We included the 9 models that successfully estimated population size at each site, excluding estimates from the M_{tb}-Burnham estimator.

Table 4.4. Simulation input for the Van Dyke's salamander population at Bean Creek. Cascade Range, Washington, 2002. Twelve trials assessed the performance of closed population estimators with variations in capture probabilities due to time, heterogeneity, and behavior. Number of replications = 1000. N = 500. Time held constant but time specific at 0.79, 1.32, 1.05, 1.05, 0.79, 0.79, 1.58, 0.53, 1.32, 0.79 for 10 trapping occasions (where 1.0 = no time effect, <1.0 = lower capture probability, >1.0 = greater capture probability). Behavior response was positive (where 1.0 = no behavioral response to capture, and >1.0 = positive response to capture). Heterogeneity is the capture probability of subsets of animals (with an equal number of animals allocated to each of 4 groups of 125 animals).

	Trial	Behavior Response	Heterogeneity
Behavior and heterogeneity as suggested by our data	1	2.0	0.2, 0.16, 0.12 0.08
Increasingly positive response to capture	2	1.1	0.2, 0.16, 0.12, 0.08
	3	1.4	0.2, 0.16, 0.12, 0.08
	4	1.7	0.2, 0.16, 0.12, 0.08
	5	2.0	0.2, 0.16, 0.12, 0.08
Slight heterogeneity, with decreasing capture probabilities	6	2.0	0.4, 0.36, 0.24, 0.16
	7	2.0	0.2, 0.16, 0.12, 0.08
	8	2.0	0.1, 0.08, 0.06, 0.04
	9	2.0	0.05, 0.04, 0.03, 0.02
Increasing behavior response, and heterogeneity with decreasing capture	10	1.1	0.2, 0.16, 0.12, 0.08
	11	1.4	0.1, 0.08, 0.06, 0.04
	12	1.7	0.05, 0.04, 0.03, 0.02

Table 4.5. Simulation input for the Van Dyke's salamander population at Clearwater Creek. Cascade Range, Washington, 2002. Twelve trials assessed the performance of closed population estimators with variations in capture probabilities due to time, heterogeneity and behavior. Number of replications = 1000. N = 85. Time held constant but time specific at 1.6, 1.0, 0.4, 1.6, 0.8, 0.4, 0.4, 1.2, 2.2, 0.4, 1.0 for 11 trapping occasions (where 1.0 = no time effect, < 1.0 = lower capture probability, >1.0 = greater capture probability). Behavior response was negative (where 1.0 = no behavioral response to capture, and <1.0 = negative response to capture). Heterogeneity is the capture probability of subsets of animals (with animals allocated to each of 3 groups, 28 animals in 2 groups and 29 in 1).

	Trial	Behavior Response	Heterogeneity
Behavior and heterogeneity as suggested by our data	1	0.55	0.16, 0.12, 0.08
Increasingly negative response to capture	2	1.00	0.16, 0.12, 0.08
	3	0.80	0.16, 0.12, 0.08
	4	0.60	0.16, 0.12, 0.08
	5	0.40	0.16, 0.12, 0.08
Slight heterogeneity, with decreasing capture probabilities	6	0.55	0.72, 0.48, 0.32
	7	0.55	0.36, 0.24, 0.16
	8	0.55	0.08, 0.06, 0.04
	9	0.55	0.04, 0.03, 0.02
Increasing behavior response, and heterogeneity with decreasing capture	10	0.60	0.36, 0.24, 0.16
	11	0.40	0.08, 0.06, 0.04
	12	0.20	0.04, 0.03, 0.02

Results from initial simulations indicated that the M_b-Zippin estimator performed the best when compared to the other closed population estimators, with the lowest percent relative bias and the best percent confidence interval coverage when considering all trials at both sites (Figures 4.5 and 4.6). The M_b-Zippin estimator had a negative, generally small, percent relative bias for both populations under study. Average percent relative bias across all trials for Bean Creek was –5.56% (SE = 0.56%), and for Clearwater Creek was –14.58% (SE = 4.84%). Average percent confidence interval coverage remained below the desired 95% coverage at both sites for all trials, but was relatively steady between trials. Average percent confidence interval coverage for Bean Creek was 76%, and for Clearwater Creek was 79%. The M_b-Zippin estimator appeared to perform fairly well, especially for simulations for Bean Creek populations. Percent relative bias was greatest for simulations with the smallest capture probabilities.

As evidenced by results for trials 1 through 5 at Bean and Clearwater Creeks, the M_b-Zippin estimator performed well consistently for populations that experienced an increase or decrease in capture probabilities due to a behavior response. However, when the behavioral response was extreme or capture probabilities were low, the estimator failed to perform as well. Otis et al. (1978) found that the M_b-Zippin estimator did not perform well for populations with small capture probabilities ($\hat{p}$ <0.2). Closer inspection of simulation results revealed that % confidence interval coverage had extremely large standard deviations in some cases, especially when capture probabilities were ≤0.10. These large % confidence interval coverage standard deviations explained why the confidence interval coverage appeared to be so good for simulations under the M_b-Zippin estimator. Additionally, there were failures of replications when input capture probabilities were low. Otis et al. (1978) found that failure of the M_b-Zippin estimator occurred more frequently when N was small (<100), therefore significantly reducing the value of Ave[$\hat{N}$].

Figure 4.5. Percent relative bias and percent confidence interval coverage for the M_b-Zippin estimator as exhibited by simulations in Program CAPTURE for the population of Van Dyke's salamanders at Bean Creek. Cascade Range, Washington, 2002.

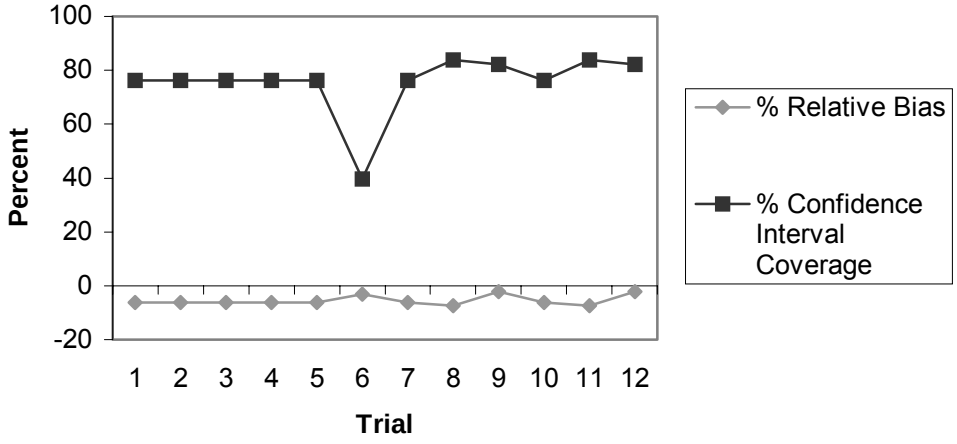
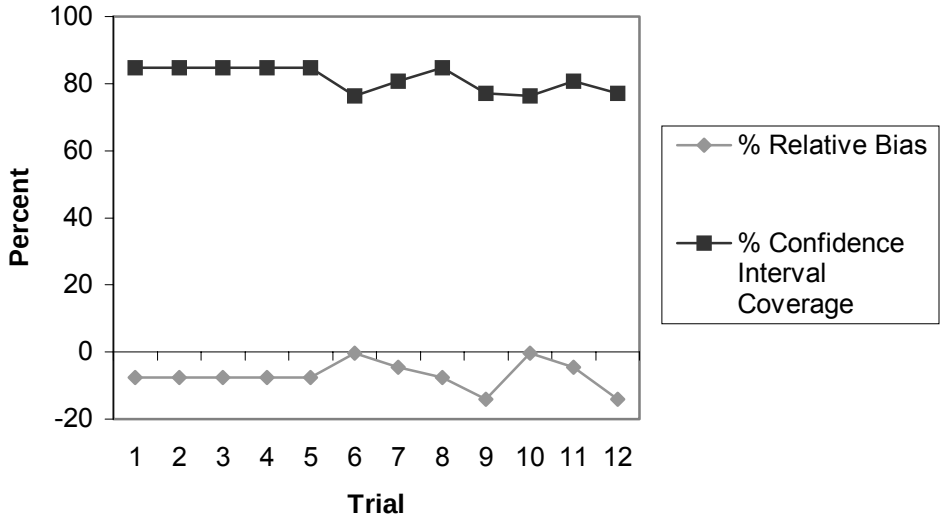


Figure 4.6. Percent relative bias and percent confidence interval coverage for the M_b-Zippin estimator as exhibited by simulations in Program CAPTURE for the population of Van Dyke's salamanders at Clearwater Creek. Cascade Range, Washington, 2002.



Otis et al. (1978) indicated that the M_b-Zippin model may not be the most appropriate estimator for populations that showed characteristics similar to the populations of Van Dyke's salamander at our two sites. Capture probabilities estimated by all models were extremely low (never above 0.1). This in itself was cause for concern with using the M_b-Zippin estimator. We reassessed how appropriate models including a behavioral response to capture were. After a closer inspection of the population estimates obtained from Program CAPTURE, and careful consideration of the biology of plethodontid salamanders, we decided there was very little evidence of a behavioral response in Van Dyke's salamanders at the two sites surveyed. Although model M_b estimated capture probabilities that varied slightly from recapture probabilities, these probabilities were so small that when a behavior response was calculated the ratio of the capture to recapture probabilities magnified the response. Differing estimates of capture probabilities under model M_b of 0.02 at Bean Creek and 0.04 at Clearwater Creek, were too small to conclude anything about the behavioral response of animals at these sites. We also felt that our survey technique (natural cover searches) and care to minimize stress on animals would act to diminish the chances of a negative behavioral response. Biologically, there was no reason to believe that Van Dyke's salamander would exhibit a positive behavior response to capture. Such responses are typically common when animals become "trap-happy" (Otis et al. 1978) (e.g. as a result of being drawn to baited traps). In the absence of a reason to believe that behavior was affecting capture probabilities, we decided to exclude models that estimate populations showing a behavioral response to capture. We chose 4 estimators considered appropriate for use with populations exhibiting variation in capture probabilities due to time effects, heterogeneity, or both. We ran additional simulations under models M_t-Chao, M_h-Chao, M_{th}-Chao, and M_t-Darroch (Tables 4.6 and 4.7). We assessed their performance when capture probabilities were extremely low, and with a small behavioral response.

Table 4.6. Simulation input for the Van Dyke's salamander population at Bean Creek. Cascade Range, Washington, 2002. Four trials assessed the performance of models M_t-Chao, M_h-Chao, M_{th}-Chao, and M_t-Darroch with variations in capture probabilities due to time, heterogeneity, and behavior. Number of replications = 1000. N = 500. Time held constant but time specific at 0.79, 1.32, 1.05, 1.05, 0.79, 0.79, 1.58, 0.53, 1.32, 0.79 for 10 trapping occasions (where 1.0 = no time effect, <1.0 = lower capture probability, >1.0 = greater capture probability). Behavior response was positive (where 1.0 = no behavioral response to capture, and <1.0 = positive response to capture). Heterogeneity is the capture probability of subsets of animals (with an equal number of animals allocated to each of 4 groups of 125 animals).

	Trial	Behavior Response	Heterogeneity
no behavior response, very little heterogeneity and low capture probabilities	13	1.0	0.1, 0.08, 0.06, 0.04
	14	1.0	0.05, 0.04, 0.03, 0.02
small behavior response, very little heterogeneity and low capture probabilities	15	1.2	0.1, 0.08, 0.06, 0.04
	16	1.2	0.05, 0.04, 0.03, 0.02

Table 4.7. Simulation input for the Van Dyke's salamander population at Clearwater Creek. Cascade Range, Washington, 2002. Four trials assessed the performance of models M_t-Chao, M_h-Chao, M_{th}-Chao, and M_t-Darroch with variations in capture probabilities due to time, behavior and heterogeneity effects. Number of replications = 1000. N = 85. Time held constant but time specific at 1.6, 1.0, 0.4, 1.6, 0.8, 0.4, 0.4, 1.2, 2.2, 0.4, 1.0 for 11 trapping occasions (where 1.0 = no time effect, < 1.0 = lower capture probability, > 1.0 = greater capture probability). Behavior response was negative (where 1.0 = no behavioral response to capture, and <1.0 = negative response to capture). Heterogeneity is the capture probability of subsets of animals (with animals allocated to each of 3 groups, 28 animals in 2 groups and 29 in 1).

	Trial	Behavior Response	Heterogeneity
no behavior response, very little heterogeneity and low capture probabilities	13	1.0	0.08, 0.06, 0.04
	14	1.0	0.04, 0.03, 0.02
small behavior response, very little heterogeneity and low capture probabilities	15	0.8	0.08, 0.06, 0.04
	16	0.8	0.04, 0.03, 0.02

Inspection of results from the second simulation exercise indicated that the 4 estimators chosen for inclusion in these simulations performed better, with general trends in percent relative bias and percent confidence interval coverage remaining generally consistent between all estimators (Figures 4.7, 4.8, 4.9, and 4.10). M_h-Chao and M_{th}-Chao appear to perform slightly better than M_t-Chao and M_t-Darroch during most simulations. Results from simulations indicate that the performance of the M_h-Chao and M_{th}-Chao were fairly similar, with negligible differences in % relative bias and % confidence interval coverage between the two estimators. Given the similarity of performance for these two models, and biological support for some changes in capture probability between trapping occasions, we chose M_{th}-Chao as the estimator that would best estimate populations of Van Dyke's salamanders at Bean and Clearwater Creeks.

Figure 4.7. Percent relative bias for the M_t-Chao, M_h-Chao, M_{th}-Chao and M_t-Darroch estimators as exhibited by simulations in Program CAPTURE for the population of Van Dyke's salamanders at Bean Creek. Cascade Range, Washington, 2002.

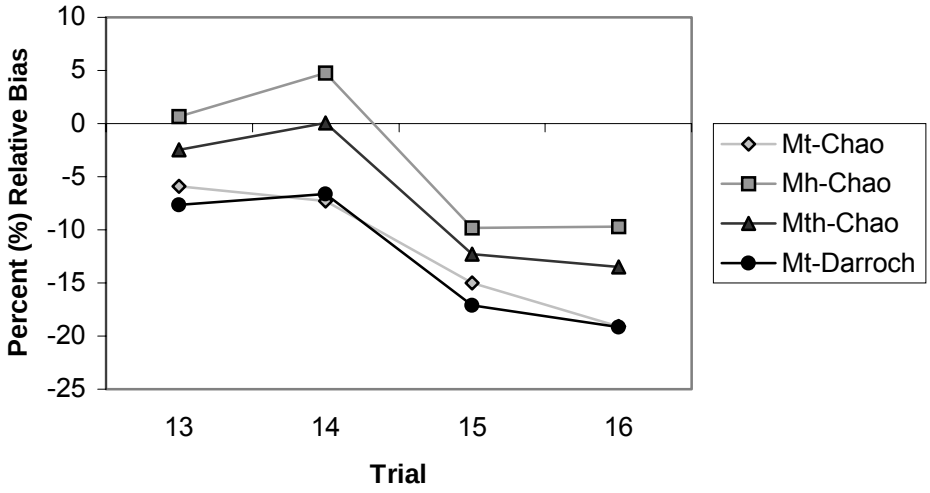


Figure 4.8. Percent confidence interval coverage for the M_t-Chao, M_h-Chao, M_{th}-Chao and M_t-Darroch estimators as exhibited by simulations in Program CAPTURE for the population of Van Dyke's salamanders at Bean Creek. Cascade Range, Washington, 2002.

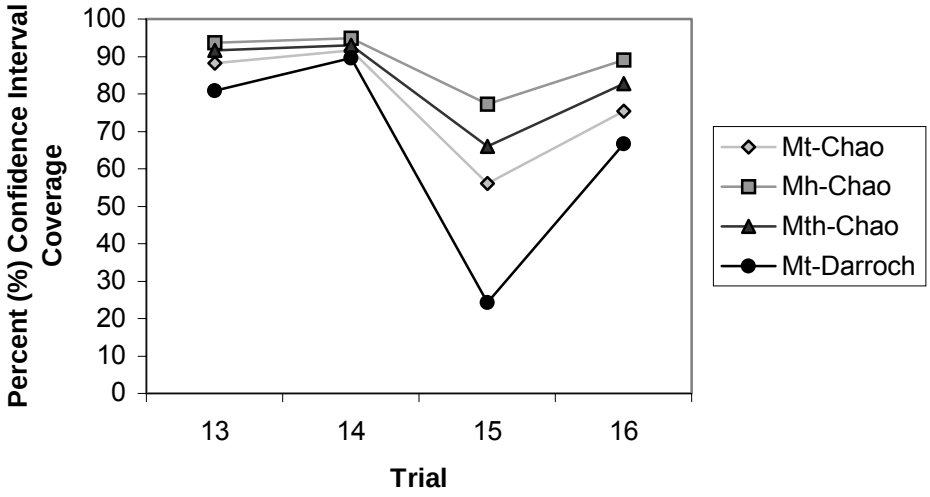


Figure 4.9. Percent relative bias for the M_t-Chao, M_h-Chao, M_{th}-Chao and M_t-Darroch estimators as exhibited by simulations in Program CAPTURE for the population of Van Dyke's salamanders at Clearwater Creek. Cascade Range, Washington, 2002.

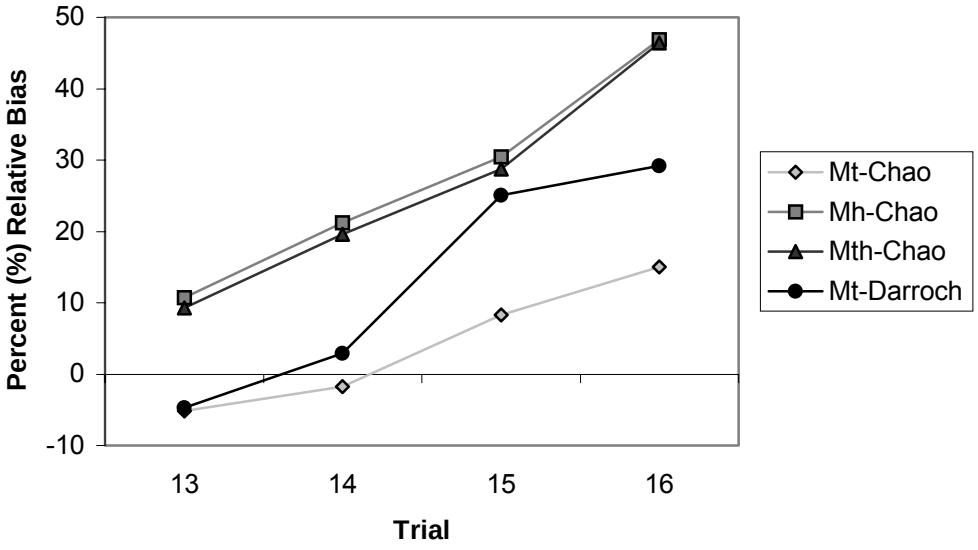
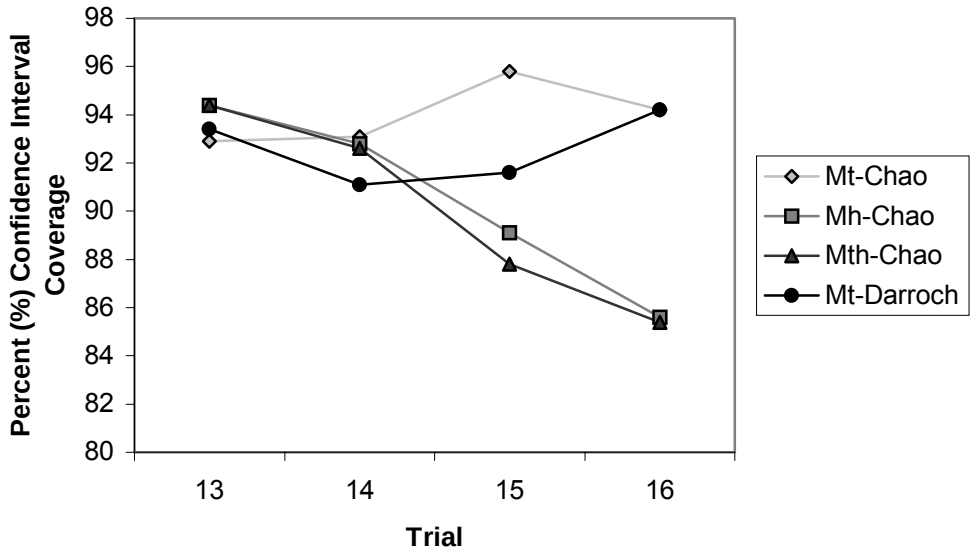


Figure 4.10. Percent confidence interval coverage for the M_t-Chao, M_h-Chao, M_{th}-Chao and M_t-Darroch estimators as exhibited by simulations in Program CAPTURE for the population of Van Dyke's salamanders at Clearwater Creek. Cascade Range, Washington, 2002.



M_{th}-Chao estimated population abundances of Van Dyke's salamanders at Bean and Clearwater Creeks to be 458 (95% CI: 306-739) and 100 individuals (95% CI: 61-209), respectively (Table 4.8), with significantly more individuals present at Bean than Clearwater Creek.

Table 4.8. Population parameters estimated for the Van Dyke's salamander using Model M_{th}-Chao in Program CAPTURE for populations at Bean and Clearwater Creeks. Cascade Range, Washington, 2002.

Site	$\hat{N}$	SE	95% CI	$\hat{p}$ for all trapping occasions
Bean Creek	458	106.75	306-739	0.03, 0.04, 0.03, 0.03, 0.03, 0.03, 0.05, 0.02, 0.04, 0.03
Clearwater Creek	100	34.70	61-209	0.07, 0.04, 0.02, 0.07, 0.03, 0.02, 0.02, 0.05, 0.09, 0.02, 0.04

Movement Patterns

Of the 125 salamanders captured at Bean Creek, 20 (16%) were recaptured at least once. Of the 37 salamanders captured at Clearwater Creek, 8 (22%) were recaptured at least once. At Bean Creek, 10 (50%) of the recaptured individuals were recaptured under the same cover object as their initial capture. The mean movement was 1.71 m (SE = 0.93 m, median = 0.27 m, range = 0.0-14.25 m, *N* = 20) at Bean Creek and 0.91 m (SE = 0.22 m, median = 0.92 m, range = 0.14-1.93, *N* = 8) at Clearwater Creek.

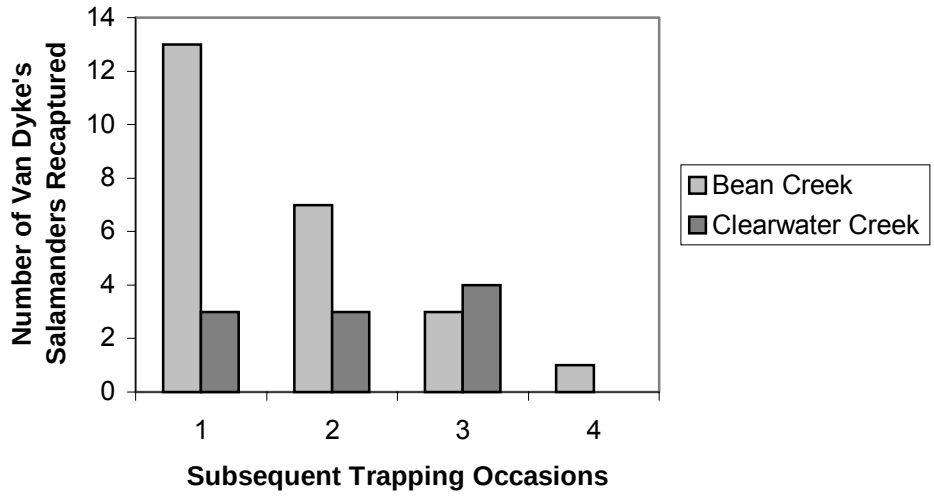
The majority of moves between capture occasions for the Van Dyke's salamander at Bean and Clearwater Creeks were <2.0 m. At Bean Creek 18 (90%) of the recaptured salamanders, and at Clearwater Creek 7 (88%) of the recaptured salamanders, moved <2.0 m between capture occasions. Considering all recapture events at Bean Creek (not just the first two captures for any individual), 2 salamanders made longer moves (>2.0 m), one salamander moving 14.25 m in an 8-day period, and the other moving 33 m in a 20-day period over 3 capture occasions. The latter animal was initially captured on one side of the stream channel,

and was recaptured on the opposite side and downstream of the original capture location 20 days later. This was the only documentation of a salamander crossing the stream channel at either site. Considering all recapture events at Clearwater Creek, we observed only one salamander that traveled >2.0 m, moving 20.85 m in a 33-day period over 3 capture occasions. Nijhuis and Kaplan (1998) found that another species of salamander with close ties to streams, the Cascade torrent salamander (*Rhyacotriton cascadae*), moved parallel to the stream channel significantly more than it moved perpendicular to the stream. The close association of Van Dyke's salamanders with stream channels, and 200 m long sampling transects, makes it unlikely that many salamanders moved off of transects throughout the course of our study.

Salamanders were more likely to be recaptured during sampling occasions closer in time to their initial capture. Among recapture salamanders at both sites, animals were always recaptured within 4 trapping occasions of their previous capture (Figure 4.11). The longest time between two successive capture occasions for any individual was 29 days at Bean Creek, and 35 days at Clearwater Creek.

The number of available cover objects at both sites was fairly similar. The mean number of cover objects turned per visit for Bean Creek was 3276 (95% CI = 2861 to 3692), and for Clearwater Creek was 3334 (95% CI = 2811 to 3857).

Figure 4.11. Number of subsequent trapping occasions between recaptures of Van Dyke's salamanders at Bean and Clearwater Creeks. Cascade Range, Washington, 2002.



DISCUSSION

Population Abundances and Movement Patterns of the Van Dyke's Salamander

There has been no previous effort to estimate population parameters for the Van Dyke's salamander. The secretive nature of land salamanders, and the influence of season and weather conditions on their detection, makes them particularly difficult to study (Jung et al. 2000). The surface activity of *Plethodon* salamanders is largely restricted to periods of rain, spring snowmelt, or high humidity (Spotila 1972, Feder 1983). Populations of Van Dyke's salamanders at both Bean and Clearwater Creeks behaved fairly similarly, with both sites exhibiting evidence of time and heterogeneity effects to capture, and low capture probabilities. There were only 3 Van Dyke's salamanders at both sites that moved distances >2 m. Other *Plethodon* salamanders have been found to have small home ranges no larger than a few square meters, and to show signs of site tenacity (Nishikawa 1990, Kramer 1993). Salamanders that find microhabitats under cover objects that can maintain favorable moisture and temperature may find it profitable to remain or return to that place frequently (Davis 2002).

Many of the salamanders observed in this study were recaptured in the exact location of initial capture. Davis (2002) observed the same phenomenon in a population of wandering salamander (*Aneides vagrans*, family Plethodontidae), as well as Taub (1961) in a population of red-backed salamander (*P. cinereus*).

Salamanders were more likely to be recaptured during a trapping occasion immediately following, or closer to, the last trapping occasion during which they were captured. Salamanders may be locating favorable microhabitats and remaining as long as conditions are stable. However, as spring run-off decreases in volume and stream levels go down, places that were favorable may become unfavorable. At this point, salamanders may be moving to new locations, again to exploit areas that are cool and moist.

Salamander capture probabilities may be influenced by the availability of cover objects at a site (Jung et al. 2000, Hyde and Simons 2001). Both of the sites included in this study appear to have similar cover object densities. The population estimate for Clearwater Creek, however, was lower than that estimated for Bean Creek. The comparable number of available cover objects and similar capture probabilities between sites suggests that salamander detection does not differ between sites. This indicates that there truly are different population abundances for each of the sites. However, other habitat characteristics such as density of underground burrows, soil moisture, and soil temperature may alter surface activities of salamanders between sites (Hyde and Simons 2001).

Estimates of abundances between the two sites differed significantly. Bean Creek is estimated to support an abundance of Van Dyke's salamanders significantly greater than the estimated abundance for Clearwater Creek. This marked difference in abundances could likely be a result of the availability of suitable habitats between the two sites. In concurrent studies (McIntyre 2003) Van Dyke's salamander occurrence both between and within sites was associated with the presence of hydrologic conditions that allow the Van Dyke's salamander to remain moist, and substrates including exposed bedrock, and small cobble. Greater population estimates for Van Dyke's salamander at Bean Creek lead us to

hypothesize that the presence of late seral class forest is not imperative for the Van Dyke's salamander, which is apparently more reliant on conditions maintained by habitats that provide thermal and hydric stability through the presence of favorable hydrological conditions and geomorphology.

Application of Closed Population Estimators

Our study illustrates the importance of simultaneously considering both the statistical tools and the biology of the organism when estimating population parameters. Life history characteristics of plethodontid salamanders, such as lunglessness and their fossorial nature, make it necessary to use models that can incorporate variability in capture probabilities, especially due to time and heterogeneity.

In the absence of biological knowledge, our data indicate that model selection and simulations may not be adequate for choosing appropriate estimators of population parameters of rare plethodontid salamanders. Estimates of population parameters are often difficult to obtain when there are not a large number of marked animals to study, and model selection is not robust when populations have extremely low capture probabilities. Estimates of capture probabilities for the Van Dyke's salamander at the two sites we investigated were extremely low (ranging from 0.02 to 0.09). Our study is not the first to estimate low capture probabilities for *Plethodon* salamanders. Welsh and Lind (1995) recaptured only 55 of 984 individually marked Del Norte salamanders (*P. elongatus*), with an average capture probability of 0.09.

Plethodon salamanders may be prone to changes in capture probability over time, heterogeneity, and behavioral response to capture. The natural history of *Plethodon* salamanders would suggest that capture probability will vary with time, as prevailing weather conditions vary (Grover 1998, Aubry 2000). Taub (1961) hypothesized that only a small number of land salamanders may be on or near the surface at any given time, and thus available for sampling. This indicates that salamanders caught on the surface may not be an

adequate or random sample of the entire population. We never recaptured individuals after more than 4 trapping occasions had passed since initial capture (Figure 4.11), indicating that salamanders may have been moving subsurface or vice versa, joining a pool of individuals either available or unavailable for capture. So, capture probabilities probably varied with heterogeneity of individuals as only certain animals were available for capture near the ground surface, while others below ground level were unavailable for capture. Finally, it is possible that some populations of plethodontid salamanders may have a behavioral response to capture. A negative response to capture (or one where animals are less likely to be recaptured after initial capture) seems the most likely, as salamanders may move post disturbance, joining others unavailable for capture below ground level. However, since recaptured salamanders were always encountered within 4 trapping occasions of the initial capture, salamanders captured during the course of our study did not appear to be immediately moving post disturbance.

When estimating population parameters for populations with small capture probabilities (<0.1) that exhibit changes in capture probabilities over time (time effects), between individuals (heterogeneity), or after initial capture (behavioral response) it is important to assess each estimator independently (beyond the application of model selection) and to consider the biology of the organism of interest. For Van Dyke's salamanders at the two study sites in the Cascade Range, the M_{th}-Chao estimator for populations exhibiting changes in capture probabilities over time and between individuals appears to be the best estimator of population parameters.

White et al. (1982) concluded that the model selection does not perform well for small population sizes unless capture probabilities are ≥0.30. Given the nature of *Plethodon* salamander populations, with generally small capture probabilities, one should apply caution when interpreting results from the model selection, especially when the population size of the species under study is small. If researchers carefully consider the biology of a species, in conjunction with output results from population estimates and simulations, we feel reasonably

certain that the correct estimator can be identified, even for populations exhibiting small capture probabilities and with small population sizes.

Conservation Implications

Surface activity of salamanders, and thus detectability, varies with landscape and weather variables such as topography, season, humidity, and climate, making them innately difficult to sample (Hyde and Simons 2001). Our estimates of population abundances for the Van Dyke's salamander, along with estimated capture probabilities at both sites, suggest that these salamanders are difficult to detect and may not be observed even where they occur. The detection of a few individuals at a site may be indicative of much larger populations. Due to the difficulty associated with observing even a single individual, the chances of not finding terrestrial salamanders at sites at which they exist is a distinct possibility (Welsh and Droege 2001). Considering its rarity, surface activities intrinsically tied to moisture and temperature conditions and nocturnal habits, it may be that the best time to conduct surveys aimed at population estimation is during periods of high rain and possibly at night.

The small movements observed for most individuals in this study imply that if human induced habitat modification occurs in areas that support Van Dyke's salamanders, dispersal of individuals to undisturbed habitats may be unlikely. Recolonization, post rehabilitation, of habitats previously used by salamanders closely associated with flowing water may be improbable (Nijhuis and Kaplan 1998). A practical strategy for conserving the Van Dyke's salamander may be the prevention of local extinctions through preservation of riparian zones.

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Chapter 5

Summary Conclusions

Van Dyke's salamander occurrence was best predicted by geological and hydrological habitat characteristics at streams and seeps within the Cascade Range of Washington, at all three spatial scales examined in our study. *Plethodon* salamanders have no physiological mechanisms to control dehydration rates, and select microhabitats that provide conditions that do not exceed their physiological tolerance limits (Spotila 1972). Models for Van Dyke's salamander occurrence at stream and seep sites indicate that deeply incised stream channels or tall seep faces, bedrock and boulder substrates, flowing water that provides a moisture gradient from dry to saturated, and rocky accumulations provide requisite conditions for this species.

Deeply incised stream channels and tall seep faces may insulate salamanders from seasonal differences by sheltering them from environmental extremes such as sun and wind exposure (Moore et al. 2001). Bedrock and boulder substrates along stream channels create splash zone areas associated with waterfall and cascade stream habitats, or force subsurface water flows to the surface forming seeps (Ziemer and Lisle 1998). These wetted areas act to diffuse harsh conditions by providing hydric and thermal stability (Hynes 1970, Huheey and Brandon 1973). The presence of a moisture gradient allows salamanders to move into areas that are adequately wet but not inundated, as seeps expand and contract during wet and dry periods (Ziemer and Lisle 1998). Finally, rocky accumulations provide a source of cover objects. Our results are consistent with the prediction that availability of cover objects can restrict the distribution and abundance of salamander species (Southerland 1986*a*).

Best approximating models at both steams and seeps included habitat variables indicative of areas with little to no overhead canopy, and the presence of grass, herb and shrub vegetation. Van Dyke's salamanders appear to be associated with microhabitats, within a broader landscape, that are incapable of supporting tree species. The presence of steep

areas of exposed bedrock, seepages that remain constantly inundated with water, and proximity to stream channel can exclude woody vegetation from areas where the Van Dyke's salamander occurs. We do not believe that there is a causal relationship between Van Dyke's salamander occurrence and the absence of woody vegetation, but rather that the relationship between salamander occurrence and herbaceous vegetation is directly linked to geological and hydrological characteristics that prevent woody species from colonizing.

Our mark-recapture efforts on the Van Dyke's salamander lend support to a growing body of evidence that indicates temporal and heterogeneity effects on capture probabilities for *Plethodons*. Temporal variation in capture probability reflects the influence that prevailing weather conditions have on plethodontid behavior and movement patterns (Spotila 1972, Feder 1983, Grover 1998). Heterogeneity in capture probabilities is most likely due to the fossorial nature of plethodontid salamanders, with some individuals being below ground and thus unavailable for capture (Taub 1961).

There is a difficulty inherent in salamander sampling due to surface activities, and consequently detectability, that varies with topography, season, humidity, climate, and other landscape variables (Hyde and Simons 2001). However, we suggest that the same physiological requirements that make plethodontid salamanders difficult to detect can be used to understand habitat characteristics influencing salamander occurrence. Our results indicate that the habitat characteristics required by the Van Dyke's salamander are closely associated with life history characteristics such as lunglessness and fossorial habits. We assert that an understanding of the physiological requirements of the Van Dyke's salamander, and other plethodontid salamanders, can aid in the understanding and prediction of habitat characteristics associated with these species.

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