56437−38, 56440. *Plectrohyla cyanomma*: MEX: OAXACA: Sierra de Juarez, 1.2 km north of crest of Cerro Pelón, UTA A-5731, 5735. *Plectrohyla mykter*: MEX: GUERRERO: Sierra Madre del Sur, 0.8 km southwest of Omilteme, UTA A-4108−11. *Plectrohyla psarosema*: MEX: OAXACA: Sierra Mixes, 5.8 km (by road) west of Totontepec, UTA A-5782 (holotype), UTA A-5771, 5776, 5783 (paratypes). *Plectrohyla sabrina*: MEX: OAXACA: Sierra de Juárez, 11.1 km south of Vista Hermosa, UTA A-52810 (paratype).

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

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Abstract.—We explored the association between Van Dyke's Salamander (*Plethodon vandykei*) and hydrologic condition, geomorphology, and vegetation structure in headwall seeps in the Cascade Range of Washington State. After conducting salamander surveys and measuring habitat characteristics at 40 seep sites from July to August of 2002, we modeled occurrence of *P. vandykei* at three site 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 for the occurrence of *P. vandykei* at the three site scales is predicted by hydrological and geological habitat characteristics. Between seeps, the probability of the occurrence of *P. vandykei* increased with increasing proportions of seep face having both dry and sheeting hydrology, and increasing proportions of seep face > 5 m high. Within seeps, the probability of the occurrence of *P. vandykei* was negatively associated with seeps where total overhead cover was > 25%. Between microhabitat sites, the probability of the occurrence of *P. vandykei* was positively associated with increases in the percent cover of small cobble, small gravel, and bedrock. *P. vandykei* appears to be associated with habitats that maintain cool thermal and hydric conditions favorable for a species that is sensitive to heat and desiccation due to physiological constraints.

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 exceptions of the Dunn's Salamander (*Plethodon dunni*) and the coeur d'Alene Salamander (*Plethodon idahoensis*; Leonard et al., 1993). *Plethodon vandykei* 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 *P. vandykei* 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 as a result of their lunglessness, making them susceptible to heat and drying (Feder, 1983; Stebbins and Cohen, 1995). Thus, they are frequently associated with cool, moist habitats.

Plethodon vandykei has been documented along high-gradient streams, in the splash zones of waterfalls, and in seeps (Nussbaum et al.,

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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). This often occurs when water percolates through coarse substrates until it reaches impermeable bedrock of a cliff face, forming what we referred to as headwall seeps (Fig. 1A).

Although habitat associations have been explored for *P. vandykei* along high-gradient streams in the southern and central Cascade Range of Washington State (McIntyre, 2003), no studies have explored the relationship of *P. vandykei* with headwall seep habitats. McIntyre (2003) found that habitat characteristics influenced by geomorphic and hydrologic conditions were indicators of the occurrence of *P. vandykei* at stream sites in the Cascade Range. The probability of the occurrence of *P. vandykei* along streams was positively associated with steep, vertical and V-shaped valley walls that lacked soil and were unable to support woody vegetation, high-gradient stream channels dominated by bedrock and boulders ($>$ 256 mm diameter), availability of small cobble (65–128 mm diameter) presumably used as cover, and the presence of valley wall seeps.

We designed this current study to assess whether the habitat characteristics that are predictive of the occurrence of *P. vandykei* at stream sites were similar to the habitat characteristics associated with the occurrence of *P. vandykei* at headwall seep sites in the Cascade Range. We developed resource selection models for *P. vandykei* in headwall seeps and assessed the influence of habitat characteristics on the occurrence of *P. vandykei* at multiple site scales: between seeps, within seeps, and microhabitat sites. *Plethodon vandykei* is rare within its range, and exploring the importance of quantifiable habitat characteristics in headwall seeps may enable us to better understand the underlying geophysical and ecological processes that determine the occurrence of *P. vandykei*.

Plethodon vandykei are difficult to detect because of their rarity and temporally restricted surface activities that are influenced by weather conditions. Habitat models provide a means for predicting suitable habitats, and can be used as a tool for narrowing the search for this species to areas that are more suitable. Although our research specifically addresses habitat modeling for *P. vandykei*, the tools that we present may be used to aid in the conservation and identification of suitable habitats for other species. These tools may prove to be particularly useful for species that share characteristics similar to *P. vandykei*, including other plethodontid salamanders, or species that are difficult to detect.

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 headwall seeps located in the Gifford Pinchot National Forest and Mount Rainier National Park. The area has been managed for multiple purposes including timber harvest, protection of ecological and geophysical conditions, research, education, and recreation. These lands have been affected by a variety of natural and anthropogenic disturbances, and ranged from old-growth coniferous forest to extensively managed young stands, and included areas impacted by the 1980 eruptions of Mount St. Helens. Headwall seep locations ranged in elevation from 450–1550 m.

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 150–1000 m in elevation and is typified by a wet, mild, maritime climate. Precipitation occurs mainly during the winter and averages 1500–3000 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 8–9°C. The Pacific silver fir zone occurs at elevations from 900–1300 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 5–6°C.

Much of the landscape supported late-seral forest 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 (*Saxifraga punctata*), Alaska saxifrage (*Saxifraga 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, sedges, and bryophytes. Our study included naturally occurring headwall seeps. Roadcut sites were not included because of the difficulty with assessing habitats that are highly altered by the presence of a road, which often truncate seeps unnaturally.

Material and Methods

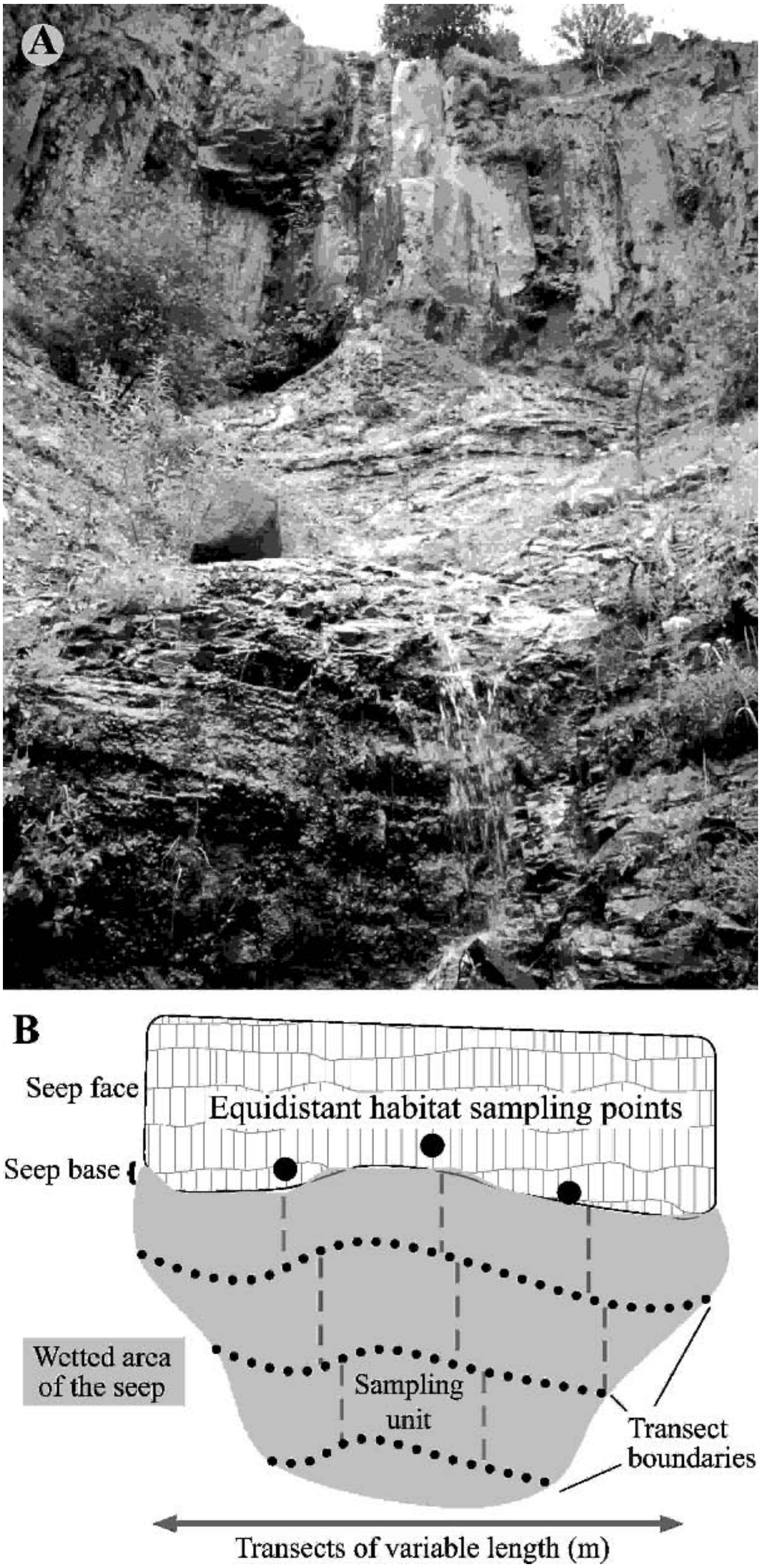
Site Selection.—Five seeps where *P. vandykei* was known to occur prior to our study were included. It was necessary to identify additional seeps where the salamander had not previously been documented to identify both undocumented seeps where the salamander was present, as well as seeps representing unoccupied habitat where the salamander was not detected. We used topographic maps and aerial photos to find high-gradient areas that were considered potential seeps. We also relied on local experts within Mount Rainier National Park to help us locate seeps. We then visited potential seep locations 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 vertical bedrock, with rocks accumulated along the base (Fig. 1A).

Because *P. vandykei* rely on moist conditions, we sampled only the wetted area of each seep. Consequently, the total area sampled among seeps varied. We placed transects along the base of the seep and parallel to the seep face (Fig. 1B). 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 parallel and contiguous with the original transect until the wetted area was covered. Subsequent down-slope transects were often not the same length as the first transect, because the wetted area tapered. 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 three equidistant points along the seep face (e.g., a 20-m seep would have equidistant point measures at 5, 10 and 15 m). Seeps > 30 m long had additional equidistant point measures, with one more equidistant point for each additional 10 m in total length (e.g., a 40-m seep would have four equidistant points).

Salamander Surveys.—Salamander surveys were conducted at each seep in July and August 2002. Sites were surveyed after snowmelt and rain, when conditions were favorable for the detection of *P. vandykei*. 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-h period prior to sampling (Jones, 1999). Transects were divided into 1 × 2 m sampling units, which were searched for salamanders by turning all available surface cover objects (e.g., rocks, wood, and bryophytes). Animal surveys were conducted immediately prior to the collection of habitat measures, with care taken to replace all cover objects to their original position.

Habitat Measures.—We recorded measures of current hydrologic condition, geomorphology, and vegetation structure. Habitat measures were recorded concurrent with animal surveys. The between-seep analysis compares habitat characteristics of seeps where *P. vandykei* was and was not detected, and included variables 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). A measure of vegetation structure was the dominant seral class in the vicinity of the seep (nonvascular, 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 *P. vandykei* might be associated with longer seeps that provided more suitable habitat. We included a measure of vegetation structure to evaluate association with seral class. *P. vandykei* is currently considered an old-growth associate, federally listed as a ''Sensitive'' species (USDA and USDI, 2004a,b).

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 *P. vandykei* animal capture location. Summaries


A
B
Seep face
Equidistant habitat sampling points
Seep base
Wetted area of the seep
Sampling unit
Transect boundaries
Transects of variable length (m)

of equidistant point measures at each site were also included in the between-seep 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 by vegetation and seep face 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 four 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°). Seep base slope was measured using a clinometer, recorded to the nearest degree. We predicted that *P. vandykei* 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 *P. vandykei* had been detected. Square quadrats measuring 0.5 m^2 were systematically placed in the center of all 1 × 2 m sampling units. 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 was based on the number of 1 × 2 m sampling units and therefore varied between sites. Quadrats representing microhabitat sites where the salamander was detected were centered on each capture location. Because we were interested in a comparison between microhabitats where the salamander was and was not detected, systematic quadrats that overlapped those centered on animal capture locations were not included in our 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 lifeform (tree, shrub, forb, bryophyte, and graminoid), wood, branch, logs, and litter. We predicted that the occurrence of *P. vandykei* 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 with the occurrence of *P. vandykei* at each of three site scales. Occurrence of *P. vandykei* was a binary response of detected versus not detected, and modeled using logistic regression (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 site scales and best approximating models for the odds of the occurrence of *P. vandykei* were selected (Burnham and Anderson, 1998). Results of logistic modeling after back-transformation from odds refer to the probability of the occurrence of *P. vandykei*.

Categorical Variable Selection.—Seven of the 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 eight categories. When there were more than two 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 1, 2, 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 equidistant point measures within a seep. For example, SEEP FACE SLOPE in the between-seep analysis is

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FIG. 1. (A) View of a headwall seep in the Cascade Range, Washington. Photo C. M. Crisafulli, (B) Transect design at a headwall seep surveyed for *Plethodon vandykei*. Cascade Range, Washington, 2002. Transects were 1 m wide; sampling units were 2 m long. Habitat characteristics were measured at equidistant points along the seep face.

TABLE 1. Variables used in the between-seep, within-seep, and microhabitat site analyses of the occurrence of *Plethodon vandykei* at seep sites located in the Cascade Range, Washington, 2002. Independent variables are either continuous (C) or binomial (B).

Analysis	Habitat characteristic	Variable	Variable type	Definition
Between seep	Hydrologic condition	STREAM PRESENCE	B	Presence or absence of a stream 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 is water flow that is significant and rapid; dry is substrate surfaces that lack water; wet is surfaces with water pooled in small surface depressions; trickling is visible water flowing over uneven rocky surfaces, where the unevenness of the rock causes turbulence in the flow of water; sheeting is water flow over smooth rock surfaces.
		SEEP HYDROLOGY	C	Proportion of seep face with both a dry and 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 $> 60^\circ$.
		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 nonvascular, grass-forb, shrub-sapling, young forest, or old growth forest.
Within seep	Geomorphology	SEEP FACE SLOPE	C	Proportion of equidistant point measures within a seep that have a seep face slope $> 80^\circ$.
		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 < 10 m.
		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).
Microhabitat site	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 for between-seep analysis.
	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).

TABLE 1. Continued.

Analysis	Habitat characteristic	Variable	Variable type	Definition
		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.
	Vegetation structure	SHRUB	C	Percent (%) quadrat covered with shrubs (woody plant species, nontree).
		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 nonround 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).

the proportion of equidistant point measures within a seep that have a seep face slope > 60°.

Model Development.—Prior to analysis we developed a suite of candidate models describing the occurrence of *P. vandykei* at each of three site 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 *P. vandykei*. To account for multicollinearity, variables with correlations > 0.5 were not included in the same model.

TABLE 2. Coefficients in best approximating models selected using BIC and fitted by logistic regression for the detection of *Plethodon vandykei* in seep habitats at three site scales. Cascade Range, Washington, 2002. Parameter estimates are log-odds ratios of occurrence.

Variable	Parameter estimate	SE	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

We identified measures of hydrologic condition, geomorphology and vegetation structure that we felt were the most important in determining occurrence of *P. vandykei* at each of the three site scales. In the between-seep analysis we identified three measures of hydrologic condition, five measures of geomorphology, and a single measure of vegetation structure (Table 1). In the within-seep analysis we identified four measures of geomorphology (Table 1). In the microhabitat site analysis we identified one measure of hydrologic condition, eight measures of geomorphology, and nine measures of vegetation structure (Table 1).

In the between seep analysis of hydrologic condition, we hypothesized that the odds of the occurrence of *P. vandykei* 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 both 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 the occurrence of *P. vandykei*.

Models that consider the influence of geomorphology on the odds of the occurrence of *P.*

TABLE 3. Rankings based on BIC for a priori models used in the between seep, within seep, and microhabitat site analyses relating the occurrence of *Plethodon vandykei* to habitat features in seeps. Cascade Range, Washington, 2002. (Meaningful models within ΔBIC 4.0 and null models shown).

Analysis	Rank	Model	ln(*L*)	K	BIC	ΔBIC	Posterior probability	$\bar{R}^2$
Between seep	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	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
Microhabitat site	1	SMALL COBBLE + SMALL GRAVEL + BEDROCK	151.02	4	173.48	0.00	0.969	0.213
	23	Null model	180.77	1	186.38	12.90	< 0.001	0.000

vandykei included seep length, seep face and base slopes, seep face height, the total overhead cover, and substrate types. We hypothesized that the odds of the occurrence of *P. vandykei* 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 the occurrence of *P. vandykei*.

The importance of vegetation structure, assessed as dominant seral class, was explored in the between-seep and microhabitat site analyses. Although *P. vandykei* is currently considered an old-growth forest obligate species, we have detected it under a range of seral classes ranging from forb-shrub dominated (in the 1980 blast area of Mount St. Helens) to old-growth forest. Thus, we hypothesized that abiotic factors such as dominant substrate and seep morphology would have a greater influence on the odds of the occurrence of *P. vandykei* 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 and branch). We hypothesized that the occurrence of *P. vandykei* 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 types of habitat measure may concurrently predict the occurrence of *P. vandykei*. 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 (Schwarz, 1978) and decreases the chances of nonsignificant variable coefficients in top models:

$$\mathrm{BIC} = -2\ln(L) + K \cdot \ln(N)$$

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 site 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 $\Delta\mathrm{BIC} < 2.0$ were likely to describe the given data equally as well as the top model. Models with a $\Delta\mathrm{BIC} < 4.0$ 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 ($\overline{\mathbf{R}}^2$) as an evaluation of the proportion of the response variation explained by each model (Nagelkerke, 1991):

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

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

$$\overline{\mathbf{R}}^2 = R^2/\max(R^2),$$

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

Results

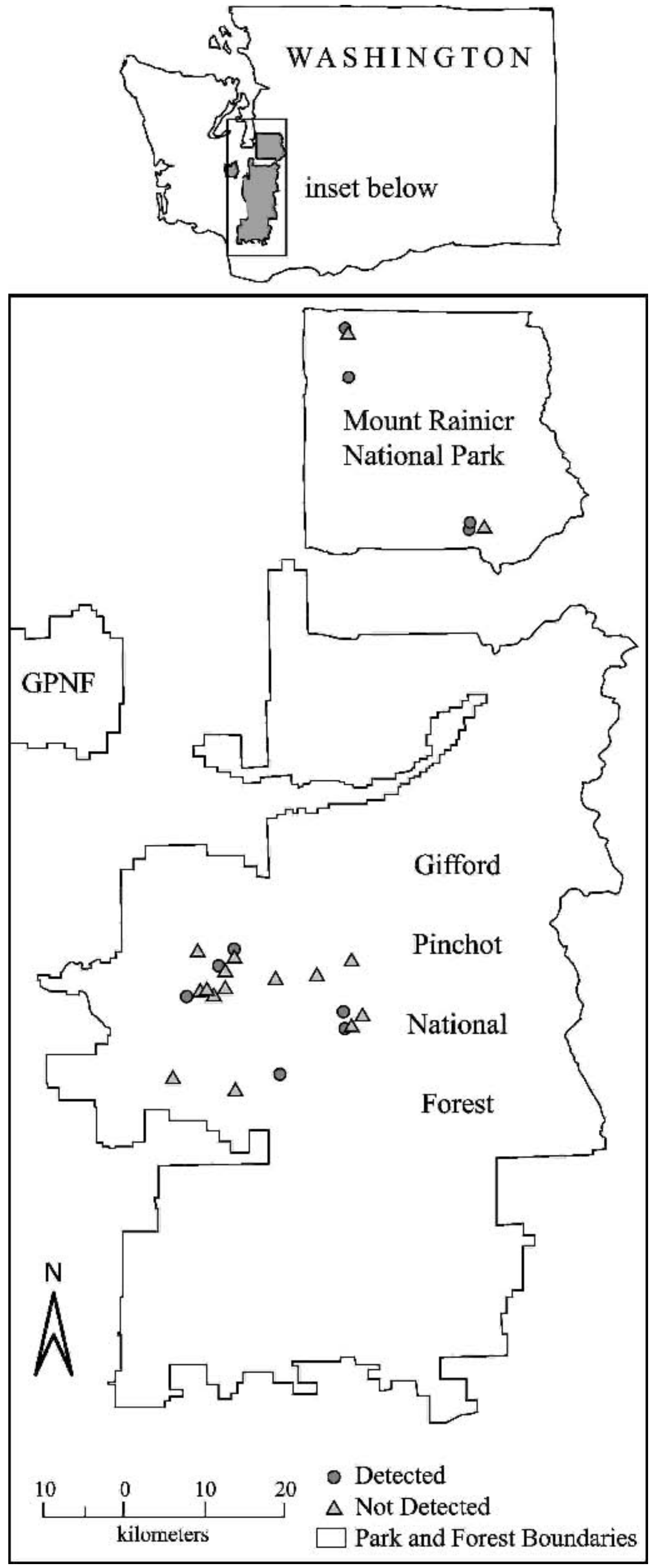
During July and August 2002 we recorded *P. vandykei* at 15 of 40 seeps surveyed (Fig. 2). We documented the salamander in 10 of 35 (28.6%) seep sites at which the salamander had never been recorded. Thirty-two *P. vandykei* were captured, with the total number detected at a seep ranging from 1–3 individuals. The mean number of *P. vandykei* captured within the 15 seeps was two individuals (SE = 0.59), and the median was 1. Only 9.6% of captured individuals were adults (with males and females reaching maturity at > 44 and 47 mm SVL, respectively [Petranka, 1998]).

Between Seep.—We used 39 seeps in the between-seep analysis, 14 seeps with *P. vandykei* detected and 25 seeps with *P. vandykei* not detected. One seep where *P. vandykei* 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 1).

The best approximating model selected using BIC and relating detection of *P. vandykei* to habitat characteristics in the between-seep analysis included two measures of habitat (Model [SEEP HYDROLOGY + SEEP FACE HEIGHT]; Table 2). The probability of the occurrence of *P. vandykei* increased as the proportion of the seep face with a dry and sheeting flow increased, and with an increase in the proportion of equidistant point measures of seep face height > 5 m (Fig. 3). A single variable model (Model [SEEP HYDROLOGY]) was a competing model with ΔBIC 1.48 (Table 3). 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 four times as likely to explain the variability in the data.

Within Seep.—We conducted the within-seep analysis using the 15 seeps at which *P. vandykei* occurred. There was a total of 81 equidistant point measures included in the analysis, 29 representing *P. vandykei* capture locations, and 52 representing systematic measures of unused habitat. Four measures of habitat were included in this analysis (Table 1).

The top model selected using BIC and relating the detection of *P. vandykei* to habitat characteristics in the within-seep analysis included one measure of habitat (Model [TOTAL OVERHEAD COVER > 25%]; Table 2). The probability of the occurrence of *P. vandykei* decreased as total overhead cover > 25% increased. When TOTAL OVERHEAD COVER > 25% was absent, the probability of occurrence of *P. vandykei* was 0.531. When TOTAL OVERHEAD COVER > 25% was present, the probability of occurrence of *P. vandykei* dropped to


WASHINGTON
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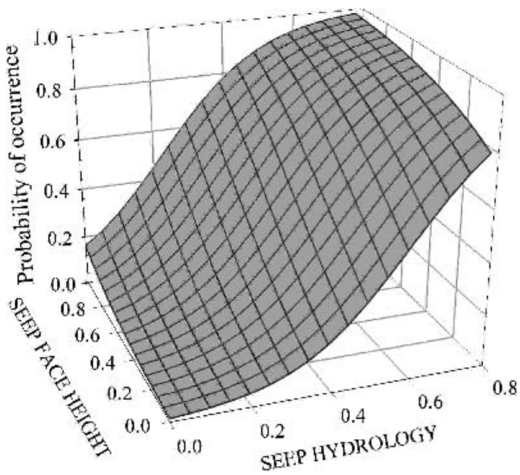

FIG. 3. Probability of the occurrence of *Plethodon vandykei* and two measures of habitat indicated by the best approximating model in the between seep analysis. Cascade Range, Washington, 2002. SEEP FACE HEIGHT is the proportion of equidistant point measures within a seep that have a seep face height > 5 m. SEEP HYDROLOGY is the proportion of the seep face with a hydrology of dry or sheeting.

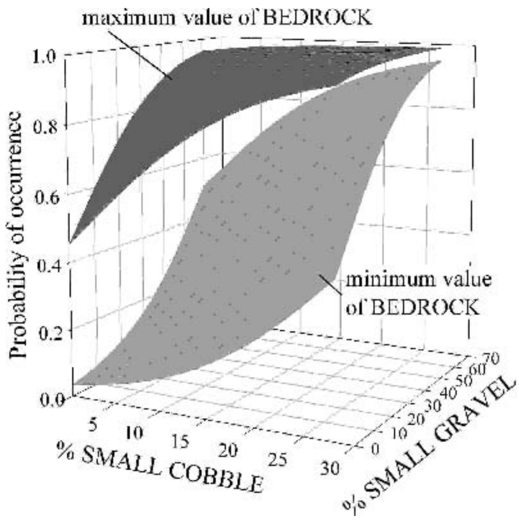

FIG. 4. Probability of the occurrence of *Plethodon vandykei* and three measures of habitat indicated by the best approximating model in the microhabitat site analysis. Cascade Range, Washington, 2002. SMALL COBBLE is the percent area of a 0.5-m^2 quadrat covered by small cobble substrate (65–128 mm 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).

0.245. There were no competing models within ΔBIC 2.0 (Table 3).

Microhabitat Site.—For the 15 seeps where *P. vandykei* occurred there was a total of 274 quadrats, 28 representing microhabitat sites where *P. vandykei* was detected and 246 representing microhabitat sites where *P. vandykei* was not detected. Eighteen measures of habitat were included in the analysis (Table 1).

The top model selected using BIC and relating the occurrence of *P. vandykei* to habitat characteristics in the microhabitat site analysis included three measures of habitat (Model [SMALL COBBLE + SMALL GRAVEL + BEDROCK]; Table 2). The probability of the occurrence of *P. vandykei* increased with an increase in small cobble, small gravel, and bedrock substrates (Fig. 4). There were no competing models within ΔBIC 2.00 (Table 3).

Because 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 the occurrence of *P. vandykei* 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 *P. vandykei* 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

Our results show that geomorphology and hydrology are indicative of, and possibly aid in the maintenance of, habitat conditions that predict the occurrence of *P. vandykei* at seep sites in the Cascade Range. Indicators of suitable habitat for *P. vandykei* included exposed bedrock, small cobble, and early seral class vegetation, in combination with hydrologic conditions that allow the salamander to remain cool and moist.

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FIG. 2. Location of seeps surveyed for *Plethodon vandykei* 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 occurrence of *P. vandykei* 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 the occurrence *P. vandykei*. These conditions along the seep face and seep base create a moisture gradient along the seep from driest to wettest. A moisture gradient along the seep allows salamanders to move into areas that are wet but not inundated with water, because seeps expand during wet periods and contract during dry periods (Ziemer and Lisle, 1998). 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, *P. idahoensis* has been observed partially submerged in water (Wilson and Larsen, 1988).

Between seeps, the occurrence of *P. vandykei* 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 the occurrence of *P. vandykei* 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 *P. vandykei* from sun and wind exposure. Tall seep faces may provide salamanders with more habitat and offer more refuge from seasonal disturbances associated with increased water flows experienced during spring snowmelt and fall rains, as well as increase the area influenced by the spray zone, further enhancing habitat.

In the within seep analysis, the occurrence of *P. vandykei* 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 *P. vandykei* along streams (McIntyre, 2003), 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 are responsible for a lack of over-story canopy at seep sites where *P. vandykei* occurs, as evidenced by a lack of soil substrates and the presence of rock accumulations that are saturated with water. The salamander was also prevalent within the 1980 blast area of Mount St. Helens, where it has survived and persisted in locations denuded by the 1980 eruption (Crisafulli et al., 2005). Seeps as defined in this study are typically characterized by cool running water and are topographically shielded from sun and wind exposure. In these habitats overstory cover is not necessary to maintain cool, moist conditions. Additionally, a thick herbaceous layer of plants often grows at the base of seeps, further ameliorating conditions that may cause desiccation.

Certain substrates were important to the occurrence of *P. vandykei* in the microhabitat site analysis, specifically an increase in small cobble, small gravel, and bedrock. Similar associations were observed at larger spatial scales among *P. vandykei* in streams. McIntyre (2003) found small cobble to be important in predicting the occurrence of *P. vandykei* between capture locations along high-gradient streams, and bedrock was positively associated with this species between and within streams. Small cobble and small gravel provide high-quality cover objects frequently utilized by *P. vandykei*. Accumulations of small cobbles may increase the amount of interstitial space important for a subterranean species (Welsh and Ollivier, 1998). Exposed bedrock helps to maintain headwall seeps by forcing subsurface flows to the surface.

Our results are consistent with those found in our concurrent study (McIntyre, 2003), in which hydrologic conditions influenced the occurrence of *P. vandykei* 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 the occurrence of *P. vandykei*. In the same study, the presence of seeps along the stream valley wall was positively associated with the occurrence of *P. vandykei*. 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.

It appears that the habitat characteristics innately present in headwall seeps are the same characteristics that *P. vandykei* is associated with in streams. The salamander is well adapted to the unique habitat characteristics provided by seep habitats. Our results indicate that *P. vandykei* may actually occupy proportionately more seeps than high-gradient streams located in the Cascade Range. We documented the salamander in 10 of 35 (28.6%) seep sites at which the salamander had never been recorded, as compared to two of 26 (7.7%) stream sites at which the salamander had never been recorded (McIntyre, 2003).

However, headwall seeps appear to be relatively rare on the landscape as compared to high-gradient streams. We hypothesize that the rarity of *P. vandykei* 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 *P. vandykei* were rare. Even so, it appears that these seeps often provide the conditions necessary for the occurrence of *P. vandykei*. We suggest that headwall seep environments are providing thermal and hydric stability, in addition to adequate amounts of cover objects.

Seeps may act to diffuse harsh conditions by providing hydric and thermal stability (Huheey and Brandon, 1973; Hynes, 1970) necessary for *P. vandykei* 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. *Plethodon 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.

Headwall seeps may be a source of connectivity for *P. vandykei*, facilitating movement between stream habitats for a species with relatively low mobility (McIntyre, 2003). This connectivity may be important for dispersing individuals, especially over landscapes with relatively low canopy cover. However, *P. vandykei* was found in low abundances at all seeps surveyed, with no more than 3 individuals captured at a seep, and adult salamanders were not often encountered (representing only 9.6% of individuals captured). A greater proportion of adult salamanders (33.7%) was found associated with streams in the Cascade Range (McIntyre, Schmitz, and Crisafulli, unpubl. data). The low number of individuals observed at seeps, in conjunction with the small proportion of adult salamanders, leads us to speculate that the ephemeral nature of some seeps may be creating habitats that are unsuitable for *P. vandykei* over longer time periods. Although *P. vandykei* may be highly adapted to habitat characteristics common in seeps, they may be unlikely to persist in seeps that are prone to seasonal drying, resulting in population sinks at these sites.

The study area is strongly influenced by volcanoes, most notably Mount St. Helens, which has had an active history of violent eruptions (Lipman and Mullineaux, 1981). 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). During this study and others (Crisafulli et al., 2005), we observed *P. vandykei* in seeps within areas severely disturbed by the 1980 eruption of Mount St. Helens. The deep tephra deposits overlying bedrock in this area makes this landscape and the hydrologic processes unique. Pumice depth and corresponding soil structure may promote a rapid downward movement of water that flows comparatively unimpeded along bedrock, emanating from valley walls as seeps. We speculate that seeps may be more common, and have different flow regimes, than in areas without tephra. Therefore, the presence and activity of volcanoes may aid in the maintenance of suitable habitat for *P. vandykei* within the Cascade Range.

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