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Strategies for Modeling Habitat Relationships of Uncommon Species: An Example Using the Siskiyou Mountains Salamander (*Plethodon stormi*)

Abstract

We analyzed environmental relationships of the Siskiyou Mountains salamander, comparing attributes at the landscape, macro- and micro-environmental scales, and the three scales combined, to determine which attributes best predicted salamander presence. Separate analyses were conducted for sites on the north and south sides of the Siskiyou Mountains which basically divide Oregon and California. We sampled 239 randomly selected sites (163 north and 76 south of the Siskiyou Crest), each in $\geq$ 5 ha of relatively homogeneous forest or post-forest (clearcut) habitat, 75 m from edge, in 7x7 m plots with $\geq$ 25 % rock cover. Measured attributes at the landscape, macro-, and micro-environmental scales totaled 230 independent variables. Subsets of 122 (North Slope) and 97 (South Slope) variables were used in hierarchical, exploratory, best subsets logistic regression, to determine the best predictors of salamander presence. We tested three analysis strategies: 1) linear relationships only; 2) linear, quadratic, and logistic relationships; and 3) linear, quadratic, and logistic relationships, and interactions among the covariates. The best models of salamander presence consisted of combined landscape, macro- and micro-environmental scale variables; included linear, quadratic, and pseudo-threshold (i.e., log) forms, and included interactions between variables. These models showed positive relationships of salamander presence with site conditions and plant assemblages characterizing old, less disturbed forest with closed canopy, moist, relatively warm microclimates, deep litter, and cobble and boulder-sized rock substrates. Our results suggest that mature to late-seral-forest attributes provide optimal habitat for the Siskiyou Mountains salamander. Stands of mature and older forests evenly distributed and interconnected across the geographical range of this species would likely best insure its long-term viability.

Introduction

One of the greatest challenges to managing for the persistence of uncommon or rare endemic species is gaining a sufficient understanding of the environmental conditions and associated habitat attributes required to sustain viable populations. The Siskiyou Mountains salamander (*Plethodon stormi* Highton and Brame 1965) is a Pacific Northwest endemic species that has a limited distribution in interior (as opposed to coastal) conifer-dominated, mixed hardwood forests in extreme southwestern Oregon and northwestern California. It is only known to occur in Jackson and Josephine counties, Oregon, and northwestern Siskiyou County, California.

The Siskiyou Mountains salamander is a California state "threatened species" and is listed as "sensitive" (critical) by the state of Oregon (Marshall et al. 1992). In 1994, the Siskiyou Mountains salamander was identified as one of five amphibian species requiring protection under the Northwest Forest Plan (USDA et al. 1994). It was recently proposed for listing under the Federal Endangered Species Act, but listing was found to be unwarranted at this time by the U.S. Fish and Wildlife Service. Development of strategies for management and conservation of this species requires a thorough understanding of environmental requirements, with particular emphasis on critical habitats and areas most affected by current and future land management.

Little information exists regarding the environmental requirements or habitat associations of this salamander. Past studies mostly focused

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on sampling along main roads (e.g., Highton and Brame 1965, Brodie 1970, Bury 1973) and, thus, surveys included only a few forest types and elevations 490 to1100 m (e.g., Highton and Brame 1965). Recent surveys have expanded the upper limit of this salamander to ~1800 m (Clayton et al. 1999). Today, information on the habitat requirements of this species is incomplete and conflicting. General studies indicate that populations of the Siskiyou Mountains salamander are found in close association with surface rock (Stebbins 1985, Herrington 1988, Blaustein et al. 1995). Nussbaum et al. (1983) reported they are associated with talus, with thin or absent litter, and Stebbins (1985) described habitat as blanketed in leaf litter from deciduous trees with moss present. More significant to land managers is their reputed association with older, mature, to late-seral forest (Ollivier et al. 2001, Bury and Welsh 2005). In the absence of more thorough information on specific habitat associations of the Siskiyou Mountains salamander, management for this species has been based on habitat models derived for a closely related species, the Del Norte salamander (*Plethodon elongatus*) (Welsh and Lind 1995, see also Welsh et al. 2006). However, the Del Norte salamander occurs closer to the marine-influenced coast, and has a broader latitudinal range compared with the Siskiyou Mountains salamander. Thus, these two sibling species may demonstrate differences in environmental associations and related distributional limitations.

Welsh and Lind (1995) used an extensive sampling approach designed to determine the "Grinellian" niche of the Del Norte salamander. This approach measures species response (e.g., detected or not) along likely important environmental gradients across the range of a species to discern limits (if any) along each gradient; these limits then define the niche dimensions (*sensu* James et al. 1984) (see Guisan and Thuiller [2005] for a critique of the niche concept). We employed this approach here with the Siskiyou Mountains salamander.

Our objective was to elucidate key environmental relationships of this salamander at multiple spatial scales, including landscape-level attributes, macro-environmental aspects of forest stand structure and plant community composition, and micro-environmental aspects such as microclimate and substrate associations. Further, we maximized model accuracy by assessing each variable's linear, quadratic, and logistic relationships; and by allowing interactions among the covariates.

Methods

Sampling occurred between 8 March 1995 and 27 June 1998, under specific weather conditions of high relative humidity and low temperatures (see below). We sampled 239 sites within the known historic range (Highton and Brame 1965, Brodie 1970, Bury 1973) and recent unpublished surveys. The upper elevation limit for the species had been reported to be 1100 m (Nussbaum 1974, Nussbaum et al. 1983, Stebbins 1985), but recent surveys found salamanders up to 1800 m (Clayton et al. 1999), so no upper elevation limit was imposed on site selection.

Site Selection

To distribute sampling across the range of the Siskiyou Mountains salamander, and derive results with the broadest possible application, we selected sites using a hierarchical multi-stage random sampling design with four nested levels as the most efficient, cost-effective method of site selection that would allow our sampling to capture the full range of each independent variable available within the range of this species (*sensu* James et al. 1984):

(1) Biogeographic, which spanned the entire range of the species, without limits on parent geology or forest type and sample sites occurred within drainages of the Klamath, Scott and Upper Applegate rivers on both public and private lands (Figure 1).

(2) Sites were randomly selected from a systematic grid across the species' range based on the U.S. Geological Survey (USGS) township and range system. Due to the small range of this species and to insure sufficient samples, all townships within the range were sampled. Within townships, 4 of the 36 one mi^2 (2.59 km^2) sections were chosen randomly. Sections with large inaccessible areas such as un-roaded wilderness requiring more than a day to access were omitted on logistical grounds and replaced by the random selection of another section. Sections lacking forest with appropriate rocky microhabitat (see below) were replaced by random selection from the eight surrounding sections.

3) Forest seral stage was designed to include sites from across the available seral continuum.

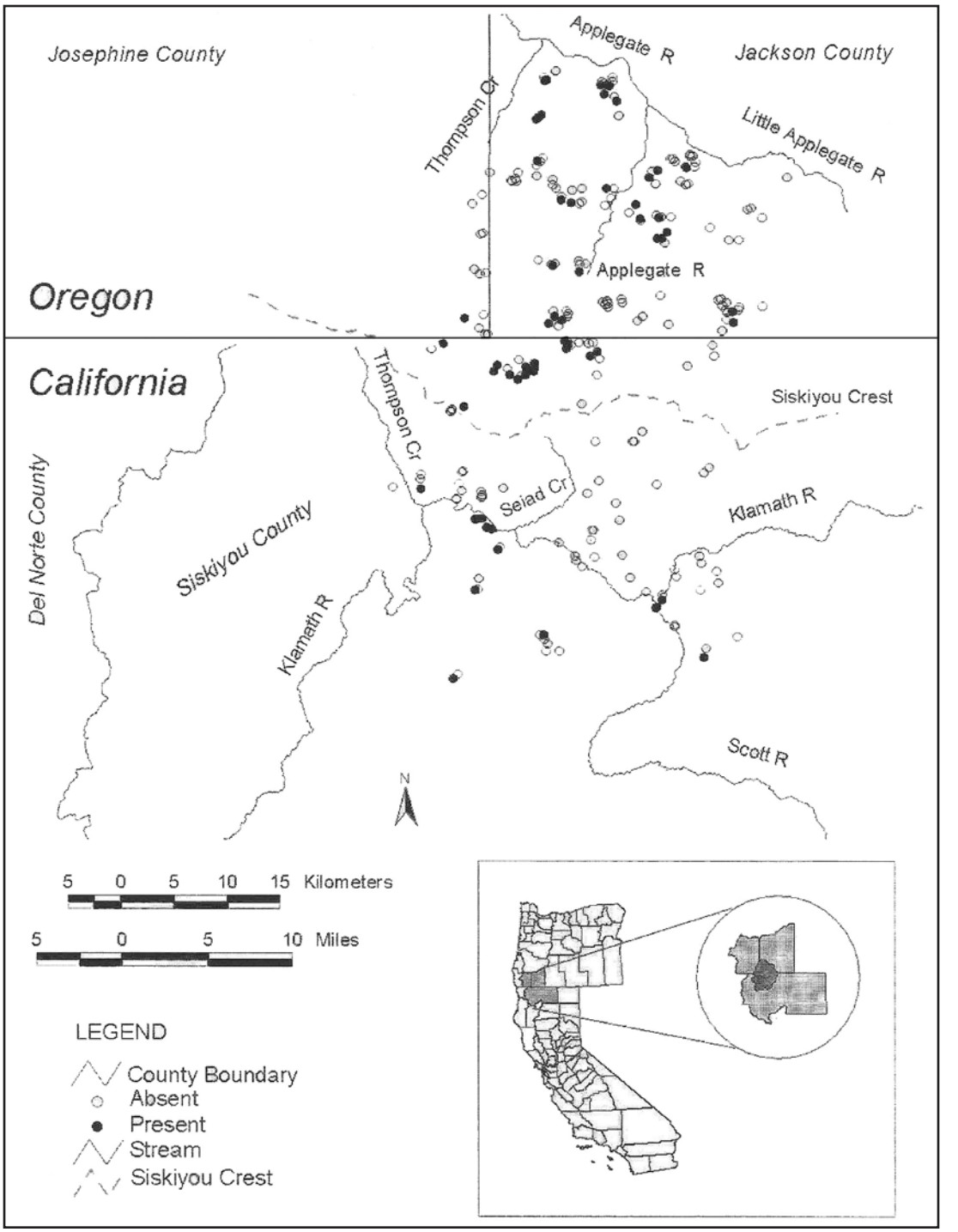

Figure 1. Location of sites sampled for the Siskiyou Mountains salamander (*Plethodon stormi*). Environmental attributes for sites on either side of the Siskiyou Crest (dashed line) were analyzed separately to model the habitat associations of the Siskiyou Mountains salamander. Solid circles indicate sites with salamander detections, open circles indicate sites with no detections.

Within each section we located with aerial photographs and ground reconnaissance, at least one, and where possible up to four, sites (one in each age class), representative of each of four seral stages: pre-canopy or clearcut (0-30 yrs), young forest (31-99 yrs), mature (100-199 yrs), and old-growth (200 + yrs) (Franklin et al. 1986, Franklin and Spies 1991). Sample plots were located in forested or clearcut sites between 5-7 ha in size with relatively uniform tree species composition and tree (or stump) size class distribution. Site visits were necessary to assess the possibility of finding potential sampling plots therein using the criterion "presence of appropriate microhabitat" (see below). Sites were not selected if disturbance (e.g., timber harvest or fire) had occurred within the last two years. Because the independent variables measured were selected to describe relatively homogeneous 5-7 ha areas, our design required that salamander sampling plots (see below) be surrounded by contiguous vegetation of relatively uniform age, structure and composition so all animal sampling plots were > 75 m from edges.

4) Minimum essential microhabitat involved the actual placement of search plots at the selected sites. Because this species was already known to be rock-associated (Herrington 1988, Leonard et al. 1993), final site selection was based on the presence of rocky substrates. Rocky substrates were classified as containing chert, slate, shale, or schist. The salamander sample plot had to contain at least some cobble-size pieces (>64 mm diameter on the short axis). This insured that at least some rock large enough to provide cover for salamanders was available. Once it was determined by visual inspection that a site contained such substrates, a plot center was established in the area of greatest rock concentration. Plots were 7x7 m with at least 25% rock; including rock covered by litter or other debris which was easily discernable. While the Siskiyou Mountains salamander may occur in areas with less rock cover, we attempted to maximize detectability by focusing on areas likely to yield sufficient captures to maximize the power of our analysis to detect additional environmental relationships. It was our intent to define habitat where resident populations might be expected to occur in numbers sufficient to be ecologically functional (Conner 1988, Davic and Welsh 2004) rather than to determine the outer extremes of their potential distribution.

Salamander Sampling

We used area-constrained searches (ACS; Welsh 1987, Bury and Corn 1990) during daylight (0800 to 1800 h), with a single visit to each site. One or more workers conducted a thorough search of surface cover in each 49-m^2 sample plot, systematically searching each site for adult, sub-adult, and juvenile salamanders (age classes based on snout to vent length after Ollivier and Welsh 2003). All cover objects were turned, and finer substrates carefully hand-sifted, down to 15 cm. Surface rock deposits with large interstitial spaces and little interstitial fill tended to make captures more difficult. However, detections in this type of microhabitat were possible with alert field crews, and salamanders observed escaping were counted.

Given the potential for high variability in the detection of plethodontid salamanders (Hyde and Simons 2001), we maximized our probability of detection (Pollock et al. 2002) by using a detailed sampling protocol (Clayton et al. 1999) and a well trained, consistent crew. This approach proved successful with the closely related Del Norte salamander, yielding a detection probability of >90% (Welsh et al. 2006). The Siskiyou Mountains salamander spends most of each year beneath the surface, and is active on the surface for limited periods during spring and fall with suitable climatic conditions. Consequently, we restricted sampling (following Clayton et al. 1999) to only: 1) during the months of March–April, and September–early November; 2) when site relative humidity was at least 45%; 3) when air temperature was 4-18° C; and 4) when the soil under the first layer of cover was moist. Because rainfall and other climatic conditions can vary by drainage, we used nearby sites in the same drainage previously known to support salamanders to verify surface activity.

Biotic and Abiotic Variables

Explanatory variables were selected using three non-exclusive criteria: 1) structural, compositional, and microclimatic aspects of the forest environment important to plethodontid salamanders as indicated by previous research (e.g., deMaynadier and Hunter 1995, Welsh and Droege 2001, Wyman 2003); 2) variables representing variation in structure and composition resulting from natural succession, timber harvesting and reforestation, or disturbances such as fire; and 3) variables incorporating aspects of the forest environment reflecting distinct spatial

scales: landscape, macro-environmental, and micro-environmental. We measured 220 continuous variables and 10 categorical variables (see Appendix, Figure 2, and Table 1 for details).

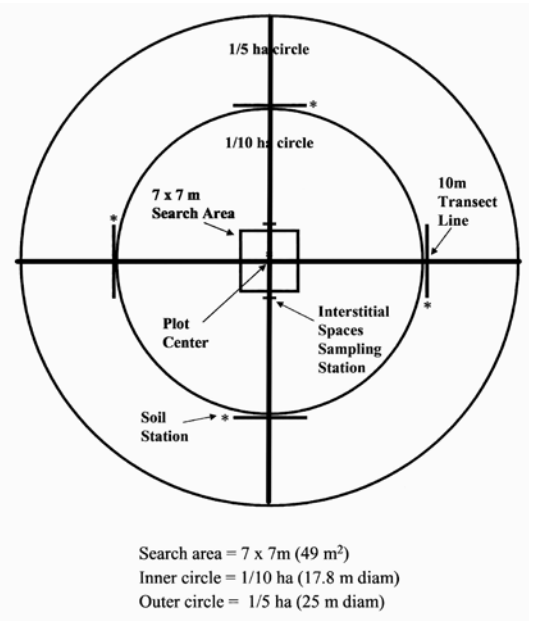

Figure 2. Diagrammatic representation of the salamander sample plots and the concentric circles and line transects used to sample the environmental attributes associated with each site (see Table 1).

Statistical Analysis

Because of pronounced differences in climate and vegetation north and south of the Siskiyou Mountains crest (Froehlich et al. 1982, Whitaker 1960), we partitioned our analyses based on locations of sites north or south of the Siskiyou Mountains crest, which roughly follows the Oregon-California border. A few sites in California but north of the Siskiyou crest were included with the North Slope sample. Sites south of the Siskiyou Crest comprised the South Slope sample, and all were in California. The North Slope sample consisted of 163 sites and the South Slope sample had 76 sites (Figure 1).

We reduced the number of explanatory variables prior to analysis using correlation statistics. To examine inter-correlations at the macro- and micro-environment scales, we aggregated variables within ecological subsets (see Table 1) into structural or climatic variable sets representing: (1) above ground or canopy conditions, (2) ground-level conditions, and (3) forest climate conditions. For the landscape scale, we conducted correlation analyses on each of the three ecological subsets in Table 1. In each analysis, for pairs of variables in which r >0.70, we retained the one showing the strongest correlation with salamander detections. This variable reduction process resulted in sets of 97 variables for the South Slope sample and 122 for the North Slope sample (Table 1).

We modeled salamander binary response (presence or not detected) as a function of environmental variables using exploratory best-subsets logistic regression analysis in S-Plus (S-PLUS 2000) and SAS (SAS Institute Inc. 1990). Given our choice of modeling approaches, it was unnecessary to standardize the covariate measurements, which allows our coefficient solutions to be understood in the context of the original scale of the variables. Consequently, the coefficient estimates in the logit models should not be compared with each other for relative statistical significance because the coefficient variable measurements are not relative in value. The test statistics and *P*-values provide an indication of the statistical significance of the coefficient estimates.

We analyzed and compared models at three spatial scales (landscape, macro-environmental, and micro-environmental) and at all three scales combined. We compared three different analysis strategies, using three alternative forms of the covariates: *strategy 1* - linear forms only; *strategy 2* - linear, quadratic, and pseudo-threshold forms; and *strategy 3* - linear, quadratic, pseudo-threshold, and 1st order interaction forms. The quadratic forms applied a quadratic (i.e., $X+X^2$), and the pseudo-threshold forms applied a log transformation (i.e., log [X +0.5]). This approach provided a more flexible range of functional forms for environmental attributes to describe potential complexities of environmental conditions suitable for salamander occurrence.

We began by using best subsets selection for logistic regression with individual subsets of related variables within each of the three spatial scales (Table 1). For example, for the South Slope data at the macro-environment scale, we analyzed models for ecological subsets "trees density," "trees size (dbh)," "dead and down wood," "shrub and understory composition," "ground-level vegetation," "ground cover," and "forest climate" (Table 1). We then compared

TABLE 1. Environmental variables (230) measured within the range of the Siskiyou Mountains salamander. Variables are arranged hierarchically by scale and ecological subset (italicized). Variables used in the analysis of the South Slope data set only are indicated by †, those used with the North Slope data set only are indicated by *. All other variables were used for both analyses. Structural aggregates used in the analyses (see text) at the macro-environmental scale consisted of Canopy attributes (2c, b, and d), ground-level attributes (2c, e, and f) and climatic attributes (2g); and at the micro-environmental scale consisted of sub-canopy attributes (3a and b), ground-level attributes (3c, d, and e) and microclimatic attributes (3f).

Scale	Variables
Landscape (1)	*Location/Condition* Latitude, longitude, elevation (m), % slope, aspect, years since disturbance *Climate* Annual precip. (cm)_e[1], precipitation (mm)_g[1], illumination (June_g, December_g), annual air temp (mean, minimum, maximum (°C)_g) *Parent geology/soil type*_g Alluvial, granite, metamorphic, miscellaneous*, ultramafic, unknown
Macro-environment (stand level) (2)	*Tree density* (2a) Forest age, conifers (all small_c[1] and b[1], all large_c and b, small Douglas-fir_c and b*, large Douglas-fir_c and b*, all pine species_c*), hardwoods (all small_c and b†, canyon live oak_c and b*, other_c*, all_c and b*, all large_b†) *Tree size (dbh)* (2b) Douglas-fir (mean, minimum, maximum), all pine species† (mean, minimum, maximum), canyon live oak* (mean, minimum, maximum), all conifers (mean, standard deviation), all hardwoods† (mean, standard deviation), other hardwoods* (mean, standard deviation) *Dead and down wood* (2c) Snags_c, stumps_c, conifer logs_c (small decayed, large decayed, all sound, small sound†), hardwood logs _c (all, decayed*), logs_l[1] *Shrub and understory composition* (2d) Bole_l, understory conifers_l (all, Douglas-fir*), understory hardwoods_l (all, canyon live oak*), poison oak_l, height II - vegetation_v1, shrubs _l (all large†, other large*), hazelnut_l* *Ground-level vegetation* (2e) Herb_l, height I - grnd vegetation_l, fern_l (all†, sword fern*) and v*, grass_v† and l*, shrubs_l (all small†, other small*), Oregon grape_l*, honeysuckle_l*, snowberry_l* *Ground cover* (2f) Exposed soil_v, exposed rock_l, gravel_v, pebble_v, cobble_v, boulder_v, leaf litter depth in cm (mean, standard deviation), moss_l† and v*, lichen_l† and v*, leaf litter_v† and l* *Forest climate* (2g) Air temperature (°C), relative humidity (%), solar index, % canopy open (mean, minimum, maximum, standard deviation), surface soil temperature in °C (mean, standard deviation), 10 cm depth soil temp in °C (mean, standard deviation)
Micro-environment (animal plot) (3)	*Shrub and understory composition* (3a) Understory conifers_l (all, Douglas-fir*), understory hardwoods_l (all, canyon live oak*), poison oak_l, large shrubs (all)_l *Ground-level vegetation* (3b) Fern_l (all, sword fern*), herb_l, grass_l, small shrubs (all)_l, Oregon grape_l*, honeysuckle_l*, snowberry_l* *Ground cover* (3c) Moss_l, lichen_l, leaf litter_l, leaf litter depth (plot center) (cm), large woody debris _av[1] *Rocky substrates* (3d) Sand_av, gravel_av, pebble_av, cobble_av, boulder_av, soil_av*, large rock_av*, rock_l* *Subsurface conditions* (3e) Mineral soil_i[1] and mean mineral soil_i, leaf litter/detritus_i* and mean leaf litter/detritus_i*, mixed soil and litter_i and mean mixed soil and litter_i *Microsite conditions* (3f) % canopy open (plot center), soil temp (surface, 10 cm depth) (plot center)

[1] e = these data were collected from the nearest USGS weather station; g = GIS variable: these data were determined using the software ARCView; climatic layers were derived using PRISM data (Daly et al. 1994); c = count variable (numbers per hectare): small trees = 12-52 cm diameter at breast height (dbh) were counted in a 1/10th-ha circle, large trees = > 53 cm dbh were counted in a 1/5th-ha circle; b = basal areas: measured for the large trees within the 1/5th-ha circle and for the small trees within the 1/10th-ha circle and were calculated using a basal area equation and reported as cm^2/ha; l = proportion of transect line: tree species were included on the transect only if they are less than 12 cm dbh; v = visual estimate (%) 1/10-ha circle; av = visual estimate (%) of salamander search area; i = interstitial space variable: the number of substrate surfaces for 10 - 0.05 m equal sections was counted for two trenches in each plot (based on Kinsolving and Bain 1990) for the prominent fill type in each trench. Fill types were: empty, mineral soil, leaf litter, or mixed. For California data analysis, leaf litter and mixed fill types were combined because of low occurrence of leaf litter fill type.

the most competitive models at each scale (using lowest AIC_c), and for all scales combined, by combining only the significant covariates from each ecological subset. We repeated this process for each strategy, employing the alternative forms of covariates, and selected the most competitive model for each strategy and spatial scale. In cases where we had too many variables to run at a single spatial scale (computational logistics limited us to a maximum of 14 covariates), we used the intermediate structural groupings (see Table 1; canopy [or sub-canopy], ground-level, and climatic [or micro-climatic] attributes) within scales to select best subsets before combining then with those of another spatial scale. Lastly, we ran groups of covariates for each of the three possible pairs of spatial scales to derive the best sub-sets of covariates that were used to derive our final combined-scales best-fitting models under each strategy.

We evaluated the competitiveness of the resulting models using the bias-corrected Akaike's Information Criterion AIC_c and Akaike weights (Burnham and Anderson 1998). With AIC_c we reported only the model with the lowest value (hereafter called the best model) at each stage of the analysis. Lists of any additional variables that comprised or contributed to models within 2 AIC_c units of the best model in each group are available from the authors on request. Akaike weight estimates the probability of each model best fitting the data, based upon its relative likelihood, given the collection of models under consideration. These weights have a Bayesian statistical interpretation as posterior probabilities of the models being the best fitting models (Stauffer et al. 2004). We also examined Nagelkerke's R^2 and the deviance D statistics (Hosmer and Lemeshow 2000). Nagelkerke's Generalized Coefficient of Determination R^2, analogous to the adjusted R^2 statistic in multiple regression, estimates the proportion of the variation in the response "captured" by the model. The deviance D statistic estimates the proportion of total deviance explained.

Finally, we evaluated the goodness-of-fit of models using estimates of correct classification, sensitivity, specificity, and the Receiver Operating Characteristic (ROC) "c" statistic (McCullaugh and Nelder 1989, Hosmer and Lemeshow 2000). Correct classification estimates the proportion of all sites correctly classified. For each candidate model, we examined correct classification results for cutoff points varying from 0% to 100% at 5% increments. Sites with predicted probabilities above the cutoff point were classified as "occupied," whereas those with predicted probabilities below were classified as "unoccupied." We used the best overall cutoff point for correct classification to estimate the correct classification, sensitivity, and specificity. Sensitivity and specificity rates presented for the models could be altered upward or downward by choosing different cutoff points. However, increases in sensitivity will result in decreases in specificity and vice versa, and will lower the overall correct classification rates. In particular, sensitivity estimates the proportion of the occupied sites correctly classified by the model, whereas specificity estimates the proportion of the unoccupied sites correctly classified. The ROC c statistic estimates the amount of area underneath the receiver operating curve, the graph of sensitivity over one-minus-specificity. The model with the highest c statistic is the best fitting overall, independent of cutoff point. Models with lower c statistics may have, in some cases, particular cutoff points that perform better for correct classification, sensitivity, and specificity.

Results

On the North Slope, we detected salamanders at 28.2% (46) of 163 sites with 137 captures (39 juveniles, 26 sub-adults, and 71 adults). On the South Slope, we detected salamanders at 20% (15) of 76 sites with 38 captures (6 juveniles, 14 sub-adults, and 17 adults). Captures ranged from 1 to 13 animals per 49-m^2 plot; 1–13 on the North Slope, and 1–6 on the South Slope. Salamander densities averaged 0.057 m^{-2} (S.D.=0.06) and 0.052 m^{-2} (S.D.=0.04) on the North and South slopes, respectively.

Habitat Models – North Slope

Of the three spatial scales, the best models for the North Slope were at the macro-environmental scale, with the *strategy 2* model (R^2=49.0%) having a lower AIC than the *strategy 1* model (R^2=51.0%) (Table 2). The best linear habitat model (*strategy 1*) was the combined scales model with an R^2 of 59.2% (Table 2; Model 4). The best model under *strategy 2* was also the combined model with an R^2 of 63.2%, consisting of 8 of the same covariates as the best model under *strategy 1*, but with several taking non-linear forms, and 4 new covariates (2

TABLE 2. Leading Siskiyou Mountains salamander habitat selection models for the North Slope, for different strategies 1-3 (see text) and spatial scales (micro, macro, landscape, and combined). k=parameters in the model including intercept; w_i=Akaike weights; CC=correct classification; sen=sensitivity; spec=specificity; c=ROC statistic (see text). The cutoff point was chosen to be the probability level p_{cutoff} = 0%, 5%, 10%, …, 95%, or 100% that maximized the correct classification rate CC. Samples i with probability $\hat{p}_i$ predicted by the model for the site i having $\hat{p}_i \geq p_{cutoff}$ were assigned predicted value $\hat{y}_i = 1$ and having $\hat{p}_i < p_{cutoff}$ were assigned predicted value $\hat{y}_i = 0$ and compared with the observed value y_i. Best model based on AIC_c is bolded.

ID	Strategy	Scale	Model (estimated logit)	k	R^2 (%)	D (%)	AICc	w_i (%)	cutoff point	CC (%)	sen (%)	spec (%)	c (%)
1	1	landscape	- 2.795 + 0.064*Precip_g + 0.289*Max air temp_g - 0.021*Illum in Jun_g - 0.947*Metamorphic soil_g	5	20.5	12.9	179.26	<0.0005	0.55	74.2	21.7	94.9	73.3
2	1	macroscale	- 2.409 – 0.124*All small conifer_b - 0.109*Douglas fir mean dbh + 0.113*All conifer mean dbh + 0.245*Other hardwood dbh std dev - 15.048*Grass_l + 13.034*Sword fern_l + 0.018*Moss_v + 2.052*Exposed rock_l + 0.052*Cobble_v - 0.006*Solar index - 0.027*% canopy open min	12	51.0	36.8	148.06	< 0.0005	0.55	79.5	47.8		92.2 88.1
3	1	microscale	- 1.069 + 2.573*All understory hardwood_l + 6.739*All fern_l - 4.769*Herb_l - 0.039*Pebble_av + 2.027*Rock_l - 0.129*Mean mixed soil and litter_i - 0.021*% canopy closed (plot center)	8	28.3	18.5	172.99	<0.0005	0.50	73.5	35.6	88.0	78.3
4	1	combined	- 0.078 + 0.315* Max air temp_g - 0.030*Illum in June_g - 0.893*Metamorphic soil_g - 0.123*All small conifer_b - 0.126*Douglas fir mean dbh + 0.136*All conifer mean dbh + 0.258*Other hardwood dbh std dev - 17.887*Grass_l + 14.199*Sword fern_l + 2.874*Rock_l - 7.191*Herb_l - 0.050*Pebble_av	13	59.2	44.6	135.73	0.213	0.65	84.0	58.7	94.0	90.5

TABLE 2. Continued

ID	Strategy	Scale	Model (estimated logit)	k	R^2 (%)	D (%)	AICc	w_i (%)	cutoff point	CC (%)	sen (%)	spec (%)	c (%)
5	2	landscape	10.411 + 0.010*Max air temp_g^2 - 0.940*Metamorphic soil_g^2 + 2.484*log(Precip_g+0.5) - 4.155*log(Illum in Jun_g+0.5)	5	21.3	13.5	178.13	< 0.0005	0.60	75.5	17.4	98.3	73.3
6	2	macroscale	4.352 + 0.268*Other hardwood dbh std dev - 0.002*Douglas fir mean dbh^2 + 0.002*All conifer mean dbh^2 - 15.201*grass_l + 18.009*Sword fern_l + 3.012*log(Exposed rock_l+0.5) - 1.394*log(Solar index+0.5)	8	49.0	35.0	142.57	0.007	0.55	79.0	45.7	92.2	87.3
7	2	microscale	85.678 – 216.100*All fern_l + 4.622*All understory hardwood_l^2 + 91.454*All fern_l^2 - 19.178*Herb_l^2 + 124.700*log(All fern_l+0.5) - 0.122*Mean mixed soil and litter_i - 0.001* Pebble_av^2 - 0.0003*% canopy open (plot center)^2	9	31.1	20.6	169.11	< 0.0005	0.55	74.1	31.1	90.6	79.6
8	2	combined	22.301 + 0.016*Max air temp_g^2 + 3.378*log(Precip_g+0.5) - 6.282*log(Illum in June_g+0.5) + 0.373*Other hardwood dbh std dev - 0.003*Douglas fir mean dbh^2 + 0.003*All conifer mean dbh^2 - 19.385*Grass_l + 5.025*log(Rock_l+0.5) + 6.620*All understory hardwood_l^2 - 28.244*All fern_l^2 + 12.277*log(All fern_l+0.5) - 0.001*Pebble_av^2	13	63.2	48.6	127.98	10.288	0.55	84.0	60.9	93.1	92.1
9	3	landscape	- 16.344 + 0.198*Max air temp_g^2 - 0.036*Max air temp_g^2*log(Illum in Jun_g+0.5) - 3.381*Metamorphic soil_g^2*log(Precip_g+0.5) + 2.126*Metamorphic soil_g^2*log(Illum in Jun_g+0.5) + 0.725*log(Precip_g+0.5)*log(Illum in Jun_g+0.5	6	26.6	17.2	173.09	< 0.0005	0.40	74.2	43.5	86.3	78.4

TABLE 2. Continued

ID	Strategy	Scale	Model (estimated logit)	k	R^2 (%)	D (%)	AICc	w_i (%)	cutoff point	CC (%)	sen (%)	spec (%)	c (%)
10	3	macroscale	+ 4.352 + 0.268*Other hardwood dbh std dev - 0.002*Douglas fir mean dbh^2 + 0.002*All conifer mean dbh^2 - 15.201*Grass_l + 18.009*Sword fern_l + 3.012*log(Exposed rock_l+0.5) - 1.394*log(Solar index+0.5)	8	49.0	35.0	142.57	0.007	0.55	79.0	45.7	92.2	87.3
11	3	microscale	- 0.349 + 4.434*All fern_l - 12.852*Herb_l^2 + 56.846*All fern_l*Herb_l^2 + 141.500*All understory hardwood_l^2*Herb_l^2 + 27.275*Herb_l^2*log(All fern_l +0.5) - 0.0002*Mean mixed soil and litter_i*Pebble_av^2 - 0.0003*% canopy closed (plot center)^2	8	23.5	15.0	162.75	< 0.0005	0.45	73.5	26.7	91.5	75.9
12	**3**	**combined**	**- 15.154 + 0.190*Max air temp_g^2 - 0.033*Max air temp_g^2*log(Illum in June_g+0.5) + 0.520*log(Precip_g+0.5)*log(Illum in June_g+0.5) + 0.295*Other hardwood dbh std dev - 0.002*Douglas fir mean dbh^2 + 0.002*All conifer mean dbh^2 - 18.326*Grass_l + 3.556*log(Rock_l+0.5) + 52.218*Herb_l^2 - 14.498*All fern_l*Herb_l^2 + 136.900*All understory hardwood_l^2*Herb_l^2 + 113.300*Herb_l^2*log(All fern_l+0.5) - 0.0001*Mean mixed soil and litter_i*Pebble_av^2**	**14**	**58.3**	**43.7**	**123.65**	**89.438**	**0.70**	**82.1**	**45.7**	**96.6**	**90.3**

log and 2 quadratic) replacing 4 linear covariates from the *strategy 1* model (Table 2; Model 8). Of all the North Slope models tested, the combined-scales model under *strategy 3*, which included many of the same covariates as the combined model under *strategy 2* (with 2 additions), but with four interaction terms included, was the best fitting overall, with an Akaike weight (w_i) of 89.44% and an R^2 of 58.3% (Table 2; Model 12). The second best model had an Akaike weight of just 10.29% (Table 2; Model 8), and AIC_c values for all of the other models were much higher than the best model (Table 2), indicating that they were not competitive.

The R^2 and D statistics for these models generally corroborated the AIC results. R^2 increased from a low of 20.5% for the best landscape scale model under *strategy 1*, to 63.2% for the combined-scales model under *strategy 2*, slightly higher than the R^2 of 58.3 for the best model overall based on lowest AIC (Table 2, Model 12). The classification results indicated that all of the resulting models were closely aligned in accuracy, with correct classification rates from 73.5% to 84.0%. With 28.2% presence of salamanders on North Slope sites, these accuracy rates are significantly better than expected based on actual rate of site occupancy. The best model had an overall correct classification of 82.1%, with a sensitivity (ability to predict presence) of 45.7%, and a specificity (ability to predict absence) of 96.6% (Table 2).

Habitat Models – South Slope

The best overall model under *strategy 1* was the combined-scales model with an R^2 of 72.4 (Table 3; Model 4). The best model under *strategy 2*, also a combined-scales model, had an R^2 of 74.1% (Table 3; Model 8). The best model under *strategy 3*, and the best fitting model overall with an Akaike weight of 66.78, was the combined scales model, with an R^2 of 76.5% (Table 3; Model 12).

Within this best model the combined effects of multiple interactions between precipitation and illumination in December, maximum air temperature, and illumination in December^2, appears to be modeling synergistic interactions of climatic and topographic attributes as overarching determinants of suitable sites for this salamander, with several macro- and micro-scale covariates acting as final arbiters of occupancy. The models for the South Slope derived under *strategy 3* were consistently better for each spatial scale than models derived under the other two strategies (Table 3). The second best ranking model, the combined-scales model of strategy 2 (Table 3; Model 8), had an Akaike weight of 22.38% and ranked within 3 AIC_c units of the best model, so it should be viewed as competitive. However, the only new variables that enter this model are the standard deviation of conifers at breast height and boulders (both positive with salamander presence) so it provides little additional information.

As with the North Slope results, the R^2 and D statistics for the South Slope models were consistent with the AIC results and the classification accuracy levels were in close agreement for all the models, ranging from 81.3% to 90.7% for overall correct classification (Table 3). Our best South Slope model had an overall correct classification of 90.7%, with sensitivity of 60.0% and specificity of 98.3%. R^2 for these models increased from a low of 26.4% for the macro-environmental scale model under *strategy 2*, to an overall high of 76.5% for the combined scales model under *strategy 3*. South Slope models explained more of the variation in salamander occupancy than the North Slope models, for all three strategies (compare Tables 2 & 3).

Model Evaluations

The optimal accuracy rates for the best fitting North Slope Model (#12) were 82.1% correct, with 45.7% sensitivity and 96.6% specificity, based upon a cutoff point probability of 0.70 (Table 2). The optimal accuracy rates for the best fitting South Slope Model (#12) were 90.7% correct, with 60.0% sensitivity and 98.3% specificity, based upon a cutoff point probability of 0.60 (Table 3).

Discussion

We had a 28% detection rate of salamander presence at sites on the North Slope and a 20% detection rate of salamander presence at sites on the South Slope. These low detection rates, all from within the known range, and mostly in evidently suitable habitats, illustrate the challenge of sampling for a rare animal with a patchy occurrence. Low detection rates and low abundances restricted our ability to fully discern the range of habitat attributes required by this salamander. Still, we believe our analyses revealed environmental conditions where

TABLE 3. Leading Siskiyou Mountains salamander habitat selection models for the South Slope, for different strategies 1-3 (see text) and spatial scales (micro, macro, landscape, and combined). k=parameters in the model including intercept; w_i=Akaike weights; CC=correct classification; sen=sensitivity; spec=specificity; c=ROC statistic (see text). The cutoff point was chosen to be the probability level p_{cutoff} = 0%, 5%, 10%, …, 95%, or 100% that maximized the correct classification rate CC. Samples i with probability $\hat{p}_i$ predicted by the model for the site i having $\hat{p}_i \geq p_{cutoff}$ were assigned predicted value $\hat{y}_i = 1$ and having $\hat{p}_i < p_{cutoff}$ were assigned predicted value $\hat{y}_i = 0$ and compared with the observed value y_i. Best model based on AIC_c is bolded.

ID	Strategy	Scale	Model (estimated logit)	k	R^2 (%)	D (%)	AICc	w_i (%)	cutoff point	CC (%)	sen (%)	spec (%)	c (%)
1	1	landscape	- 9.563 + 0.002*Precip_g + 0.465*Max air temp_g - 0.024*Illum in Dec_g	4	39.0	28.4	62.63	0.001	0.60	86.8	40.0	98.4	82.3
2	1	macroscale	- 3.783 - 0.047*All pine min dbh + 0.029*All pine max dbh + 0.069*All conifer dbh std dev - 0.241*Gravel_v - 0.013*Solar index + 0.405*10 cm depth soil mean temp	7	38.0	27.5	70.09	< 0.0005	0.60	81.3	20.0	96.7	84.7
3	1	microscale	- 5.614 – 48.326*All fern_l + 0.278*Leaf litter depth (plot center) + 0.042*Boulder_av + 0.360*10 cm depth soil temp (plot center)	5	39.8	29.0	64.17	0.001	0.50	82.7	26.7	96.7	88.2
4	1	combined	- 25.180 + 1.099* Max air temp_g - 0.030*Illum in Dec_g + 0.120*All conifer dbh std dev + 0.641*10 cm depth soil mean temp - 82.466*All fern_l + 0.068*Boulder_av	7	72.4	61.2	44.81	10.774	0.55	88.0	60.0	95.0	95.9
5	2	landscape	- 6.041 + 0.003* Precip_g - 0.061*Illum in Dec_g + 0.016*Max air temp_g^2 + 0.0002*Illum in Dec_g^2	5	45.9	34.4	60.41	0.004	0.75	85.5	26.7	100.0	86.0
6	2	macroscale	- 2.969 - 0.935*log(Gravel_v+0.5) + 0.019*10 cm depth soil mean temp^2	3	26.4	18.2	67.71	< 0.0005	0.55	84.0	20.0	100.0	77.0
7	2	microscale	-7.570 + 0.356*Leaf litter depth (plot center) + 0.149*Boulder_av + 0.471*10 cm depth soil temp (plot center) - 2338.5*All fern_l^2 - 0.002*Boulder_av^2	6	47.0	35.2	61.87	0.002	0.50	82.7	40.0	93.3	85.6

TABLE 3. Continued

ID	Strategy	Scale	Model (estimated logit)	k	R^2 (%)	D (%)	AICc	w_i (%)	cutoff point	CC (%)	sen (%)	spec (%)	c (%)
8	2	combined	- 15.345 - 0.029*Illum in Dec_g + 0.041*Max air temp_g^2 + 0.119*All conifer dbh std dev + 0.031*10 cm depth soil mean $temp^2$ + 0.072*Boulder_av - 2589.700*All $fern\_l^2$	7	74.1	63.1	43.35	22.380	0.35	88.0	80.0	90.0	95.9
9	3	landscape	- 3.639 - 0.00006*Precip_g*Illum in Dec_g + 0.00002*Precip_g*Max air temp_g^2 + 0.0000002*Precip_g*Illum in Dec_g^2	4	47.3	35.6	57.22	0.022	0.65	86.8	40.0	98.4	85.7
10	3 -	macroscale	- 3.6254 + 0.027*10 cm depth soil mean $temp^2$ - 0.009*log(Gravel_v+0.5)*10 cm depth soil mean $temp^2$	3	29.7	20.8	65.80	< 0.0005	0.40	82.7	33.3	95.0	76.3
11	3	microscale	- 7.766 + 0.382*Leaf litter depth (plot center) - 3776.400*All $fern\_l^2$ + 0.005*$Boulder\_av^2$ + 0.526*10 cm depth soil mean temp - 0.00006*Boulder_av *$Boulder\_av^2$	6	54.8	42.5	56.41	0.033	0.60	85.3	40.0	96.7	89.5
12	**3**	**combined**	**- 7.548** **- 0.00009*Precip_g*Illum in Dec_g** **+ 0.00003*Precip_g*Max air temp_g^2** **+ 0.0000003*Precip_g*Illum in Dec_g^2** **+ 0.041*10 cm depth soil mean $temp^2$** **- 0.010*log(Gravel_v+0.5)*10 cm depth soil mean $temp^2$** **- 989.600*All $fern\_l^2$**	**7**	**76.5**	**66.0**	**41.16**	**66.78**	**0.60**	**90.7**	**60.0**	**98.3**	**96.7**

populations are likely to persist. Our models reveal important non-linear relations and environmental interactions that were not uncovered by an earlier more traditional linear modeling approach using discriminant function analysis (Ollivier et al. 2001). The inclusion of landscape level variables generated in GIS (that were not available in the earlier analysis) revealed the importance of processes at broad spatial scales in influencing the current distribution of this salamander. Still, the two analyses produced results that were similar. In both instances, climatic variables (e.g., annual precipitation, solar incidence, and soil temperature) predominated in the best multi-scale models, as did forest interior climate surrogates such as amount of canopy closure and the presence of certain plant species (either moisture-loving or moisture-averse).

North Slope versus South Slope

Our analysis of habitat relations suggests that the populations on each slope respond differently to the environmental parameters we measured. The best habitat models under all three analysis strategies had consistently higher predictive abilities for South Slope sites compared with those on the North Slope (i.e., % correct classification, sensitivity and specificity values in Tables 2 and 3). Exceptions were model sensitivity (correctly predicting occupancy) where several of the North Slope models were slightly better than those of the South Slope. We think that the better prediction of South Slope models are the result of landscape-specific differences in population-level responses to available moisture, which is likely the ultimate controlling factor for plethodontid salamander occurrence (Spotila 1972, Feder 1983, Grover 2000). Precipitation on the north side of the Siskiyou Crest is more consistent both across the landscape and over time compared to the south side. Site moisture is retained for longer periods on the north side due to the northerly aspect of the mountain range and the direction of prevailing weather patterns from northwest to southeast (Froehlich et al. 1982). The coefficient of variation for precipitation is 26.0% for the North Slope sites and 35.2% for the South Slope sites. We suggest that this difference in predictable precipitation across versants explains why the more fine-grained micro-environmental models, which had moisture-sensitive plant attributes, were consistently better than the landscape scale models for the North Slope; a situation that was not reflected with the South Slope models (see Tables 2 and 3). On the South Slope where precipitation is less predictable, the combined scales model that included several interaction terms with precipitation and other climatic and topographic attributes, along with three finer scale attributes and their interactions (Model 12), was the best model (Table 3) and far exceeded the predictive capabilities of the best North Slope model (Table 2, Model 12).

Because of these moisture differences, there is less suitable habitat for this salamander on the South Slope, and it is more patchily distributed. Where it does occur, it is easier to distinguish on the landscape and thus to model. Also, as a result of these distinct dominant weather patterns within the relatively small range of this salamander (Figure 1), available moisture on both the North and South Slopes tends to increase from north to south, and is indicated by the dominant covariate signs in the leading models. On the North Slope, moisture increases north to south with the increase in elevation towards the Siskiyou Mountains crest. On the South Slope, moisture also increases north to south due to the rain shadow effect immediately south of the Siskiyou Mountains crest. The presence of the variable "Illumination in December" as a more prominent (negative) variable in the South Slope models, compared with "Illumination in June" (also negative) for the North Slope, is likely an expression of the greater desiccating potential on this landscape. These results suggest that, to a large degree. it is landscape-scale processes that shape and determine the arrangement of populations of this salamander across the available terrain, with the stand-level (macro-scale) attributes providing the critical ameliorating conditions that allow them to persist when conditions are stressful.

Substrate moisture is the single most limiting physiological factor for terrestrial salamanders, playing a critical role in every aspect of their biology (Spotila 1972, Feder 1983, Grover 2000). Plethodontid salamanders are lungless, with respiration occurring through the moist skin. The forest landscapes of the Klamath-Siskiyou Mountains are a mosaic of suitable habitat patches. The relationship between a particular patch (e.g., slope, aspect, elevation, and amount of forest cover) and the prevailing climate determines the suitability of the microclimate within each patch (Chen et al. 1999). The length of time that equable surface

microclimates are within the tolerance limits of these salamanders may be of critical importance because it is only then that they can carry out surface activities (e.g., Jaeger and Forester 1993, Houck and Verrell 1993, Verrell and Mabry 2000).

Most of the recently disturbed sites we sampled on the South Slope appeared to be "sink" habitat for populations (Pulliam 1988, 2000). This was suggested by the age class distribution of the few animals we found on recently disturbed sites (both slopes combined, pre-canopy and young sites; N=15 salamanders), which were mostly juveniles and sub-adults (73.0% of detections), with fewer adults present compared with mature and old-growth sites (H. Welsh, unpublished data). Overall, juveniles and sub-adults together comprised only 50.0% of captures on mature and old-growth sites (both slopes combined, N=20). Further, body condition of salamanders (see Karraker and Welsh 2006) on young sites (both slopes combined) was significantly lower than it was on mature sites (H=8.90, df=2, P=0.01, H. Welsh et al., unpublished manuscript). The higher proportions of young salamanders on recently disturbed sites may have consisted largely of animals from more suitable nearby habitats that were displaced by competition with adults on established territories (i.e. despotic dispersal) (see Jaeger and Forester 1993, Gabor 1995, Maerz and Madison 2000).

Modeling Habitat at Landscape and Macro-environmental Scales on the North Slope

The landscape scale models for the North Slope indicate that sites with higher precipitation (those closer to the Siskiyou Mountains crest at the center of the range) had a greater likelihood of salamander presence (Table 2). The leading landscape model (Model 9) illustrates the importance of interactions between the prevailing climate and both geologic and topographic attributes, represented here by the GIS-derived variable 'Illumination in June' and the parent geologic variable 'metamorphic soil,' for predicting species occurrence. Both of these variables are negative with salamander presence in the linear model (Model 1), but when interacting with other key variables the results are positive predictors of the likelihood of occurrence (Model 9). This model with interaction terms was the best of the three landscape scale models (Table 2). Our results here clearly illustrate the benefits of examining higher order and interaction effects as part of the modeling process.

The macro-scale habitat models for the North Slope, comprised of tree covariates, along with grass, sword ferns, moss, substrate covariates, and stand-level climatic covariates (solar index and percent canopy open) (Table 2), appear to consist of both forest structural attributes, and plant surrogates for site specific microclimatic conditions. Grass (negative with salamander presence) is a surrogate for open habitats; moss and sword fern (both positive with salamander presence) are interior forest floor plants requiring relatively higher and more dependable moisture (see Frost 1997). The macro-scale models for the North Slope were consistently better than the micro- or landscape scale models for predicting presence or absence of salamanders, and, the model was not improved when including interaction terms (Table 2).

Modeling Habitat at Landscape and Macro-environmental Scales on the South Slope

The landscape scale models for the South Slope were consistently better predictors of the potential for landscape mosaics patches to support salamanders at this spatial scale than were the North Slope models. Conversely, the macro-environmental models for the South Slope were poor compared with those for the North Slope, and were the weakest of the three spatial scales (Table 3). The South Slope linear macro-scale model (Table 3, Model 2) consisting of three stand structure (tree) covariates—one describing substrate and two describing climatic attributes—was the best of the three forms, explaining the most variation at this scale (R^2=38.0%). In contrast, the macro-environmental models for the North Slope were, collectively the best models of the three scales. The linear model had seven vegetation, two substrate, and two climatic covariates (Table 2; Model 2), and explained the most variation (R^2=51.0%).

Vegetation differences between the two slopes, largely a result of the differences in macro-climatic regimes (Whittaker 1960), may contribute to the lower detection rates for salamanders on the South Slope, and to weaker models at the macroscale where differences in vegetation are most effectively modeled. The South Slope supports less of a shrub layer, slower growing trees, and greater prevalence of drought-resistant species such as manzanita (*Arctostaphylos* spp.), canyon live oak (*Quercus chrysolepis*), and poison oak (*Toxicodendron diversilobum*). The plant assemblages and stand structure on the South Slope

sites indicate a warmer, drier climate; and, thus, provide less suitable salamander habitat (and by implication fewer salamander populations) on a similar amount of landscape compared to the vegetation assemblages on the cooler, moister North Slope sites.

Modeling Habitat at the Micro-environmental Scale

The micro-environmental models for the North Slope were consistently weaker than the macroscale models but better than the landscape scale models, with the best of these (under strategy 3) explaining 23.5% of the variation in salamander occurrence (Table 2). Covariates in these models were all indicative of fine-scale ground cover, substrate, and microclimatic attributes. The hardwood understory variable is likely an indication of enhanced leaf litter provided by this deciduous vegetation. Forest leaf litter provides both salamander cover and moisture-storing capacity, and is the primary food of many of the invertebrates that form the prey base of plethodontid salamanders (e.g., Wyman 1998).

The North Slope models consisted of several different measures of canopy closure plus solar index (Table 2; see both macro- and micro-scale models). Forest stand microclimates are strongly influenced by the amount of canopy closure provided by the tree crowns, which together comprise a structural element of critical importance in determining stand-level microclimatic conditions (Chen et al. 1999). Welsh and Lind (1995) found that of 43 measurements of the forest environment they measured, canopy closure was the single best indicator of Del Norte salamander presence (see also Welsh et al. 2006).

The micro-scale models for the South Slope also contained covariates indicative of substrate attributes and conditions (leaf litter and soil temperature), but they also included a plant indicator in ferns (all) (negative with salamander presence). This negative relationship with ferns at first appeared counter-intuitive, but the category of 'all ferns' consisted mainly of bracken fern, which grows in drier, more open grassland habitats.

Modeling with Multiple Forms and Interactions

Although it is tempting for researchers to "keep it simple" (i.e., readily explainable) when modeling the relationships of animals to their environments, many such relationships are complex and not linear. Modeling of environmental relationships can be greatly improved by the inclusion of non-linear forms and covariate interactions because so many organism/environment relationships are non-linear and often derive from complex interactions among environmental attributes. While we often label such attributes 'independent variables', this is clearly a misnomer given how often they interact to affect each other and in combination act to influence the responses of organisms, often in complex non-linear ways.

Linking the Best Models with Salamander Ecophysiology and Life History

Across spatial scales, those models that either directly or indirectly modeled climatic conditions, including microclimates, were the best predictors of salamander presence. The habitat models for both slopes collectively appear to emphasize the importance of closed canopied, moist, relatively cool forest stands capable of sustaining stable moist microclimates (see Chen et al. 1999). This is not surprising because of the physiological limits of these salamanders (Spotila 1972, Feder 1983, Grover 2000), which have several key aspects of their life history that directly influence population fitness. These include the activities of courtship, mating, and feeding (Feder 1983, Jaeger and Forester 1993, Houck and Verrell 1993, Verrell and Mabry 2000), all of which may require surface activity and could be restricted to a relatively narrow window of suitable surface conditions. Salamanders naturally move vertically through the substrate in response to climatic changes, and the presence or absence of suitable surface microclimatic regimes best explains variation in their vertical distribution (Taub 1961). However, the proportion of a given population at or near the surface at a given time is not known for any plethodontid species (Scott and Ramotnick 1992, Bailey et al. 2004). We also do not know how long a population may remain viable if surface conditions are not amenable and all individuals have to remain subsurface to avoid physiological stress.

Because of the relative rareness of the Siskiyou Mountains salamander, the small size of our search plots, and the resulting small sample sizes, our choices of analysis options with which to evaluate habitat relationships were limited. We were not able to regress habitat attribute values

against salamander numbers, one of the best ways to detect and demonstrate strong environmental relationships. Still, our habitat analyses based upon a presence/absence response from both slopes of the Siskiyou Mountains salamander's range indicated strong relationships with interior forest conditions, exemplified by stable microclimates, moisture-loving plant species, and a long-duration disturbance regime (i.e. late-succession forests). While such conditions may exist outside of mature and late-seral forests, they might be limited in the interior (as opposed to coastal) range of the Siskiyou Mountains salamander. Thus, we suggest that this salamander is likely a mature to old-growth-forest-associate that exists at its biological optimum (Thompson 2004) under conditions found primarily in later seral stages of mixed conifer-hardwood forests in northwestern California and southwestern Oregon.

It is important to use caution when interpreting correlative studies in the absence of data that demonstrate a cause and effect relationship. However, we think that our study clearly links this salamander species with conditions that are found more consistently and reliably within older forests in the drier interior region of the Klamath-Siskiyou Bioregion. These results suggest an "ecological dependence" (Ruggiero et al. 1988) by the Siskiyou Mountains salamander on attributes and conditions found primarily in mature to late-seral forests (see also Welsh et al. 2006).

Many of the biotic and abiotic requirements necessary for long-term viability for the Siskiyou Mountains salamander remain undetermined. However, because of their relative rarity, small range, low mobility, and consequent limited dispersal abilities (e.g., Karraker and Welsh 2006), their viability may depend upon well-distributed mature forests throughout its range. Further, we suggest that salamanders are likely avoiding harvested forest sites, which can act as sink habitat (Pulliam 1988, 2000) and possible barriers to dispersal (Johnston and Frid 2002 and cites therein). Therefore, to assure long-term viability of the Siskiyou Mountains salamander, we suggest that a matrix of intact forests be interconnected across the landscape within their range (Richards et al. 2002) as the best way to assure that vital source populations are maintained on these fragmented forest landscapes over the long term (see Saunders et al. 1991, Cushman 2006).

A Note on Taxonomy and Habitat Relationships

We did not make any effort here to distinguish potential "evolutionarily significant units" (ESU's) within the geographic range of the Siskiyou Mountains salamander (e.g., DeGross 2004, Mead et al. 2005). We ignored these potential ESU's because we believe, based on evidence from other plethodontid salamander complexes with similar levels of genetic differentiation (Larson et al. 1984), that such differences, while interesting historical artifacts and compelling examples of vertebrate evolution, do little if anything to alter their basic eco-physiological limits (e.g., Spotila 1972, Feder 1983) and consequent similar environmental requirements imposed by the plethodontid life form. This life form is shared by all of the potential ESU's within the complex of salamanders occupying the interior forest habitats of the Klamath-Siskiyou Region, all of which occur in conifer-dominated forests.

Conclusions

This study provides a collection of leading models that are most effective at predicting the presence or absence of the Siskiyou Mountains salamander in its northern California and southern Oregon range. Although we have tested these models for goodness-of-fit with accuracy assessment (Tables 2 and 3), we acknowledge the exploratory nature of best subsets selection analysis for this poorly understood species. Our results are subject to the possible effects of compounded Type I error and over-fitting of models. For more definitive results, we recommend further analysis, based upon additional sample data, using the parsimonious *a priori* model selection and inference strategy advocated by Burnham and Anderson (1998), including this collection of candidate models as a subset. However, our tentative results suggest that the best habitat selection models are those with complex relationships between habitat attributes and salamander response, incorporating higher order and interaction effects at several scales. The effects of particular attributes themselves may be biologically and statistically insignificant but in combination with non-linear forms and interactions in the best fitting models may be effective in distinguishing between the occupied and unoccupied habitats of the salamander. It is becoming increasingly clear that carefully designed studies

that collect presence-absence data can provide the critical information on habitat requirements and distributional limits of rare endemic species required to guide informed conservation efforts (Dunk et al. 2004, Edwards et al. 2004, this paper).

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Appendix

Methods Used for Determing Biotic and Abiotic Variables.

Elevation was taken from USGS topographic maps, slope was measured with a clinometer across the search area, aspect was measured in degrees and converted to 1 of 9 directions for analysis (5 was equivalent to both due east and due west, numbers <5 are increasingly more northerly, and numbers >5 are increasingly more southerly). The parent geology/soil type for each site was derived using soil coverages from the relevant National Forests or counties in a GIS environment using the software ARCView (Table 1; g). Climatic layers (including "Illumination") were similarly derived in GIS using PRISM data (Daly et al. 1994) which has a 2 km^2 resolution. "Years since disturbance" was determined from U. S. Forest Service Ranger District or timber company fire and timber harvest records for each site and pertains to these two types of disturbance. Solar index is an estimate of annual solar incident radiation based on latitude, slope, and aspect (Frank and Lee 1966). Count variables (Table 1; c) were calculated as numbers per hectare; the small trees (= 12-52 cm diameter at breast height [dbh]) were counted in a 1/10th-ha circle centered on the salamander search area, the large trees (= >53 cm dbh) were counted in a 1/5th-ha circle similarly situated (Figure 2). Basal areas of the large trees were measured within a 1/5th-ha circle, and for small trees within a 1/10th-ha circle (Figure 2), and were calculated using a basal area equation and reported as cm^2/ha. Forest age was measured using tree core data from three canopy member conifer trees of the dominant size class. The trees were cored, aged and the mean value was used to age the site. The three trees were selected within the 1/5th-ha circle and spaced evenly around the search area (Figure 2). "All conifer species" (Table 1) includes western red cedar (*Thuja plicata*), incense cedar (*Calocedrus decurrens*), Pacific yew (*Taxus brevifolia*), Douglas-fir (*Pseudotsaga menziesii*), true fir species, and all pine species. "All hardwood species" (Table 1) includes madrone (*Arbutus menziesii*), bigleaf maple (*Acer macrophyllum*), Pacific dogwood (*Cornus nuttallii*), California black oak (*Quercus kelloggi*), chinquapin (*Chysolepis chrysophylla*), canyon live oak (*Q. chrysolepis*) and Oregon white oak (*Q. garryana*). "All pine species" (Table 1) includes Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*P. ponderosa*), western white pine (*P. monticola*), and sugar pine (*P. lambertiana*). "Other hardwoods" (Table 1) includes madrone, bigleaf maple, Pacific dogwood, California black oak, and chinquapin. Line transect variables (Table 1; l) were recorded as a proportion of 50 m of transect line per site (Figure 2) (tree species were included only if they are less than 12 cm dbh). Variables derived by visual estimation were percent estimates of the surface of the 1/10-ha circle (Table 1; v) or percent estimates of the 7 x 7 m salamander search area (Table 1; av) (Figure 2). Shrub and understory vegetation consisted of vegetation > 0.5 m (Table 1; Height I). Ground-level vegetation consisted of vegetation < 0.5 m (Table 1; Height II). Small shrubs were < 2 m and large shrubs were > 2 m. "All shrubs" included all woody shrubs not including tree species. Snags and stumps were counted within the 1/5 ha circle. Snags had to be > 12 cm dbh and over 2 m in height to be counted. Small logs were < 50 cm mean diameter, large logs are ≥ 50 cm mean diameter; both size classes were counted irrespective of length, but only those logs > 10 cm in diameter were counted. Leaf litter depth, surface soil and 10 cm soil temperatures were measured with a thermometer at 4 equidistant points on a 1/10-ha circle surrounding the search area (Figure 2), with the mean value used to characterize each site. Canopy cover was measured at the plot center (Table 1, 3f), and at each of four soil stations (Figure 2) (Table 1, 2g); an average of 4 readings taken at each point using a Type B (concave) spherical densiometer was used to estimate each canopy value in the analysis. Air temperature was measured with a thermometer and relative humidity was measured with a sling psychrometer at the search site at the time of animal sampling. Subsurface conditions (Table 1, 3e) consisted of the number of interstitial substrate surfaces for 10 0.05-m long sections that were counted for each of two trenches dug at each plot (Figure 2) (based on Kinsolving and Bain 1990) and estimated for each of the fill type

in each trench. Fill types were: empty, mineral soil, leaf litter, or mixed. For the South Slope data analysis, leaf litter and mixed fill types were combined because of low occurrence of leaf litter. Large rock (Table 1, 3d) includes % boulder and % bedrock combined. Substrate grain size was classified as: sand = 0.06-2.0 mm, gravel = 2.0-32.0 mm, pebble = 32.0-64.0 mm, cobble = 64.0-256.0 mm, boulder = 256.0+ mm.

Those variables that could model relationships at more than one spatial scale (e.g., canopy closure, temperature), were assigned to a particular scale and ecological subset based on the scale at which the variable was measured (Table 1, Figure 2). This approach has practical application for resource managers because these ecological subsets represent aspects of forest structure manipulated or altered during activities such as timber harvesting and road building.