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# Habitat Correlates of the Del Norte Salamander, Plethodon elongatus (Caudata: Plethodontidae), in Northwestern California

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ABSTRACT.--A stratified systematic sampling design was used to quantify the habitat relationships of the Del Norte salamander (*Plethodon elongatus*) in northwestern California. We sampled 57 sites, each within at least 5-7 ha of relatively homogeneous forest or post-forest habitat, where we measured 83 characteristics of the environment. Salamander sampling consisted of area-constrained sampling of 7 x 7 m plots with at least 25% rock cover at each site. A subset of 43 variables was used in a hierarchical analysis of habitat associations using discriminant analysis and regression. Variables included attributes at the landscape, macrohabitat, and microhabitat scales. Results indicate a significant association of the Del Norte salamander with older forests with closed, multi-storied canopy (composed of both conifers and hardwoods), with a cool, moist microclimate, and rocky substrates dominated by cobble-sized pieces. These habitat attributes appear optimal for survival and reproductive success throughout most of the range of this species. The Del Norte salamander may require ecological conditions found primarily in late seral stage forests.

The Del Norte salamander (*Plethodon elongatus*) is the southernmost member of the six species of Pacific Northwest *Plethodon* and has a relatively restricted distribution in the three southwestern counties of Oregon and the four northwestern counties of California. It occurs in isolated populations throughout its range, occasionally in relatively high densities (Welsh and Lind, 1992; Diller and Wallace, 1994). It is generally associated with rocky substrates in low-elevation (< 1250 m) mixed conifer-hardwood forests (Stebbins, 1954, 1985; Nussbaum et al., 1983; Herrington 1988; Welsh and Lind 1991; Leonard et al., 1993), but little is known about specific habitat affinities.

Previously the USDA Forest Service conducted research to test the association of vertebrates with forest age in the Douglas-fir mixed hardwood forests of northwestern California. The Del Norte salamander was found in significantly greater abundance in late seral stage forests (old-growth) compared with early seral stages (Welsh, 1990). These results are in need of confirmation because only 21 of the 54 study sites fell within the range of this salamander, although Raphael (1988) reported similar results.

The apparent association of the Del Norte salamander with old-growth forests and the rapid loss of these late seral habitats due to timber harvesting (Thomas et al., 1988), have resulted in its being listed as a "species of special concern" by the State of California (Steinhart, 1990; Jennings and Hayes, unpubl.) and a candidate (C2) species by the U.S. Fish and Wildlife Service (Drewry, 1989). Clearly, more information on the habitat associations of this species is needed. A better understanding of its habitat relationships might explain the lower numbers found in early successional forests and provide a basis for management alternatives that could reverse the loss of individuals and decline in populations due to forestry practices.

This paper reports on a study of habitat as

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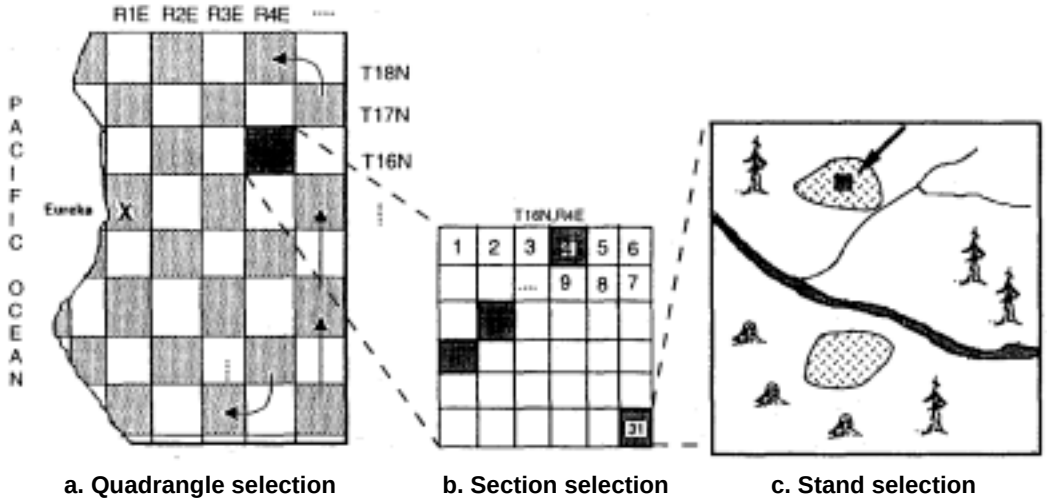



FIG. 1. Stratified systematic site selection procedure, with a random component (see text), used to locate sampling sites for the Del Norte salamander (*Plethodon elongatus*) across its range in northwestern California.

sociations of the Del Norte salamander at sites across the successional continuum in the mixed conifer-hardwood forests of northwestern California. Our objectives were to (1) examine the association with late seral stage forests and clarify the nature of that relationship; (2) investigate and elucidate other possible habitat requirements; and (3) evaluate the potential impacts of continued habitat alterations on populations of this species.

## MATERIALS AND METHODS

*Site Selection*.-To distribute sampling across the range of the Del Norte salamander within northwestern California and avoid the biases inherent in many museum collections (e.g., site proximity to major roads), we chose sites using a stratified systematic design, with a random component, at four nested levels (Fig. 1): (1) biogeographic, (2) township and section, (3) seral stage, and (4) minimum essential microhabitat.

The first level (biogeographic) sampled across the range of the species and within its attitudinal limits in northwestern California (Stebbins,1985; Jones and Raphael, 1990). All sample sites occurred within the drainages of the Smith, Klamath, and Trinity rivers on public lands from near the Oregon border south to north central Humboldt and Trinity counties, California (latitude 40°30'N), and east from the Pacific Ocean to western Siskiyou and Trinity counties (longitude 123°20'W).

The second level (township and section) selected sites randomly, while simultaneously spacing them systematically across the sampling domain. It was based on the U.S. Geological Survey township and range system; each quadrangle is composed of 36 one $mi^2$ sections. We randomly selected the first quadrangle in the vicinity of the southeastern corner of the range. Each additional quadrangle was evenly spaced until 50 quadrangles (our desired minimum sample size) were designated across the range (Fig. la). Within selected quadrangles, we randomly chose four sections to search for appropriate forest stands by picking numbers from 1 to 36 (Fig. lb).

The third level (seral stage) sampled across the seral stages of the region's forests in proportion to their relative abundance. Within each section we located up to four sites, in each of four forest age classes, where possible (Fig. lc): clear-cut (0-30 yrs), young forest (31-99), mature forest (100-199), and old-growth forest (200+) (Franklin et al., 1986). Sampling areas were then located in at least 5-7 ha of contiguous forest or clear-cut (no edge habitat) with uniform age, structure, and composition (relatively homogeneous stands). We visited sites to assess potential for sampling, and stands were either accepted or rejected on the basis of our finial criterion, the presence of appropriate microhabitat.

The fourth nested level, for placement of 7 x 7 m (49 $m^2$) salamander sampling plots, was based on documented minimum microhabitat requirements (minimum essential microhabitat or MEM). The intent was to maximize time, effort, and the usefulness of data sets by not sampling for the species at a site where it had little or no possibility of occurrence. Rocky substrate was the required microhabitat which in this

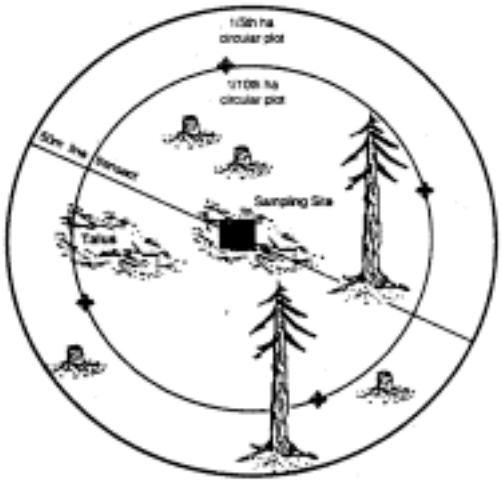



FIG. 2. Sampling methods used to measure forest environment variables (Table 1) collected in association with sampling for the Del Norte salamander (*Plethodon elongatus*). Crosses mark locations for soil and climate measures. Circles not drawn to scale.

study consisted of any rock type (chert, slate, shale, etc.) with at least some cobble-size pieces (64-256 mm diameter) on the surface (i.e., rocks large enough to provide cover). Pilot sampling indicated ≥25% surface rock cover within the 49 $m^2$ as a minimum amount to yield sufficient animals (if present) for comparative analysis. Once we found that a stand could meet this condition, a 49 $m^2$ sample plot was placed in the rockiest area with at least 25% (visual estimate) of the surface covered by rock. Rock covered by leaf litter or other organic debris could be easily discerned and was included. All plots were at least 75 m from any forest edge.

If a site failed to contain 49 $m^2$ of substrate with 25% rock cover it was rejected. Because this minimum amount of rock substrate was used to define sample sites, the absence of rock was not evaluated; however, the range of variation for this parameter was examined in this analysis.

*Animal Sampling*.- Intensive area-constrained searches (Welsh, 1987; Corn and Bury, 1991) were conducted during daylight hours at each sampling site to determine the number of animals present. This approach required the thorough searching of the 7 x 7 m sample area by one or more workers. Each site was systematically searched with all cover objects turned over, and other substrates raked or sifted, down to 15 cm unless we saw a salamander escaping deeper, in which case we pursued it. In this way all animals on or near the surface were captured. We sampled only when obvious surface moisture was present under cover objects and when air temperatures were ≥ 9.0C.

*Measuring Forest Biotic and Abiotic Parameters.*-We selected habitat variables using three criteria: (1) parameters that reflected structural, compositional, and microclimatic aspects of the forest environment relevant to the Del Norte salamander as indicated by previous research (Stebbins, 1954, 1985; Nussbaum et al., 1983; Welsh, 1990; Welsh and Lind, 1991); (2) parameters that represented changes in structure and composition of the forest resulting from management practices like timber harvesting and reforestation, or natural successional events such as fire, landslide, or flood; and (3) variables that incorporated aspects of the forest environment based on three scales of spatial organization: landscape, macrohabitat, and microhabitat.

Our approach was to initially estimate a wide range of parameters and then eliminate redundant variables prior to statistical analyses. Measurements of general locators (landscape scale), forest structure (macrohabitat scale), and microhabitats resulted in a total of 83 variables (see Welsh [1993] for details and methods of measurements). Methods for these variables included (Fig. 2): (1) measurements of general site characteristics with instruments and from topographic maps; (2) the Braun-Blanquet (1932) cover abundance scale; (3) a 50-m line transect for ground and understory vegetation cover (Canfield, 1941; Brown, 1974); (4) tree counts in 1/10 ha and 1/5 ha circles centered on the sample site; (5) point measurements of soil and litter characteristics (average of four measurements); and (6) estimates of sampling area microhabitat and substrate composition.

*Statistical Analyses.* -Rotenberry (1986) and Rice et al. (1986) advocated a combined statistical approach—regression analysis plus discriminant analysis—when conducting studies of habitat relationships over a large scale and involving heterogeneous habitat types. This approach allows for cross-validation between methods. Regression analysis explores how the number of individuals vary as a particular feature of the habitat varies. A limitation of the regression approach is that factors other than habitat can cause variation in numbers along a habitat gradient and thus complicate interpretation (cf. Van Horne, 1983). Discriminant analysis can compare the variation in average habitat between sites with and without the species of interest, regardless of differences in population size. This approach addresses the question of what range of attributes of the habitat can provide suitable conditions for the species to exist. Used together, these techniques can reveal aspects of the habitat that may be limiting for a species and also indicate those aspects of habitat that might be managed to maintain or increase animal numbers.

We first address what attributes of habitat de-

termine the presence or absence of this species rather than the question of why salamander numbers might vary among sites. Therefore, regression was used as a second tier of analysis to further examine relationships with the most significant variables derived from the discriminant analysis.

We performed preliminary descriptive analyses to review the distributions of the initial 83 habitat variables. Histograms, normal score plots, and measures of skewness and kurtosis (SAS, 1990) were used to assess the normality of distributions, and deviations were, corrected by appropriate transformations (log, square root, or arcsine [Sokal and Rohlf, 1981]). Reduction of variables prior to analysis based on elimination of redundancy (those showing the best correlation with salamander numbers were retained) and omission of those with mostly zero values (>80%) resulted in 43 variables for analysis (Table 1). In the subsequent multivariate statistical analysis we assumed (but did not test) that univariate normality implied multivariate normality.

For multivariate analyses we grouped variables into subsets (ecological components) based on similarity of spatial scale and vertical stratum of the forest environment (Table 1). Dueser and Shugart (1978) and Bingham and Sawyer (1991) used a similar approach. For those variables that could model relationships at more than one spatial scale, the assignment to a particulars cale and ecological component was based on the scale at which the variable was measured (see Table 1, Fig. 2). An ecological component was defined as a group of variables that together described a logical class of structural, compositional, or climatic attributes of the forest environment. This approach has application for resource managers, because these ecological components are related to those aspects of forest structure commonly manipulated or altered during timber harvesting and road building. Significant variables from each subset from the ecological component analyses can subsequently be combined to derive composite habitat models that incorporate multiple components and scales. Although we believe this approach holds promise for both analytical and management applications, it will benefit from further evaluation and experimentation.

A two-group discriminant analysis (DA) (SAS, 1990) was run for each ecological component using a stepwise procedure to select variables. We tested the null hypothesis that a given habitat variable does not add any additional discriminatory power. Variables were entered into models if their P values for the partial F statistic were $\leq 0.10$. For model-building, we chose a moderate significance level (*alpha* < 0.10) because: (1) it permitted more variables to enter the models, thus providing the best discrimination power given the limits of our sample size (Costanza and Afifi, 1979); (2) a more moderate level reduces the chances of type II errors (accepting a false null hypothesis); and (3) a moderate *alpha*-level provided a criterion more appropriate for detection of ecological trends (Toft and Shea, 1983; Toft, 1991). Once the variables were selected, a linear discriminant function was determined on the basis of those variables.

Besides the assumption of multivariate normality required for statistical inferences, DA also assumes homogeneous variance-covariance structure among groups (Neff and Marcus, 1980). We tested for heterogeneity among variance-covariance matrices using Bartlett's modification of the likelihood ratio test (with alpha = 0.05; SAS, 1990) and compared results of classification success for both linear and quadratic functions where appropriate. However, we present all results in terms of linear functions because quadratic functions yielded classification results similar to those of the linear functions, linear functions are easier to interpret, and the stepwise technique used to choose variables was linear. Standardized structure coefficients are presented as an indication of the relative contribution of each variable chosen by stepwise DA to the discriminant function (Rencher, 1992).

We employed a jackknife procedure (SAS, 1990) to evaluate the classification success of each model. Cohen's Kappa (Titus et al., 1984) was computed for each test to indicate classification success compared with chance; the level of acceptable performance was set at alpha = 0.05. In classification tests based on the discriminant functions, we assumed that our random systematic site selection yielded a proportion of sites with and without salamanders that reflects the true proportion. Thus, we adjusted the prior probabilities of group membership. accordingly (priors proportional) (SAS, 1990).

We examined the relationships between salamander abundance and all significant variables from the DA using regression. This analysis was performed on sites with salamanders only, and one outlier site with very high captures was removed. Simple linear and standard non-linear curves (logarithmic, exponential, and second-order polynomial) were fit to untransformed data, and the variables with the best $R^2$ are presented.

## RESULTS

We sampled 57 sites for the Del Norte salamander from 27 February to 6 June 1989 (see Fig. 1. of Welsh and Lind, 1992). Thirty sites had salamanders, with a total of 146 captures: 78 juveniles and sub-adults (19-40 mm snout-

TABLE 1. Hierarchical arrangement[1] of ecological components represented by 43 measurements of the forest environment taken in conjunction with sampling for the Del Norte salamander (*Plethodon elongatus*).

| II. Landscape Scale | III. Macrohabitat or Stand Scale | | | | | | IV. Microhabitat Scale |
|---|---|---|---|---|---|---|---|
| A. Geographic relationships | A. Trees: density by size | B. Dead & down wood: surface area & counts | C. Shrub & understory composition (>0.5 m) | D. Ground-level veg. (<0.5 m) | E. Ground cover | F. Forest climate | A. Substrate composition[5] |
| Latitude (degrees)<br>Longitude (degrees)<br>Elevation (m)<br>Slope (%)<br>Aspect (degrees) | *Small conifers__C [2]<br>*Small hardwoods__C<br>Large conifers__C<br>*Large hardwoods__C<br>Forest age (years)[3] | *Stumps-B<br>All logs-decayed__C<br>*Small logs-sound__C<br>*Sound log area__L<br>*Conifer log-decay. area__.<br>*Hrdwd. Log-decay. area__L | *Understy conifer__L<br>*Understy hardwoods__L<br>*Large shrub__L<br>*Small shrub__L<br>Bole__L<br>Height II-ground veg__B (0.5-2 m) | *Fern__L<br>*Herb__L<br>*Grass__B<br>Height I-ground veg__B (0-0.5 m) | *Moss__L<br>*Lichen__B<br>Leaf__B<br>*Exposed soil__B<br>Litter depth (cm)<br>Dominant rock__B<br>Co-dom. Rock---B | Air temp. (°C)<br>Soil temp. (°C)<br>Solar index[4]<br>% canopy closed<br>Soil pH<br>Soil relative humidity (%)<br>Rel. humidity (%) | Pebble__P (% of 32-64 mm diameter rock)<br>Cobble__P (% of 64-256 mm diameter rock)<br>Cemented__P (% of rock cover embedded in soil/litter matrix) |

[1] Spatial scales arranged in descending order from coarse to fine resolution (see Wiens, 1989). Level l relationships (the biogeographic scale) were not analyzed because all sampling occurred within the range.

[2] C = count variables which are numbers per hectare; B = Braun-Blanquet variables which are % cover in 1/10-ha circle; L = Line transect variables which are percent of 50-m line transect; P = % of 49-$m^2$ salamander search area. Small trees = 12-53 cm DBH (dia. at breast height), large trees = > 53 cm DBH.

[3] Based on mean of cores from three trees in dominant size class on site; classes used = 12-27 cm, 27-53 cm, 53-90 cm, 90-120 cm, and +120 cm DBH.

[4] Solar index is an estimate of annual incident solar radiation based on latitude, slope, and aspect (Frank and Lee, 1966).

[5] Rock particle sizes from Platts et al. (1983).

* Variable was transformed for statistical analyses.

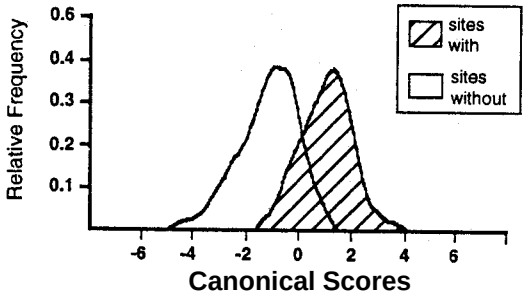
TABLE 2. Two-group stepwise discriminant analyses of 57 sites sampled for the Del Norte salamander *(Plethodon elongates)* across its range in northwestern California. Independent variables were grouped for separate analyses by ecological component (Table 1); standardized structure coefficients are presented for those variables that entered each model. Means and standard deviations are presented in the actual measured units, although some variables were transformed prior to analyses (Table 1). Models were, tested for classification success with a jackknife procedure. Cohen's Kappa statistic indicates the classification success compared with chance. An asterisk indicates a model with heterogeneous variance-covariance matrices.

| Ecological component | Sites with salamanders (n = 30) Mean | SD | Sites without salamanders (n = 27) Mean | SD | Standardized structure coefficient |
|---|---|---|---|---|---|
| II. Landscape Scale | | | | | |
| A. Geographic relationships | | | | | |
| Slope | 30.33 | 8.20 | 25.15 | 7.15 | 1.000 |
| Wilks' Lambda = 0.888; F (df = 1,55) = 6.95; *P* = 0.0109 | | | | | |
| Jackknife success (%) = 61.4; Cohen's Kappa = 0.226; *P* = 0.0445 | | | | | |
| III. Macrohabitat Scale | | | | | |
| A. Trees: density and size class | | | | | |
| Small hardwoods | 241.33 | 235.82 | 98.93 | 179.52 | 0.541 |
| Forest age | 215.80 | 210.61 | 53.89 | 101.93 | 0.694 |
| *Wilks' Lambda = 0.754; F (df = 2,54) = 8.81; *P* = 0.0005 | | | | | |
| Jackknife success (%) = 75.40; Cohen's Kappa = 0.509; *P* = <0.0001 | | | | | |
| B. Dead and down wood: surface areas and counts | | | | | |
| No variables entered the model. | | | | | |
| C. Shrubs and understory composition (>0.5 m) | | | | | |
| Understory hardwoods | 24.56 | 19.15 | 11.44 | 14.09 | 1.000 |
| Wilks' Lambda = 0.828; F (df = 1,55) = 11.46; P = 0.0013 | | | | | |
| Jackknife success (%) = 71.91; Cohen's Kappa = 0.437; P = 0.0005 | | | | | |
| D. Ground level vegetation (<0.5 m) | | | | | |
| Herb | 4.28 | 9.74 | 8.49 | 13.09 | 0.816 |
| Fern | 5.25 | 9.38 | 1.62 | 3.90 | -0.722 |
| Wilks' Lambda = 0.849; F (df = 2,54) = 4.80; *P* = 0.0121 | | | | | |
| Jackknife success (%) = 70.20; Cohen's Kappa = 0.392; *P* = 0.0019 | | | | | |
| E. Ground cover | | | | | |
| Moss | 20.08 | 27.82 | 6.89 | 15.79 | 0.899 |
| Co-dominant rock | 18.37 | 16.66 | 30.06 | 19.88 | -0.718 |
| Wilks's Lambda = 0.696; F (df = 2,54) = 11.77; *P* = 0.0001 | | | | | |
| Jackknife success (%) = 77.21; Cohen's Kappa = 0.540; *P* = <0.0001 | | | | | |
| F. Forest climate | | | | | |
| Relative humidity | 75.17 | 17.81 | 61.22 | 15.78 | 0.675 |
| Canopy closed (%) | 72.47 | 29.42 | 35.70 | 36.12 | 0.846 |
| Wilks' Lambda = 0.630; F (df = 2,54) = 15.85; *P* = 0.0001 | | | | | |
| Jackknife success (%) = 68.42; Cohen's Kappa = 0.364; *P* = 0.0031 | | | | | |
| IV. Microhabitat Scale | | | | | |
| A. Substrate composition | | | | | |
| Cobble | 44.83 | 23.53 | 34.70 | 17.75 | 1.000 |
| Wilks' Lambda = 0.943; F (df = 1,55) = 3.31; *P* = 0.0744 | | | | | |
| Jackknife success (%) = 57.89; Cohen's Kappa = 0.156; *P* = 0.1210 | | | | | |

vent length [SVL]) and 68 adults (>40 mm SVL). Captures at sites with salamanders ranged from one to 30 animals in the $49^2$ m plots.

*Discriminant Analysis*.-Slope was the only landscape scale variable that significantly discriminated between sites with and without salamanders (Table 2: IIA). Sites with salamanders had slightly greater slopes. This single variable model was able to discriminate between sites with and without salamanders with 61.4% accuracy, 22.6% better than by random chance.

Five of six ecological components at the macrohabitat scale yielded models with discriminatory power (Table 2: III). The trees component indicated that sites with salamanders both were greater in age and contained more small hardwoods than did sites with no salamanders (Table 2: IIIA). This highly significant model




Variables in Composite Model

low ← % canopy closure → high
low ← relative humidity → high
high ← co-dom rock → low
low ← % cobble → high
low ← % slope → high

FIG. 3. Frequency curves (kernel method; Silverman [1986]) of canonical scores for sites with (N = 30) and without (N = 27) the Del Norte salamander (*Plethodon elongatus*) based on the composite habitat model (Table 3). Values of variables (i.e., high or low) represent trends relative to canonical scores.

distinguished sites with and without salamanders at 75.4%, 50.9% better than chance for the jackknife test. The dead and down wood component failed to yield a model (Table 2: IIIB). Within the shrub and understory component the function was based on a single variable (understory hardwoods), which were more abundant on sites with salamanders (Table 2: IIIC). This model accurately predicted salamander presence or absence at 71.90%, 43.7% better than chance. The component model of ground level vegetation was derived from two variables: ferns (more on sites with salamanders) and herbs (fewer on sites with salamanders) (Table 2: IIID). This model had 70.20% of sites correctly classified, 39.2% better than chance (jackknife procedure). The ground cover component model was derived from two variables: moss (greater on sites with salamanders) and percent co-dominant rock (the second most abundant rock size) (less on sites with salamanders) (Table 2: IIIE). The ground cover component model was the best model overall based on jackknife success, with 77.21% of sites correctly classified; 54.0% better than chance. The forest climate model, consisting of relative humidity and percent canopy closed (both higher on sites with salamanders) (Table 2: IIIF), had the highest model *F* statistic of all component models. It ranked fourth overall in classification success with 68.4% of sites correctly classified, 36.4% better than chance.

The single component at the microhabitat scale, substrate composition, yielded a single variable model based on percent cobble (greater on sites with salamanders) (Table 2: IVA). However, the classification test results were the poorest of all the component models.

The final composite discriminant model provided a means to evaluate the relative influence of significant variables derived from the component analyses. The composite model was derived from four ecological components, with variables entering in the following order: percent canopy closed, relative humidity, co-dominant rock, cobble, and slope (Table 3, Fig. 3.) This model had classification success of 82.50%, 64.8% better than chance.

*Regression Analyses.*- The regression analysis

TABLE 3. Multiple component discriminant model. All variables derived from the anlayses of ecological components (Table 2) were combined in a two-group discriminant analysis (across all scales and ecological components) to derive a multiple component model of the habitat of the Del Norte salamander. Standardized structure coefficients indicate the relative contribution of each variable to the discriminant function.

| Step | Variable | F-statistic | *P* | Standardized structure coefficient |
|---|---|---|---|---|
| 1 | Canopy closed (%) | 17.90 | 0.0001 | 0.503 |
| 2 | Relative humidity | 10.65 | 0.0019 | 0.370 |
| 3 | Co-dominant rock | 5.85 | 0.0190 | -0.287 |
| 4 | Cobble | 7.83 | 0.0072 | 0.216 |
| 5 | Slope | 6.53 | 0.0136 | 0.313 |
| | Forest age | | | |
| | Small hardwoods | | | |
| | Understory hardwoods | | | |
| | Ferns | | | |
| | Herb | | | |
| | Moss | | | |

Wilks' Lambda = 0.437; F (df = 5,51) = 13.13; *P* = 0.0001
Jackknife success (%) = 82.50; Cohen's Kappa = 0.648; *P* = <0.00001

of sites with salamanders only, examining all those variables derived from the DA of ecological components, indicated that three variables were highly significant predictors of increased numbers of salamanders at a site. Percent canopy closure was the best ($R^2$ = 0.297) (Fig. 4a). The 95% confidence interval (C.I.) (based on sites with captures only) indicated that the true mean canopy closure for sites with salamanders was between 61.9% and 83.0%. Sites without salamanders had a 95% C.I. of 22.0% to 49.4% canopy closure. Number of small hardwoods was the second best single variable for predicting salamanders ($R^2$ =0.271) (Fig. 4b). Here, the 95% C.I. for sites with captures contained 156.9-325.7 small hardwoods/ha, while sites without salamanders had a 95% C.I. of 31.21-166.6 small hardwoods/ha. The third best predictor of abundance was forest age ($R^2$ = 0.119) (Fig. 4c). The 95% C.I. for forest age for sites with salamanders was from 140.4 to 291.2 yrs, and for sites without salamanders, 15.4 to 92.3 yrs.

## DISCUSSION

*Landscape Scale*.-Three of the five variables in the geographic relations component (elevation, latitude, longitude; Table 1) were held within narrow limits because the sampling domain was restricted to sites within the published geographic and elevational range of the Del Norte salamander (sea level to 1250 m) in northwestern California. (Work subsequent to ours has found this species occurring up to 1460 m in western Siskiyou Co., California [S. Cuenca and D. Clayton, pers. comm.].) This, species showed little variation in numbers along these spatial trajectories. However, the discriminant analysis (DA) indicated that slope was greater on sites that contained salamanders. Diller and Wallace (1994) reported such a relationship for coastal populations of this species, and Ramotnick and Scott (1988) found a similar relationship for *P. neomexicanus* in the southern Rocky Mountains. As suggested by the above authors, our data also show that the positive relationship with slope probably results from the accumulation of rocky debris in a layered fashion at the bottoms of steeper slopes (talus piles). Such conditions increase subterranean interstitial spaces as the rock layers aggregate and are buried under the accumulating forest litter. These sites usually yield the highest numbers of captures per unit effort for this species (pers. obs.). Maiorana (1978) presented evidence of the importance of subterranean retreat space in regulating numbers in other plethodontid salamander populations.

Another important factor possibly contrib.-uting to this relationship with slope is the effect

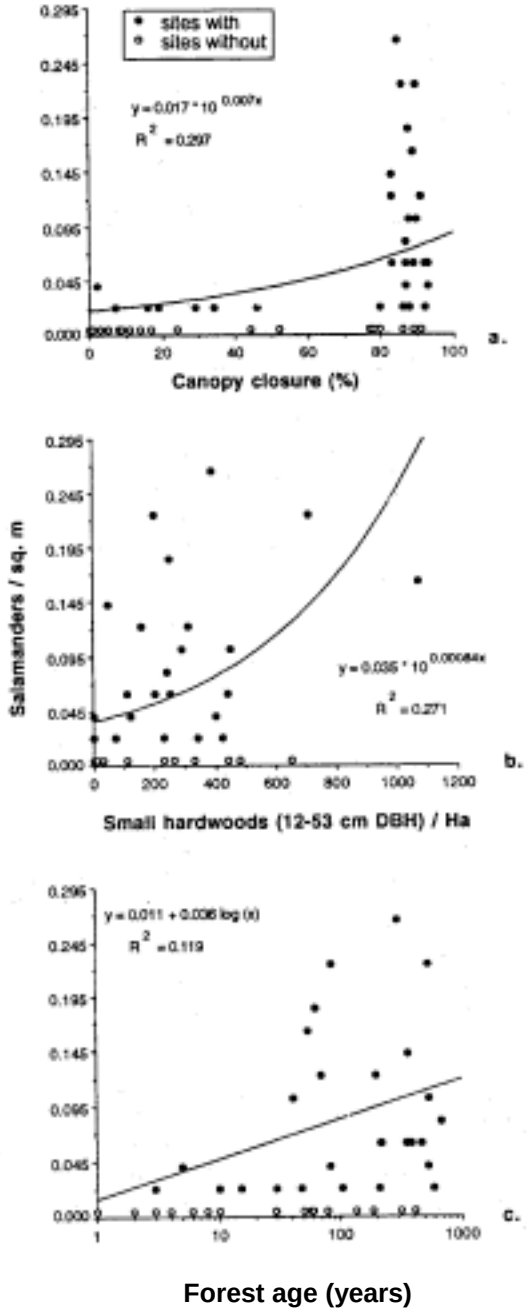



FIG. 4. Bivariate scatter plots for the three best habitat variables based on highest RI values: a. percent canopy closure; b. number of small hardwoods; c. forest age (mean of three conifers in dominant size class at site) (x axis is log scale). Regression lines and Rz values apply to sites with salamanders only (filled circles; N = 30); sites without salamanders (empty circles; N = 27) are included to show overall distributions. Some overlapping points are obscured.

of ongoing timber harvesting. Timber harvesting in northwestern California has progressed from areas with little or no slope to increasingly steeper areas. As a result, older forest is today more abundant on areas with greater slope; forest age and slope were significantly correlated ($r = 0.322$; $P = 0.015$).

*Macrohabitat Scale*.-The trees component yielded a highly significant model (DA), with excellent predictive power (Table 2). The regression analysis yielded similar results. Increased forest age and numbers of small hardwoods were two of the best indicators of both salamander presence and increased abundance (Table 2: IIIA, Fig. 4b, c). The relationship with forest age agrees with earlier evidence of an association with late seral forests (Raphael, 1988; Welsh and Lind 1988; Welsh 1990). The DA also showed a positive relationship with understory hardwoods (see shrubs and understory component; Table 2: IIIC); as did Raphael (1988). Welsh and Lind (1991) reported a significant relationship between basal area of hardwoods and increased numbers of Del Norte salamanders. Why hardwoods are good predictors of the presence and abundance of this species has not yet been determined. Possibly, the increased biomass of deciduous vegetation, with the consequent leaf fall, may support a more abundant and diverse community of forest floor insects than would a pure conifer forest. Small terrestrial invertebrates are the primary food for Del Norte salamanders (Nussbaum et al., 1983). Another aspect of the hardwood component that may be important for the salamanders is that of forest structure. In the characteristic mature mixed conifer-hardwood forests of northwestern California, hardwoods tend to form the sub-canopy and understory (Bingham and Sawyer, 1991, 1992). This complex multilevel forest structure forms an essentially closed canopy and contributes to a relatively cool and stable microclimate on the forest floor. Such conditions are optimal for terrestrial plethodontid salamanders (see Feder, 1983).

The DA yielded no model for the dead and down wood component. Down wood is apparently not important to this rock associated species, although Del Norte salamanders occasionally use woody debris for cover when it occurs in conjunction with rocky substrates (Welsh and Lind, 1991). In contrast, other western plethodontid salamanders show strong associations with dead and down woody material (Whitaker et al., 1986; Aubry et al., 1988; Bury and Corn, 1988; Corn and Bury, 1991; Gilbert and Allwine, 1991; Welsh and Lind, 1991).

The DA of the shrubs and understory component indicated a positive relationship with hardwood shrub species and abundance of Del Norte salamanders, but the nature of this relationship is not understood (see discussion of hardwood trees above).

The DA of the ground-level vegetation component indicated that sites containing Del Norte salamanders were characterized by more ferns and fewer herbs than sites with no salamanders (Table 2: IIID). We are unaware of any evidence that ferns play a direct role in the biology of the Del Norte salamander, but ferns are indicative of the cool, moist microclimatic conditions which also favor plethodontid salamanders (Feder, 1983). Spies (1991), Spies and Franklin (1991), and Frost (1992) reported more mesothermal-adapted herb species in older, closed canopy forests. The negative relationship between herbs and salamanders is thus contrary to other macrohabitat relationships demonstrated here, which indicate a strong association with characteristics of late seral forests. It may be that the rock-dominated substrates preferred by this salamander are edaphically poor sites for many forest herb species.

The two-variable DA model from the ground cover component had the greatest predictive power of all component models according to the jackknife test. These results attest to the importance of substrate conditions in the biology of the Del Norte salamander. In this DA model the variable co-dominant rock showed a negative relationship with salamander presence (Table 2: IIIE). This variable was defined as the percent cover of the second most abundant size class of rock within the 1/10 ha circle (nine size classes were possible [Welsh; 1993]). The presence of rock was a minimum essential microhabitat (MEM) site selection criterion, so all sites sampled contained at least 25% surface covering of rock. However, sites with salamanders, as well as those with higher numbers of salamanders, were sites that also had a relatively low percent of surface area covered by a smaller co-dominant rock size class. We interpret this as indicating that the presence of a large (=cobble) dominant size class of rocks, with few small rocks between them, created the maximum amount of interstitial space for cover.

The significantly higher values for moss cover (Table 2: IIIE) on sites with salamanders are probably indicative of sites with cooler, moister microclimates. Bingham and Sawyer (1991) noted that moss was more abundant in the older forests of northwestern California than in younger forests.

The model derived from the forest climate component proved to be the most significant in our DA based on model F statistic (Table 2: IIIF). Percent canopy closed (positive with salamander numbers) was the most influential variable in the DA model, and the relationship holds for the bivariate regression (Fig. 4a). This variable indirectly measures the amount of light

(and heat) that penetrates the canopy and reaches the forest floor. As such, it indicates average annual microclimatic conditions (surface temperatures and moisture) at ground level. These microclimatic conditions are known to be markedly cooler, moister and more stable in interior (closed canopy) forests than forest edge or openings (Chen et al., 1993). However, Diller and Wallace (1994) reported no relationship between salamander presence and canopy cover for coastal populations.

Relative humidity (Table 2; IIIF: positive relationship) was a measure of site conditions at the time of sampling. Our sampling was timed to coincide with the late winter to early spring rainy season, a period of high surface activity for this species (Welsh and Lind, 1992). This variable in the climate model indicated that even during high seasonal activity periods, sites with relatively greater humidity promote greater surface and near surface activity and probably also support denser populations of this species compared with relatively drier sites.

Welsh (1993), reporting on an all-possible-subsets (APS) regression analysis of this data set, found several additional macrohabitat scale attributes that varied with salamander numbers. Increased numbers of large hardwoods, greater leaf litter depth, and increased epiphytic lichen (wind fall) were significant predictors of greater salamander abundance; while increased stumps (a surrogate for clearcuts), decayed logs, grass, height I (< 0.5 m) ground vegetation, and air temperature were significant predictors of decreased salamander abundance.

Collectively, these macrohabitat models indicate the importance of a relatively cool, moist climatic regime for this species. The importance of such climates has a strong physiological basis in the biology of plethodontid salamanders (Feder, 1983). The presence or absence of suitable surface microclimatic regimes appears to be the best explanation for the variation in the vertical distribution of salamanders (Taub, 1961). They move horizontally and vertically in the soil column, depending on both the weather and the season (Heatwole, 1962; Fraser, 1976; Jaeger, 1979, 1980). However, the proportion of a given population at or near the surface at a given time is not known for plethodontid salamanders (Scott and Ramotnick, 1992). We also do not know how long a population could remain viable if surface climatic conditions were not amenable and all individuals had to remain submerged to avoid physiological stress. Behavioral data suggest that at least some surface activity may be critical for reproduction and feeding (Fraser, 1976) in these salamanders (Verrell, 1989).

*Microhabitat Scale*.-Cobble entered both the component and composite level DAs, but it demonstrated low classification success by itself (Tables 2, 3). We believe the poor performance of our substrate composition DA model to be an artifact of the sampling design, which required all 7 x 7 m plots to contain at least 25% rock cover. The habitat characteristic of rocky substrates constituted the minimum essential microhabitat (MEM) requirement for placement of our sample plots. Cobble was the most common rock size at 34 of 57 plots. Such use of documented habitat specializations permits a sampling strategy in which random sites can be rejected in cases where MEM is completely lacking. This approach provides a more focused, yet randomized, study design that can address questions about the nature of salamander distributions among and within sites with requisite microhabitat. While this minimum requirement may constitute a sampling bias against detection of animals in low numbers in suboptimal habitat across the successional sequence, we believe it is a valid approach for a comparative study as long as all sites sampled meet the minimum requirement for the relevant parameter. The importance of rocky substrates for this species is well established, so this sampling approach is sound. However, this model would no doubt have been a better predictor of salamander presence had this criterion not been imposed by the study design.

Welsh's (1993) microhabitat scale APS model consisted of cobble plus "cementedness," a variable that estimated the percent of rock substrate that was "glued" in by decomposing leaf and needle litter and organic soil above the mineral soil layer. This model was a significant predictor of increased salamander abundance. Cobble in a matrix of decomposing organic materials appears to form the best substrate conditions for these salamanders because numerous small, protected interstitial spaces are created as the rock accumulates in layers covered by leaf litter and soil. Such a matrix is favored by Del Norte salamanders, possibly because of the increased protected cover, more favorable microclimatic conditions within, and the greater invertebrate forage such conditions would support.

The variables that demonstrated the strongest relationships in both the DA (Table 2) and the bivariate regression analysis (Fig. 4) and are thus indicative of both presence and increased abundance of Del Norte salamanders were percent canopy closure, small hardwoods, and forest age. Other indicators of salamander presence from the DA included greater slope, more understory hardwoods, more ferns, fewer herbs, more moss, less secondary (co-dominant) rock, increased relative humidity, and more cobble for sites with salamanders than those lacking them. These results indicate the niche (sensu Grinell; see James et al., 1984) of the Del Norte salamander is com-

posed of: (1) a mixed coniferous/ hardwood late seral stage forest with a closed, multi-story canopy; (2) cool, moist microclimate with moss and fern ground cover, lichen downfall, and a deep litter layer; and (3) rocky substrates dominated by cobble. Welsh and Lind (1991) quantified the niche of this species on the basis of a small sample size, but the results are highly consistent with those reported here. Welsh and Lind (1991) found that Del Norte salamander abundance varied positively with forest age, basal area of hardwoods, percent cover of rock, and large trees, and varied negatively with small conifers (5-80 cm DBH) (but see Diller and Wallace, 1994).

Our habitat model suggests that the Del Norte salamander has evolved in close association with conditions that predominate in late seral forests (Welsh 1990). However, this study also indicated that this species occurs in younger forests, but in significantly lower abundances (see also, Raphael, 1988). What densities of salamanders may be required for long-term viability or ecological function (Conner, 1988) remain open questions.

Dense and apparently viable populations have been reported from young redwood forests and from rocky embankments along open road cuts within these forests, along California's north coast (Diller and Wallace, 1994). However, despite their large sample, all localities reported by Diller and Wallace were within the marine-influenced, coastal belt, which represents only a small portion of the range of this species. Diller and Wallace (1994) attributed differences in the habitat requirements of coastal and more interior populations of this species to the pronounced climatic differences between these two geographic regions. We concur because most of the sites we sampled here and in earlier work (Welsh and Lind, 1988, 1991; Welsh, 1990) were interior sites.

Our data are from across the range of the Del Norte salamander in northwestern California. Most populations, and the highest densities, occurred in older forests. Thus, we consider this salamander to be an old-growth associated species that exists at its biological optimum under conditions found primarily in late seral forests of mixed conifer-hardwood in northwestern California and southwestern Oregon. It is important to use caution when interpreting correlative studies because cause and effect relationships cannot be conclusively demonstrated. However, we believe our data link the Del Norte salamander with conditions that exist primarily in late successional forests throughout all but the marine-influenced coastal areas of its range. Ruggiero et al. (1988) argued that habitat preferences are evidence of ecological dependence because they are based on evolved behavior and thus relate directly to the probability of persistence. They stated, "When patterns of species abundance and measures of survival and reproductive success show a close association with a particular environment(s), we should conclude that the environment(s) is required for species persistence" (Ruggiero et al., 1988). This study demonstrates an ecological dependence by the Del Norte salamander on attributes and conditions found primarily in late seral forests. These conclusions argue for modified forest management practices that take into account the ecological requirements of this salamander, at least throughout the interior portions of its range.

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