

**DISTRIBUTION AND HABITAT OF THE THREATENED CHEAT MOUNTAIN
SALAMANDER (*PLETHODON NETTINGI*) AT MULTIPLE SPATIAL SCALES
IN WEST VIRGINIA FORESTS**

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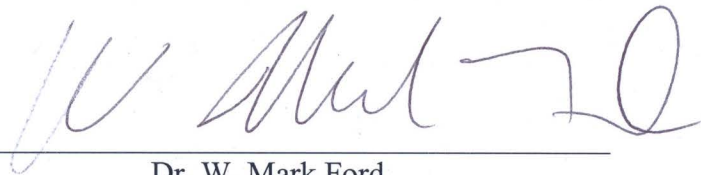
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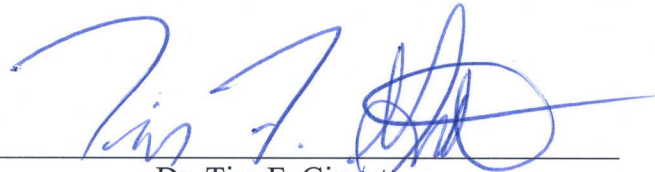
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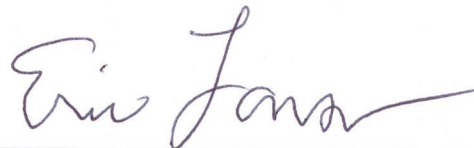
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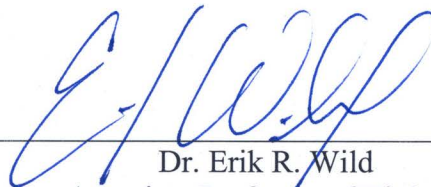
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ABSTRACT

Effective conservation of vertebrate diversity increasingly requires understanding influences of habitat composition and structure at multiple spatial scales. In particular, patterns of amphibian occurrence across broad spatial scales have been poorly elucidated. The federally threatened Cheat Mountain salamander (*Plethodon nettingi*; hereafter CMS) is known to occur in approximately 70 small, scattered populations in the Allegheny Mountains of eastern West Virginia, USA. However, current conservation and management efforts on federal, state, and private lands involving CMS must largely rely on small scale, largely descriptive studies of habitat associations from a few sample sites. In this study, I used comparative modeling approaches to explain the range-wide distribution and habitat relationships of CMS in relation to a suite of biotic and abiotic habitat variables measured at both the landscape- and site-level.

At a landscape-level, I collected data on 13 explanatory, Geographic Information System (GIS)-based habitat variables at CMS-occupied ($n = 180$) and random ($n = 180$) sites within the northern high Allegheny Mountains ecological subsection. Prior to analyses, data were divided randomly into sets for model development (75%) and validation (25%). I then examined CMS-landscape habitat relationships using *a priori*, logistic regression models with information-theoretic model selection, classification and regression tree (CART) modeling, and discriminant function analysis (DFA). Among logistic regression models, a model containing the variables elevation, aspect, slope, and geology type received the strongest empirical support, although a model containing these variables and current vegetation type also received limited support. Variable selection within my CART and DFA modeling was consistent with logistic regression results. Common variables in all three approaches indicated that the probability of finding CMS

at a landscape-level increased in areas with higher elevations and sandstone geology. Validation of models with empirical support using reserved data indicated that classification accuracy was $\geq 80\%$ for all three analytical methods. Finally, I linked model outputs from all three methods to GIS coverage maps that predicted CMS occupancy within the study area.

At a site-level, I collected data on 18 explanatory habitat variables at CMS-occupied ($n = 67$) and random ($n = 37$) sites, measured during the summer of 2006, and examined CMS habitat relationships using *a priori*, logistic regression models with information-theoretic model selection. Among 16 specified models, a model containing the variable depth to rock received the strongest empirical support, although five competing models containing additional abiotic variables (emergent rock ground cover, rocky outcrops, seeps) and biotic variables (canopy closure, conifer density, bryophyte ground cover) received limited support. Overall, results of model selection indicated that the probability of CMS occurrence at the site-level increased in areas with shallower depth to rock, areas proximal to rocky outcrops but distal to seeps, areas with higher densities of bryophytes, and areas with high densities of red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). Habitat models at both landscape- and site-levels contained a high degree of congruency and indicated that associations between CMS and geophysical habitat features may be primary predictors of occurrence, although vegetation associations interact with these features to form more precise habitat relationships within forested landscapes. Information gained from this multi-scale study will increase the capacity of managers to plan for the continued persistence and conservation of CMS, as well as their associated habitats.

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PREFACE

The two chapters comprising this thesis consist of separate, but related manuscripts submitted for publication that investigate the distribution and habitat of Cheat Mountain salamanders (CMS; *Plethodon nettingi*) at multiple spatial scales. The Cheat Mountain salamander is a small terrestrial plethodontid endemic to high-elevation forests of the Allegheny Mountains in Tucker, Randolph, Pocahontas, Grant, and Pendleton counties of eastern West Virginia. The species is believed to consist of approximately 70 isolated populations distributed across an area of approximately 1800 km². Most (ca. 75%) known CMS populations appear to comprise of ≤ 10 individuals, and $\geq 80\%$ of populations occur on the Monongahela National Forest. Cheat Mountain salamanders were listed as a threatened species in 1989 by the U.S. Fish and Wildlife Service. Historically, the range of CMS probably was more extensive than the current restricted distribution. However, exploitative logging and large wildfires in the region eliminated $>93\%$ of red spruce (*Picea rubens*) forests by 1920. Many CMS populations were thought to have been extirpated during this period. In addition to legacy habitat disturbance, recent or ongoing forest management, surface mining, road building, and recreational development activities, as well as competition with sympatric red-backed salamanders (*Plethodon cinereus*) and Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*) have been hypothesized to limit current CMS distribution and abundance. Because extant CMS populations are small and geographically isolated, loss of genetic diversity also is thought to threaten the species.

Despite the threatened status of CMS, required protection under the Endangered Species Act, continuing concerns about habitat disturbance effects, and a key recovery

plan task indicating the need for quantitative habitat assessments, relatively little has been published regarding CMS habitat relationships. Because the distribution of CMS is discontinuous and important habitat features are poorly quantified, extensive surveys for occupancy must be conducted prior to most forest management or other land-disturbing activities in the region. Only small scale, largely descriptive studies of CMS-vegetation associations or microhabitat relationships currently are available to guide conservation and management efforts on federal, state, and private lands across the species' range. Accordingly, the goal of my research was to quantitatively model how geophysical and other abiotic features interact with vegetation composition at both broad and fine scales to influence range-wide CMS distribution and habitat associations.

In the first chapter, I created landscape-level occurrence models for CMS and used those models to predict the probability of CMS occupancy across the range of the species. Specifically, I (1) developed and validated the classification accuracy of three statistical approaches for modeling CMS-occupied and random points using coarse-scale spatial data (i.e., Geographic Information System-based) readily available to resource managers; (2) examined the role of biotic and abiotic habitat characteristics for predicting CMS occurrence at a coarse scale; (3) evaluated the influence of modeling approach on characterization of CMS habitat relationships; and (4) examined the use and limitations of large-scale modeling for amphibian conservation.

In the second chapter, I used pre-existing data on CMS presence combined with fine-scale habitat characteristics that I quantified at a subset of CMS-occupied and random locations to develop site-level habitat models of CMS occurrence across the predicted range of the species. Specifically, I (1) examined if logistic regression

modeling of site-level habitat characteristics with information-theoretic model selection could reliably differentiate between CMS-occupied and random locations; (2) evaluated the relative importance of biotic and abiotic habitat features for describing CMS habitat relationships; and (3) compared these findings to both my landscape-scale habitat modeling results (Chapter I) and to previous, qualitative descriptions of CMS habitat associations.

CHAPTER I:
LANDSCAPE-LEVEL OCCURRENCE MODELS FOR THE THREATENED
CHEAT MOUNTAIN SALAMANDER *PLETHODON NETTINGI*: THE
IMPORTANCE OF GEOPHYSICAL FEATURES

Abstract. Effective conservation of vertebrate diversity increasingly requires understanding influences of habitat composition and structure at large spatial scales. In particular, patterns of amphibian occurrence across broad spatial scales are not well studied. The federally threatened Cheat Mountain salamander (*Plethodon nettingi*; hereafter CMS) is known to occur in approximately 70 small, scattered populations in the Allegheny Mountains of eastern West Virginia. I used a comparative modeling approach to explain the landscape-level distribution and habitat relationships of CMS in relation to a suite of biotic and abiotic habitat variables measured across the species' range. I collected data on 13 explanatory landscape-level habitat variables at CMS-occupied ($n = 180$) and random ($n = 180$) sites. Prior to analyses, data were divided randomly into sets for model development (75%) and validation (25%). I then examined CMS-landscape habitat relationships using *a priori*, logistic regression models with information-theoretic model selection, classification and regression tree (CART) modeling, and discriminant function analysis (DFA). Among logistic regression models, a model containing the variables elevation, aspect, slope, and geology type received the strongest empirical support, although a model containing these variables and current vegetation type also received limited support. Variable selection within my CART and DFA modeling was consistent with logistic regression results. Common variables in all three approaches

indicated that the probability of finding CMS at a landscape-level increased in areas with higher elevations and sandstone geology. Validation of models with empirical support using reserved data indicated that classification accuracy was $\geq 80\%$ for all three analytical methods. Finally, I linked model outputs from all three methods to GIS coverage maps that predicted CMS occupancy within the study area. My results indicate that geophysical and ecological characteristics measured at large spatial scales may be useful for quantifying salamander habitat relationships in forested landscapes, and more specifically increase the capacity of managers to locate and plan for the continued persistence and recovery of CMS.

INTRODUCTION

Conservation of vertebrate diversity increasingly requires elucidating habitat relationships at large spatial scales (Guisan and Zimmermann 2000, Maurer 2002). However, habitat relationship studies for most taxa remain focused on characterizing habitats at small, site-level scales. In particular, patterns of amphibian distribution across large spatial scales remain poorly known (Hecnar and M'Closkey 1996, Johnson et al. 2002). Because amphibians have limited dispersal abilities and small home ranges (Duellman and Trueb 1986), site-specific habitat factors often are assumed to have an overriding influence on patterns of amphibian distribution. However, there is increasing evidence that habitat characteristics measured at broad spatial scales are important predictors of amphibian occurrence and abundance (Diller and Wallace 1996, Gustafson et al. 2001, Russell et al. 2004a, 2005, Stoddard and Hayes 2005). Moreover, development of effective habitat conservation strategies for amphibians may be limited

by the historical paradigm that condition of site-level vegetation is equivalent to habitat suitability. Although vegetation composition and structure often exert a strong influence on amphibian distribution and abundance (deMaynadier and Hunter 1995, Russell et al. 2004b), recent research indicates the importance of abiotic habitat features such as geology, topography, and climate have not been sufficiently recognized (Diller and Wallace 1996, Sutherland and Bunnell 2001, Russell et al. 2004a, 2005).

The Cheat Mountain salamander (*Plethodon nettingi*; see Fig. 1) (hereafter CMS) is a small terrestrial plethodontid endemic to high-elevation, red spruce (*Picea rubens*)-dominated forests of the Allegheny Mountains in Tucker, Randolph, Pocahontas, Grant, and Pendleton counties of eastern West Virginia (Green 1938, Green and Pauley 1987). The species is restricted to approximately 70 isolated populations distributed across an area of approximately 1800 km² (Pauley and Pauley 1997, Petranka 1998). Most (75%) known CMS populations appear to consist of ≤ 10 individuals and $\geq 80\%$ of populations occur on the Monongahela National Forest (MNF; U.S. Fish and Wildlife Service 1991).

Cheat Mountain salamanders were listed as a threatened species in 1989 by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1991). Historically, its range possibly was more extensive than the current restricted distribution (U.S. Fish and Wildlife Service 1991). However, exploitative logging combined with large wildfires in the region eliminated $>93\%$ of red spruce forests by 1920 (Clarkson 1964, Clovis 1979, Mielke et al. 1986) that in turn was thought to have caused the extirpation of many CMS populations. Although no published studies have directly assessed the impacts of these landscape events on CMS, presumably this species' response is analogous to that of other woodland salamanders to the microclimatic, vegetational, and structural changes that

occur after forest disturbances such as timber harvest (deMaynadier and Hunter 1995, Russell et al. 2004b). Pauley and Watson (2003) found that CMS abundance increased with distance from forest opening edge created by forest regeneration areas, ski trails, and roads. In addition to legacy habitat disturbance, recent or ongoing forest management, surface mining, road building, and recreational development activities, as well as competition with sympatric red-backed salamanders (*P. cinereus*) and Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*) have been hypothesized to continue limiting CMS distribution and abundance (Highton 1972, Pauley 1980a, Pauley 1998). Because extant CMS populations are small and geographically isolated, loss of genetic diversity also is thought to threaten the species (U.S. Fish and Wildlife Service 1991, Kramer et al. 1993).

Despite the threatened status of CMS and continuing concerns about habitat disturbance, few quantitative data on CMS habitat relationships have been collected. Cheat mountain salamanders largely occur in coniferous and mixed conifer-deciduous forest stands with a bryophyte (*Bizzania* spp.)-dominated forest floor ranging in elevation from 805-1482 m (Green and Pauley 1987, Pauley and Pauley 1997). Brooks (1945, 1948) indicated that CMS were restricted to pure stands of red spruce or mixed red spruce-yellow birch (*Betula alleghaniensis*) forests with highest abundances in young-growth red spruce forests rather than mature stands. However, mature red spruce forests were uncommon on the landscape at that time (Clarkson 1964). Clovis (1979) and Pauley (1980b) found CMS to be more cosmopolitan, occurring not only in red spruce forests but also in northern hardwood stands dominated by red maple (*Acer rubrum*),

yellow birch, black cherry (*Prunus serotina*) and other hardwoods with little or no conifer component.

Because the distribution of CMS is discontinuous and important habitat features are poorly quantified, extensive surveys for occupancy must be conducted prior to most forest management or other land-disturbing activities in the region. However, only small scale, largely descriptive studies (Brooks 1948, Pauley 1980*b*, Pauley and Pauley 1997, Pauley 1998) of CMS-vegetation associations or microhabitat relationships currently are available to guide conservation and management efforts on federal, state, and private lands in the area. Accordingly, studies are needed that quantitatively model how geophysical and other abiotic features interact with vegetation composition at a broad scale to influence CMS distribution. Quantitative models that can reliably (1) describe habitats known to be occupied by CMS; (2) predict CMS distribution at a landscape level; and (3) be linked to Geographic Information System (GIS) data readily available to resource managers should increase the efficacy of ground surveys, more effectively evaluate potential impacts of future management activities on CMS, and aid in species regulatory as well as recovery efforts. Moreover, an understanding of the distribution and landscape-level habitat associations of CMS may assist in the conservation of other high-elevation obligate species of concern in the area such as the Virginia northern flying squirrels (*Glaucomys sabrinus fuscus*; Menzel et al. 2006), northern goshawks (*Accipiter gentiles*), and saw-whet owls (*Aegolius acadicus*) as well as the broader goal of restoring red spruce ecosystems widely regarded as one of the most endangered forest communities in eastern North America (Shuler et al. 2002).

My objectives were to create landscape-level occurrence models for CMS and to use those models to predict the probability of CMS occupancy across the range of the species in West Virginia. Specifically, I (1) developed and validated the classification accuracy of three different statistical approaches for modeling CMS-occupied and random points using spatial data readily available to resource managers; (2) examined the role of biotic and abiotic habitat characteristics for predicting CMS occurrence at a coarse, landscape scale; (3) evaluated the influence of modeling approach on characterization of CMS habitat relationships; and (4) examined the use and limitations of large-scale modeling for amphibian conservation.

STUDY AREA

The known distribution of CMS lies entirely within the northern high Allegheny Mountains ecological subsection (M221Ba; Keys et al. 1995) in eastern West Virginia, USA (Fig. 2). Therefore, I constrained my modeling to this area. This 320,081-ha landscape included portions of the MNF, Canaan Valley National Wildlife Refuge (CVNWR), Canaan Valley Resort State Park, Blackwater Falls State Park, as well as large areas of corporate and non-industrial private forest ownership. Geoclimatic conditions include steep slopes, broad mountaintops and ridges, narrow valleys with small, high-gradient streams, high precipitation, and cool temperatures. Elevation ranges from 291 to 1482 m with an average of 951.7 ± 210.1 m. Geologic formations are of sedimentary origin and include sandstone, shale, and limestone. Area soils have high moisture content with thick humus, while soil fertility and pH vary depending upon parent material (Kochenderfer 2006). Over a 30-year period (1961-1990), average

annual minimum temperature was 2.6 ± 0.3 °C, average annual maximum temperature was 13.5 ± 1.4 °C, and average annual precipitation was 131.3 ± 11.0 cm/year.

Mountains and some higher valleys within the study area generally are wholly forested whereas lower elevation valleys have been converted in part to pasture (McCay et al. 1997). At middle elevations, covering most of the region, the forest cover was an Allegheny hardwood-northern hardwood type dominated by American beech (*Fagus grandifolia*), yellow birch, sugar maple (*A. saccharum*), red maple, and black cherry. Remnant stands of red spruce and eastern hemlock (*Tsuga canadensis*) were present at the higher elevations and along sheltered riparian areas. Species from mixed mesophytic forest associations such as yellow poplar (*Liriodendron tulipifera*), basswood (*Tilia americana*), sweet birch (*B. lenta*), and northern red oak (*Quercus rubra*) occurred at lower elevations (Ford et al. 2002a). Although relatively rare locally, on some xeric exposures oak (*Q. spp.*)-dominated or oak-pine (*Pinus spp.*) cover types occurred (McCay et al. 1997, Ford et al. 2002a, Kochenderfer 2006).

METHODS

Salamander occurrence and random point data

To determine CMS presence, I acquired locations from GIS databases maintained by MNF ($n = 204$) and CVNWR ($n = 49$) where ≥ 1 CMS was found during previous field surveys. For my analytical use, I specified that locations must (1) have data available for all habitat variables (Table 1) and (2) be separated by ≥ 60 m to increase the likelihood of independence for CMS detections and reduce the potential for spatial autocorrelation of habitat data (Legendre 1993). Although CMS occurrence data were available from

private lands within the study area, most habitat data were not readily obtainable.

Therefore, only data from public lands were used for analyses. Using these criteria, 180 occupied CMS points were retained for model development.

To represent habitats currently “unoccupied” by CMS, I selected an equal number ($n = 180$) of random points from the study area. Because true absence of CMS at these points is unknown, I used the term “pseudo-absence” in conjunction with random sites. Prior to selecting random points, I buffered all occupied points with a 60-m radius area using ArcView 3.3 (ESRI 2002). I assumed these buffers prevented overlap of occupied and random sites. Terrestrial plethodontid salamanders are relatively sedentary, with small home ranges (e.g., $<1\text{-}25\text{ m}^2$) and very limited dispersal abilities (citations in Petranka 1998). Moreover, the apparent rarity of CMS across the landscape increases the likelihood of salamander absence outside the 60-m buffers. Within my defined pseudo-absence area, I generated random points using a random point generator (Jenness 2005). I required that random points met habitat data and minimum distance criteria as described above for occupied locations.

Habitat variables

For each occupied and random location, I characterized a set of biotic and abiotic landscape habitat variables that potentially explained CMS distribution. I selected variables for modeling that were (1) indicated by previous research to be potentially important habitat correlates of plethodontid salamanders (see deMaynadier and Hunter 1995, Russell et al. 2004b), (2) capable of being mapped at large spatial scales, and (3) readily available to natural resource managers. This initial selection process resulted in the identification of 13 landscape-level variables (Table 1). I derived elevation, aspect,

slope, and terrain shape index (TSI) of each location from a 30-m resolution digital elevation model obtained from the United States Geological Survey (USGS) National Elevation Database. Aspect was linearized using the equation:

$$[1-\cos(\text{aspect in radians})] + [1-\sin(\text{aspect in radians})]$$

so that mesic, northeasterly aspects had low values and xeric, southwesterly aspects had high values (Ford et al. 2002*b*). Terrain shape index quantifies the surface shape of a plot, ranging from convex (TSI <-0.05) to concave (TSI >0.05). These landscape variables previously have been used to characterize landforms and related biological attributes of the central and southern Appalachian Mountains (McNab 1989, Odom and McNab 2000). I determined surficial geology from a digitized version of a 1:250,000-scale 1968 state geologic map of West Virginia, obtained from the Natural Resource Analysis Center (NRAC) at West Virginia University. Locations of streams, lakes, and other aquatic habitats were obtained from the 1:24,000-scale USGS National Hydrography Dataset. Distance from each location to the edge of the nearest water source was measured using an ArcView extension (Jenness 2004). Thirty-year (1961-1990) average precipitation and temperature (minimum and maximum) data, modeled using the PRISM model (Daly et al. 1997), were obtained from the NRAC at a resolution of 1-km².

Current vegetation cover of the study area was characterized from MNF (1:24,000 scale) and CVNWR (1:12,000 scale) land cover maps. I combined these data sources and grouped vegetation cover into three forested categories and one non-forest type appropriate for Appalachian systems (following Braun 1950, McNab and Avers 1994, Mueller 1996). Forested categories included red spruce-montane, northern hardwood,

and mixed mesophytic. Shrubs, grasses, and other non-forested uplands were combined into the non-forest category. Historical land cover (primary forest, second or third-growth forest, and agricultural) was determined from a digitized version of a 1:443,520-scale 1910 state forestry map of West Virginia produced by the NRAC. Historic fire regime (based on fire frequency and severity) and potential natural community type data (Cleland et al. 1997) were obtained from MNF GIS coverages at a scale of 1:24,000. Potential natural vegetation was grouped into the same categories as current vegetation. All data layers were incorporated into a GIS (ESRI 2002, 2005) for visualization and analyses.

Modeling overview

I used three comparative statistical methods to model CMS habitat relationships: logistic regression using information-theoretic model selection (Burnham and Anderson 2002), classification and regression tree modeling (CART; Breiman et al. 1984), and discriminant function analysis (DFA; McGarigal et al. 2000). For all analyses, the dependent variable was the presence or pseudo-absence (as represented by random points) of CMS. Logistic regression is widely used for examining patterns of species occupancy (O'Connor 2002), including modeling the landscape-level habitat relationships of salamanders (Russell et al. 2004a, 2005, Stoddard and Hayes 2005). I used CART as an adjunct to logistic regression because it is relatively free of statistical assumptions, has been increasingly used in wildlife habitat modeling (Anderson et al. 2000, O'Brien et al. 2005), and produces decision trees that are easily visualized and applied in a management context. Classification tree analysis also has been shown to produce better prediction of species distributions than other popular modeling approaches

(Castellon and Sieving 2006). Unlike logistic regression, CART produces a binary outcome rather than a continuous probability of occurrence. Finally, I selected DFA as a third analysis approach because it also is frequently used to model species presence/absence data (McGarigal et al. 2000). Similar to CART, DFA produces a binary outcome of occurrence but differs in that it assumes equal covariance structure and multivariate normality (McGarigal et al. 2000).

Prior to modeling, all location data were divided randomly into sets for model development and validation. Division of data was based on a Bernoulli distribution and resulted in approximately 75% and 25% of data used for development and validation, respectively. Therefore, I was able to assess how well models classified data not used in model development. I reported the overall classification accuracy of the model development dataset and the validation dataset for each model. Logistic regression and DFA analyses were performed using SPSS software (SPSS 2005) and CART modeling was performed using CART 5.0 (Salford Systems 2002).

Logistic regression modeling

Prior to model development, I eliminated redundant variables (Spearman's $r \geq 0.70$) and retained 10 variables for inclusion in models (Table 1). I then specified a set of *a priori*, candidate logistic regression models (Burnham and Anderson 2002) to determine the probability of occurrence of CMS in relation to the landscape level habitat variables. I specified models based on (1) a review of published literature on habitat relationships of CMS and other woodland salamanders, and (2) my previous experience with these species. I specified 13 models: a global model containing all 10 variables and subset models representing potential influences of biotic and abiotic attributes on CMS

presence (Table 2). Each model represented a competing hypothesis of the determinants of CMS occurrence. I did not consider all possible combinations of variables, as this strategy typically inflates the number of models beyond the number that can be reliably analyzed (Burnham and Anderson 2002). Prior to model selection, I examined fit of global models following recommendations of Burnham and Anderson (2002) that included examining residuals, measures of fit (Nagelkerke's rescaled $R^2 = 0.59$), classification tables (overall accuracy = 81.9%), and histograms of expected probabilities.

I used Akaike's Information Criterion (AIC; Hurvich and Tsai 1989, Burnham and Anderson 2002) for model selection. Because the number of occupied and random sites ($n = 360$) was small relative to the number of variables (K) in several models (i.e., $n/K < 40$), I used AIC corrected for small sample size (AIC_c) for model selection (Hurvich and Tsai 1989, Burnham and Anderson 2002). I used the formulas presented in Burnham and Anderson (2002) to calculate AIC_c from the log-likelihoods for each model. I ranked all candidate models according to their AIC_c values and the best model (i.e., most parsimonious) was the model with the smallest AIC_c value (Burnham and Anderson 2002). I drew primary inference from models within 2 units of AIC_{cmin} , although models within 4-5 units may have limited empirical support (Burnham and Anderson 2002). I calculated Akaike weights (w_i) to determine the weight of evidence in favor of each model (Burnham and Anderson 2002). To assess model fit of supported models, I calculated Nagelkerke's rescaled R^2 . All categorical variables were transformed into dummy variables (Cohen and Cohen 1983) and coefficients were calculated relative to the most frequently occurring category for each variable (Russell et al. 2004a, 2005). Models with empirical support were used to create GIS maps (mapping unit = 30 m \times 30

m) of the study area that classified the probability of occupancy by CMS into classes of 0-25%, 25-50%, 50-75%, and 75-100%.

CART modeling

Classification and regression tree modeling is a non-parametric approach that recursively partitions a dataset (the root node) into subsets (nodes) that are increasingly homogeneous with regard to a response variable. The method is appropriate for complex ecological data sets that include imbalance, nonlinear relationships, and intercorrelation (Breiman et al. 1984). The CART models consist of a decision tree with binary (i.e., yes-no) splits based on specific values of predictor variables. Each step in the tree-building process finds a rule (node) dependent on all previous steps based on a single variable that is most important in reducing remaining variation in the dataset. A terminal node is one that cannot be split further because the number of cases is less than a specified criterion, or when all cases belong to the same class. Terminal nodes are assigned a final outcome based on group membership of the majority of observations (i.e., for CMS either “occupied” or “pseudo-absent”). Using these methods, CART can create a tree that will completely describe the data, and at extreme classification, terminal nodes can be occupied by a single case. As with other stepwise procedures, adding variables (nodes) will continuously increase model fit, but at the cost of increasing the true misclassification rate in an independent data set. To avoid this, Breiman et al. (1984) recommend that trees be overgrown, then “pruned” upward using a variety of methods. The pruned output tree represents a parsimonious set of nested ecological dependencies among habitat factors that expose how they interact to predict the probability of CMS presence.

Within the CART modeling context, the specific type of model for my analysis was a classification tree (Breiman et al. 1984) because my response variable was categorical. To construct my original tree, I split nodes with a minimum size of 10 observations using the standard Gini impurity measure (Breiman et al. 1984), which tends to split off the largest category into its own group (De'ath and Fabricius 2000). I specified equal priors for my data because I sampled an equal number of CMS-occupied points and random points. After the initial classification tree was specified, I used the minimum misclassification error of the validation dataset (Breiman et al. 1984) to select the optimal number of nodes, and pruned the original tree to this size. A GIS map of the study area (mapping unit = 30 m × 30 m) was created from the optimal CART model, predicting areas as occupied or unoccupied (i.e., pseudo-absent) by CMS.

Discriminant function analysis

Lastly, I used a multivariate DFA to evaluate which habitat variables were most useful for differentiating between CMS-occupied and pseudo-absent (random) locations. As with my logistic regression analyses, I eliminated redundant variables (Spearman's $r \geq 0.70$ and retained 10 variables (Table 1) for analyses. Categorical variables were transformed into dummy variables (Cohen and Cohen 1983). Some transformed variables failed to meet assumptions of normality based on Kolmogorov-Smirnov tests ($P < 0.05$). However, DFA is robust for non-normally distributed data with larger sample sizes (e.g., $n > 100$; Tabachnick and Fidell 1996). I used Box's M-test as recommended by McGarigal et al. (2000) to test for equality of population covariance matrices. Because covariance matrices departed significantly from equality, I conducted DFA classification using group covariance matrices of the canonical discriminant functions as

recommended by Tabachnick and Fidell (1996). At each step of the forward stepwise DFA, the variable that minimized the overall Wilks' λ and had a P -value of ≤ 0.05 was entered. I used the model Wilks' λ value to test for statistical significance and determined relative habitat variable importance by examining the magnitude of the standardized canonical correlation coefficients. A GIS map of the study area (mapping unit = 30 m \times 30 m) was created from the final DFA model, differentiating areas as occupied or unoccupied (i.e., pseudo-absent) by CMS.

RESULTS

Logistic regression modeling

Of 13 logistic regression models explaining the landscape-level occurrence of CMS, “landform/geology” was selected as my best-approximating model (Table 2). The presence of CMS was positively associated with increasing elevation, sandstone surficial geology, and northeasterly aspects, but negatively associated with other geological types and steep slopes (Table 3). The second-best model, “landform/geology/vegetation,” received limited empirical support ($\Delta AIC_c = 4.65$; Table 2). This model indicated that in addition to geological and topographical features, CMS occurrence was positively associated with the presence of red spruce-montane forest cover (Table 3). Weight of evidence ($w_{\text{best model}}/w_{\text{second-best model}}$) in favor of my “landform/geology” model was about 10 times greater than that of my “landform/geology/vegetation model” (Table 2), indicating little uncertainty in selection of the best candidate model (Burnham and Anderson 2002). The remaining 11 models received no empirical support ($\Delta AIC_c \geq 11.99$, $w_i = 0.0$; Table 2).

The “landform/geology” model had an overall classification accuracy of 80.1%. When applied to the reserve data, this model had a validation accuracy of 84.3%. The probability of CMS occupancy using the “landform/geology” model was mapped across the study area (Fig. 3a). The “landform/geology/vegetation” model had an identical overall classification accuracy of 80.1% and a validation accuracy of 86.7%. The predicted distribution of CMS was similar to that for the “landform/geology,” model (Fig. 3b). However, private lands were excluded from the “landform/geology/vegetation” predictive map because vegetation data from privately-owned areas were unavailable.

CART modeling

My initial CART model contained 23 terminal nodes, but I minimized misclassification error of the validation dataset at a tree size of four terminal nodes (Fig. 4). My optimum, pruned model contained three habitat variables and indicated that the majority of CMS occupied locations were best explained by the presence of sandstone geology or mixed shale-sandstone geology, and an average annual precipitation of >127.19 cm. My model also indicated that some CMS locations were associated with limestone or shale geology types when elevation was >1206.5 m. The final CART model did not include any biotic variables (i.e., vegetation). My CART model had an overall classification accuracy of 84.1% and a validation accuracy of 85.5%. Areas predicted as occupied and unoccupied by CMS were mapped across the study area using model parameters (Fig. 3c).

Discriminant function analysis

The stepwise DFA model was statistically significant (Wilks $\lambda = 0.572$, $F_{4, 272} = 50.87$, $P < 0.001$) and included four habitat variables (in order of importance): sandstone

geology, distance to water, mixed shale-sandstone geology, and elevation. These variables had standardized correlation coefficients of 0.867, 0.278, 0.277, and 0.222, respectively. An examination of discriminant scores (Fig. 5) indicated that CMS occupancy was best explained by the presence of sandstone or mixtures of shale-sandstone, greater distances from water, and higher elevations. The stepwise DFA model did not include any biotic variables (i.e., vegetation). My DFA model produced an overall classification accuracy of 79.4% and a validation accuracy of 84.3%. Areas predicted as occupied and unoccupied by CMS were mapped across the study area using model parameters (Fig. 3d).

DISCUSSION

Models of CMS distribution

My research provides the first quantitative assessment of factors potentially influencing the landscape-level distribution of CMS. Regardless of modeling approach, the probability of CMS occurrence was influenced primarily by geophysical characteristics rather than by coarse-scale patterns of vegetation composition. In particular, all four models with empirical support indicated that CMS distribution was predicted by higher elevations and the presence of sandstone geology. Although earlier observations suggested the potential importance of elevation in defining CMS distribution (Pauley 1980a, U.S. Fish and Wildlife Service 1991), my research is the first attempt to explicitly model this putative relationship. The positive association between CMS presence and higher elevations may reflect location-dependent relationships with other environmental variables rather than a direct effect of elevation *per se*. For example,

in my study area higher elevations generally have greater average annual precipitation and cooler average annual temperatures when compared to lower elevations. Therefore, high-elevation areas may best provide the moist, cool environments required for cutaneous respiration by CMS and other lungless salamanders (Petranka 1998). Moreover, my final CART model indicated that average annual precipitation was an important predictor of CMS distribution, with higher levels of precipitation at occupied sites when compared to random locations.

Alternatively, the association of CMS with higher elevations may reflect interspecific competition with other species of salamanders that are more abundant at lower elevations. Both red-backed salamanders (*P. cinereus*) and Allegheny Mountain dusky salamanders (*D. ochrophaeus*) have been hypothesized to competitively dominate CMS and therefore potentially restrict its distribution (Highton 1972, Pauley 1980a, Adams et al. 2007). For example, areas currently occupied by CMS are above the elevation of many headwater stream networks, thereby allowing CMS to avoid interspecific competition with more aquatic *Desmognathus* spp. (Pauley 1980a). Moreover, my final DFA model indicated that CMS-occupied sites were farther from water sources when compared to random locations, potentially lending support to the hypothesis that CMS may be competitively excluded from areas where densities of more aquatic salamanders are high (Pauley 1980a).

Researchers in the Pacific Northwest have documented landscape-level associations between surficial geology and the distribution of stream amphibians (e.g., Diller and Wallace 1996, Sutherland and Bunnell 2001, Russell et al. 2004a, 2005) and plethodontid salamanders (e.g., *Plethodon vandykei*; McIntyre et al. 2006). However, I

am unaware of any literature identifying correlations between eastern plethodontids, including CMS, and specific geology types. My landscape models indicated a consistent association between CMS occupancy and the presence of sandstone geology.

Throughout much of the Appalachian Plateau of the central Appalachian Mountains, higher-elevations are capped by resistant sandstone parent materials (Fenneman 1938). Therefore, the relationship between CMS occupancy and geology type could represent an inherent intercorrelation with elevation. However, at high elevations (i.e., >1000 m) in my study area, 54.5% of the surficial geology consists of shale, whereas only 35.7% is sandstone and 5.9% is mixed shale-sandstone geology. Accordingly, it is plausible that the independent combination of these two geophysical features do actually best predict CMS occupancy at the landscape level.

The strong association between CMS distribution and sandstone I observed certainly reflects the surface and subsurface habitats produced by this geology type. In my study area, sandstone parent materials generally weather to produce abundant emergent rocks and colluvial breakdown. Emergent rocks and other cover objects are used during the day by surface-active CMS to avoid desiccation and predation (Green and Pauley 1987, Pauley 1998, Petranka 1998). Larger rock outcrops, resulting from similar weathering patterns have been hypothesized to have served as important refugia for CMS that allowed this species to persist during exploitative logging and widespread wildfires in the early 20th century (Pauley 1998). Moreover, fracturing of exposed sandstone outcrops from intense freeze-thaw cycles in the higher Alleghenies provides conduits to the underlying layers of sandstone, which often exist as a collection of rocks with abundant interstitial spaces. Other plethodontid salamanders, and presumably CMS,

use such underground refugia to avoid dry, hot weather during summer and to overwinter (Petranka 1998). Additionally, I speculate that the association between sandstone geology and CMS may provide further evidence of spatial segregation from competitively dominant *P. cinereus*. Populations of *P. cinereus* usually reach their greatest numbers in forested habitats with deep soils, but are absent or occur at low densities in shallow, rocky soils (Petranka 1998). In a study of Shenandoah salamanders (*P. shenandoah*), a sibling species to CMS, Jaeger (1970) reported that *P. shenandoah* appeared to avoid competition with sympatric *P. cinereus* by inhabiting accumulations of talus (rock fragments).

Both logistic regression models indicated that aspect and slope were important predictors of CMS distribution. Many plethodontid salamander species are positively associated with north-facing aspects where lowered solar radiation helps maintain moist conditions (deMaynadier and Hunter 1995, Petranka 1998, Ford et al. 2002b). Therefore that warmer, more xeric southerly exposures may limit the presence of CMS is not surprising. Other researchers have reported positive associations between the presence of plethodontid salamanders and steeper slopes (Petranka 1998). In contrast, I observed a negative association between slope and the occurrence of CMS. However, in the Appalachian plateau region, gentle slopes are common at higher elevations, which may at least partially explain this relationship.

Although the landscape-level distribution of CMS was primarily related to geophysical features, one logistic regression model with empirical support indicated that CMS occurrence was positively associated with the presence of red spruce forest cover. This finding corroborates previous, qualitative descriptions of CMS habitat that

suggested an association between the historic or current distribution of red spruce forests and the range of CMS (Brooks 1948, U.S. Fish and Wildlife Service 1991). Because of historic timber harvest, >93% of the original red spruce acreage in my study area and surrounding region has been replaced by northern hardwood cover types with a much reduced conifer component (Mielke et al. 1986, Schuler et al. 2002). Most remnant red spruce stands in the region are restricted to isolated patches at the highest elevations (Menzel et al. 2006). Therefore, it is unclear whether coarse-scale associations between the current distributions of CMS and red spruce forest reflect an intercorrelation with elevation, or the opposite.

Moreover, the functional importance of red spruce for CMS remains unknown. Densities of many plethodontid salamanders, including *P. cinereus*, appear to be lower in coniferous forests than deciduous forests (Petranka 1998, Brooks 2001). There are CMS populations in Allegheny hardwood-northern hardwood forest types without significant conifer components (Clovis 1979, Green and Pauley 1987, Pauley and Pauley 1997). Therefore, quantitative site-level and microhabitat studies that explicitly examine CMS presence and population densities in relation to structural attributes of red spruce stands, other forest types, and associated abiotic features are needed to evaluate the inferred dependence of this species on high-elevation red spruce ecosystems.

My findings indicate that geophysical features do exert an overriding influence on the landscape-level occurrence of CMS, supporting Highton's (1972, 1995) description of *P. nettingi* as a relictual species tied to higher elevations. However, I do not suggest that CMS are insensitive to vegetation composition and other biotic attributes. Rather, the relative importance of abiotic and biotic features for shaping CMS distribution is likely

scale-dependent (Mitchell et al. 2001). Associations of CMS with abiotic landform features may reflect biological constraints manifested at the population- or species-levels, whereas constraints on individual salamanders may operate at fine spatial scales (Russell et al. 2004a, 2005, Stoddard and Hayes 2005). For example, surficial geology, elevation, and aspect are indirect predictor variables (Guisan and Zimmermann 2000) that may have no direct physiological relevance for survivorship of individual salamanders. However, these features indirectly reflect site-level and microhabitat variables such as availability of cover objects, soil moisture, vegetation composition, prey availability, and competitive sympatric salamander density that obviously would influence habitat use and occupancy by individual CMS and other plethodontid salamanders (deMaynadier and Hunter 1995, Petranka 1998).

Landform influences on site-level habitats (e.g., rock substrates) also may have interacted with previous vegetation disturbance from exploitative timber harvest or subsequent wildfire and presence of other salamander species to shape the current distribution of CMS (Highton 1972, Pauley 1980a, Pauley 1998). I think that variation in these site-level habitat attributes may be a source of much of the unexplained variation in my models. Incorporating fine-scale variables should result in more refined predictions of CMS occurrence. However, this will require intensive measurement of habitat and population data that are not readily available from existing sources. Unfortunately, current permitting restrictions involving CMS have largely precluded researchers from collecting these much-needed data (Adams et al. 2007).

Modeling comparison

The three modeling approaches I employed showed remarkable consistency in the variables chosen as important predictors of CMS occupancy. Furthermore, all models produced maps that predicted similar patterns of CMS occupancy, and the classification accuracy of models derived from each method was reasonably high using both model development and validation datasets. However, the empirically supported logistic regression models required 4-5 variables to accurately predict occupancy, whereas the CART and DFA models required only 3 variables. The CART approach has the advantage of producing a decision tree (Fig. 4) that can be easily interpreted by natural resource managers than the other two methods. Additionally, results of CART analyses are not affected by interactions among predictor variables, or by nonlinear relationships between predictor variables and the response variable. Of course the considerable limitation of CART and DFA models is that output maps (Figs. 2c-d) only allow binary predictions of occupancy (i.e., present or unoccupied), whereas logistic regression provides a continuous level of predicted CMS occupancy across the study area (Figs. 2a-b). Continuous probability maps may be more useful in a management context, allowing flexibility as to what level of predicted occupancy corresponds to a certain level of conservation status or field survey priority.

Despite my consistently high percentage of correct classification, wildlife habitat modeling is replete with assumptions. Because my research relied on previous ground surveys to determine occupancy, I assumed that ≥ 1 CMS was still present at each location and that habitat conditions had not changed dramatically between the original surveys and my modeling effort. I also assumed that all random locations were currently

unoccupied but potentially available to CMS (Manly et al. 1993). Available CMS data were restricted to occurrence; my modeling effort does not address landscape level influences on CMS abundance, densities, or range-wide population viability. Finally, because I emphasized parsimony in each of my modeling approaches and used relatively coarse landscape-level data, I recognize the potential for fine-scale errors in my occupancy maps. For example, one logistic regression model (Fig. 3a) and the DFA model (Fig. 3d) predicted CMS occurrence in a few bands in the extreme northeastern portion of the northern high Allegheny Mountains ecological subsection where CMS does not occur. Therefore, I urge a conservative approach when applying my results for conservation or management purposes.

Relevance to conservation planning

Managers of large, heterogeneous landscapes need readily available information on the spatial distribution of threatened, endangered and sensitive species. My research represents the first attempt to quantitatively model the range-wide habitat associations of CMS, and indicates that identification of potentially occupied CMS habitat should move beyond a traditional focus on vegetation composition and integrate geophysical factors including topography and geology. I think my effort should be useful to natural resource managers as it delineates where potentially critical or optimal habitats from an occupancy perspective exist on the MNF and CVNWR. My models generated predictions over very large areas and used spatial data that were readily available to many land managers. Therefore, my methodologies should be easily adapted to predicting distributions of other amphibian species (e.g., *P. hubrichti*, *P. punctatus*, *P. shenandoah*), in other regions where similar occupancy and spatial data exist (Gustafson et al. 2001, Knapp et al. 2003).

My research provides an example of how integration of biological knowledge, habitat modeling, and GIS-based data can reveal important aspects of landscape-level habitat associations of amphibians.

Secondly, if CMS depend on areas outlined by my models, the resulting maps show where the highest concentrations of CMS habitat (and presumably CMS) are probable. Because the distribution of CMS is discontinuous and important habitat features are poorly quantified, extensive surveys for occupancy should be conducted prior to land-disturbing activities. My models should reduce the time and effort associated with future CMS surveys, including the identification of new populations.

Finally, my models provide a landscape-level baseline for future management efforts designed to restore CMS habitats that are linked to ongoing efforts to restore high elevation red spruce ecosystems in the region (Shuler et al. 2002). My results suggest such efforts may be more effective if situated in areas of high predicted probability (e.g., ≥ 0.5) of CMS occurrence, including 1) high elevation sites with sandstone geology, 2) areas with northeasterly aspects, moderate slopes, higher relative annual precipitation, and 3) areas further from surface water. However, single species management efforts often fail over the long term, whereas ecosystem-based efforts that restore landscape-level forest composition and structure typically benefit a greater number of species (Carey 2003, Aubry et al. 2004, Menzel et al. 2006). For example, there is a high degree of congruence (including identification of specific predictor variables) between my occupancy maps for CMS and those developed for Virginia northern flying squirrels (Menzel et al. 2006). Accordingly, I think my habitat models for CMS may aid in the

development of multi-species ecosystem management and restoration efforts in the Allegheny Mountains (Schuler et al. 2002, Menzel et al. 2006).

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LITERATURE CITED

- Adams, D. C., M. E. West, and M. L. Collyer. 2007. Location-specific sympatric morphological divergence as a possible responses to species interactions in West Virginia *Plethodon* salamander communities. *Journal of Animal Ecology* 76:289-295.
- Anderson, M. C., J. M. Watts, J. E. Freilich, S. R. Yool, G. I. Wakefield, J. F. McCauley, and P. B. Fahnestock. 2000. Regression-tree modeling of desert tortoise habitat in the central Mojave desert. *Ecological Applications* 10:890-900.
- Aubry, K. B., C. B. Halpern, and D. A. Maguire. 2004. Ecological effects of variable-retention harvests in the northwestern United States: the DEMO study. *Forest Snow and Landscape Research* 78:119-137.

- Breiman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth and Brooks, Monterey, California, USA.
- Brooks, M. 1945. Notes on amphibians from Brickle's Knob, West Virginia. *Copeia* 1945:231.
- Brooks, M. 1948. Notes on the Cheat Mountain salamander. *Copeia* 1948:239-244.
- Brooks, R. T. 2001. Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. *Forest Ecology and Management* 149:197-204.
- Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner Press, New York, New York, USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Carey, A. B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forests: inducing spatial heterogeneity with variable-density thinning. *Forestry* 76:128-136.
- Castellon, T. D., and K. E. Sieving. 2006. Landscape history, fragmentation, and patch occupancy: models for a forest bird with limited dispersal. *Ecological Applications* 16:2223-2234.
- Clarkson, R. B. 1964. Tumult on the mountains. McClain Printing, Parsons, West Virginia, USA.
- Cleland, D. T., P. E. Avers, W. H. McNab, M. E. Jensen, R. G. Bailey, T. King, and W. E. Russell. 1997. National hierarchical framework of ecological units. Pages 181-

- 200 in M. S. Boyce and A. Haney, editors. Ecosystem management applications for sustainable forest and wildlife resources. Yale University Press, New Haven, Connecticut, USA.
- Clovis, J. F. 1979. Tree importance values in West Virginia red spruce forests inhabited by the Cheat Mountain salamander. *Proceedings of the West Virginia Academy of Science* 54:58-64.
- Cohen, J., and P. Cohen. 1983. Applied multiple regression–correlation analysis for the behavioral sciences. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.
- Daly, C., G. H. Taylor, and W. P. Gibson. 1997. The PRISM approach to mapping precipitation and temperature. *Proceedings of Applied Climatology Conference* 10:10-12.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178-3192.
- deMaynadier, P. G., and M. L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* 3:230-261.
- Diller, L. V., and R. L. Wallace. 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. *Journal of Herpetology* 30:184-191.
- Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. The Johns Hopkins University Press, Baltimore, MD, USA.
- ESRI (Environmental Systems Research Institute, Inc.). 2002. ArcView 3.3. ESRI, Redlands, California, USA.

- ESRI (Environmental Systems Research Institute, Inc.). 2005. ArcGIS 9.1. ESRI, Redlands, California, USA.
- Fenneman, N. E. 1938. Physiography of eastern United States. McGraw-Hill, New York, New York, USA.
- Ford, W. M., B. R. Chapman, M. A. Menzel, and R. H. Odom. 2002a. Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. *Forest Ecology and Management* 155:131-141.
- Ford, W. M., M. A. Menzel, and R. H. Odom. 2002b. Elevation, aspect and cove size effects on southern Appalachian salamanders. *Southeastern Naturalist* 1:315-324.
- Green, N. 1938. A new salamander, *Plethodon nettingi*, from West Virginia. *Annals of the Carnegie Museum* 27:295-299.
- Green, N., and T. K. Pauley. 1987. Amphibians and reptiles in West Virginia. University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.
- Guisan, A., and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. *Ecological Modeling*. 135:147–186.
- Gustafson, E. J., N. L. Murphy, and T. R. Crow. 2001. Using a GIS model to assess terrestrial salamander response to alternative forest management plans. *Journal of Environmental Management* 63:281-292.
- Hecnar, S. J., and R. T. M'Closkey. 1996. Regional dynamics and the status of amphibians. *Ecology* 77:2091-2097.
- Highton, R. 1972. Distributional interactions among eastern North American salamanders of the genus *Plethodon*. Pages 139-188 in P. C. Holt, editor. The distributional history of the biota of the Southern Appalachians. Part III: vertebrates. Research

Division Monograph 4. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

- Highton, R. 1995. Speciation in eastern North American salamanders of the genus *Plethodon*. *Annual Review of Ecology and Systematics* 26:579–600.
- Hurvich, C., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297-307.
- Jaeger, R. G. 1970. Potential extinction through competition between two species of terrestrial salamanders. *Evolution* 24:632-642.
- Jenness, J. 2004. Nearest features extension for ArcView 3.x, version 3.8a. Jenness Enterprises, Flagstaff, Arizona, USA.
- Jenness, J. 2005. Random point generator extension for ArcView 3.x, version 1.3. Jenness Enterprises, Flagstaff, Arizona, USA.
- Johnson, C. M., L. B. Johnson, C. Richards, and V. Beasley. 2002. Predicting the occurrence of amphibians: an assessment of multiple-scale models. Pages 157-170 *in* J. M. Scott, P. J. Heglund, J. B. Haufler, M. L. Morrison, M. G. Raphael, W. B. Wall, and F. Sampson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D.C., USA.
- Keys, J. E., Jr., C. A. Carpenter, S. L. Hooks, F. G. Koenig, W. H. McNab, W. E. Russell, and M. L. Smith. 1995. *Ecological units of the eastern United States: first approximation*. USDA Forest Service, Atlanta, Georgia, USA.
- Kochenderfer, J. N. 2006. Fernow and the Appalachian hardwood region. Pages 17-39 *in* M. B. Adams, D. R. DeWalle, and J. L. Hon, editors. *The Fernow Watershed Acidification Study*. Springer Press, Dordrecht, Netherlands.

- Knapp, R. A., K. R. Matthews, H. K. Preisler, and R. Jellison. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. *Ecological Applications* 13:1069– 1082.
- Kramer, P. N., N. Reichenbach, M. Hayslett, and P. Sattler. 1993. Population dynamics and conservation of the peaks of otter salamander, *Plethodon hubrichti*. *Journal of Herpetology* 27:431-135.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659– 1673.
- Manly, B. F. J., L. McDonald, and D. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.
- Maurer, B. A. 2002. Predicting distribution and abundance: thinking within and between scales. Pages 125-132 in J. M. Scott, P. J. Heglund, J. B. Haufler, M. L. Morrison, M. G. Raphael, W. B. Wall, and F. Sampson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.
- McCay, D. H., M. D. Abrams, and T. E. Demeo. 1997. Gradient analysis of secondary forests of eastern West Virginia. *Journal of the Torrey Botanical Society* 124:160–173.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York, New York, USA.
- McIntyre, A. P., R. A. Schmitz, and C. M. Crisafulli. 2006. Associations of the Van Dyke's salamander (*Plethodon vandykei*) with geomorphic conditions in headwall seeps of the Cascade Range, Washington State. *Journal of Herpetology* 40:309-322.

- McNab, W. H. 1989. Terrain shape index: quantifying effect of minor landforms on tree height. *Forest Science* 35:91-104.
- McNab, W. H., and P. E. Avers, compilers. 1994. Ecological subregions of the United States: section descriptions. USDA Forest Service Administrative Publication WOWSA-5. USDA Forest Service, Washington, D.C., USA.
- Menzel, J. M., W. M. Ford, J. W. Edwards, and L. J. Ceperley. 2006. A habitat model for the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the central Appalachian Mountains. Research Paper NE-729. USDA Forest Service, Northern Research Station. Newtown Square, PA, USA.
- Mielke, M. E., D. G. Soctomah, M. A. Marsden, and W. M. Ciesla. 1986. Decline and mortality of red spruce in West Virginia. USDA Forest Service Report 86-4. USDA Forest Service, Fort Collins, Colorado, USA.
- Mitchell, M. S., R. A. Lancia, and J. A. Gerwin. 2001. Using landscape-level data to predict the distribution of birds on a managed forest: effects of scale. *Ecological Applications* 11:1692–1708.
- Mueller, R. F. 1996. Biodiversity: Central Appalachian plant distributions and forest types. *Wild Earth* 6:37-43.
- O'Brien, C. S., S. S. Rosenstock, J. J. Hevert, J. L. Bright, and S. R. Boe. 2005. Landscape-level models of potential habitat for Sonoran pronghorn. *Wildlife Society Bulletin* 33:24-34.
- O'Connor, R. J. 2002. The conceptual basis of species distribution modeling: Time for a paradigm shift? Pages 25-33 *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. B.

- Haufler, M. G. Raphael, W. B. Wall, and F. Sampson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D.C., USA.
- Odom, R. H., Jr., and W. H. McNab. 2000. Using digital terrain modeling to predict ecological types in the Balsam mountains of western North Carolina. USDA Forest Service Research Note SRS-8, USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Pauley, B. A. 1998. The use of emergent rocks as refugia for the Cheat Mountain salamander, *Plethodon nettingi* Green. Thesis. Marshall University, Huntington, West Virginia, USA.
- Pauley, B. A., and T. K. Pauley. 1997. Range and distribution of the Cheat Mountain salamander, *Plethodon nettingi*: an update. Proceedings of the West Virginia Academy of Science 69:3.
- Pauley, T. K. 1980a. Field notes on the distribution of terrestrial amphibians and reptiles of the West Virginia mountains above 975 meters. Proceedings of the West Virginia Academy of Science 52:84-92.
- Pauley, T. K. 1980b. The ecological status of the Cheat Mountain Salamander (*Plethodon nettingi*). Unpublished report to the U.S. Forest Service, Elkins, West Virginia, USA.
- Pauley, T. K., and M. B. Watson. 2003. Determination of the size of buffer zones to prevent detrimental effects on the Cheat Mountain Salamander (*Plethodon nettingi*). Unpublished report to the U.S. Fish and Wildlife Service, Elkins, West Virginia, USA.

- Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.
- Russell, K. R., T. J. Mabee, and M. B. Cole. 2004*a*. Distribution and habitat of Columbia torrent salamanders at multiple spatial scales in managed forests of northwestern Oregon. *Journal of Wildlife Management* 68:405-417.
- Russell, K. R., T. B. Wigley, W. M. Baughman, H. G. Hanlin, and W. M. Ford. 2004*b*. Responses of southeastern amphibians and reptiles to forest management: a review. Pages 319-334 *in* H. M. Rauscher and K. Johnsen, editors. *Southern forest science: past, present, and future*. USDA Forest Service General Technical Report. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Russell, K. R., T. J. Mabee, M. B. Cole, and M. J. Rochelle. 2005. Evaluating biotic and abiotic influences on torrent salamanders in managed forests of western Oregon. *Wildlife Society Bulletin* 33:1413-1424.
- Salford Systems. 2002. CART Version 5.0 for Windows. Salford Systems, San Diego, California, USA.
- Shuler, T. M., W. M. Ford, and R. J. Collins. 2002. Successional dynamics and restoration implication of a montane coniferous forest in the central Appalachians, USA. *Natural Areas Journal* 22:88-98.
- SPSS. 2005. SPSS Version 14.0 for Windows. SPSS, Inc., Chicago, Illinois, USA.
- Stoddard, M. A., and J. P. Hayes. 2005. The influence of forest management on headwater stream amphibians at multiple spatial scales. *Ecological Applications* 15:811-823.

- Sutherland, G. D., and F. L. Bunnell. 2001. Cross-scale classification trees for assessing risks of forest practices to headwater stream amphibians. Pages 550-555 *in* D. H. Johnson and T. A. O'Neill, managing directors. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.
- Tabachnick, B. G., and L. S. Fidell. 1996. Using multivariate statistics. HarperCollins College Publishers, New York, New York, USA.
- U.S. Fish and Wildlife Service. 1991. Cheat Mountain salamander recovery plan. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts, USA.

TABLE 1. Biotic and abiotic habitat variables used for modeling landscape-level habitat relationships of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006.

Variable	Units	Abbreviation	Additional description
Elevation	m	ELV	Elevation of point
Aspect	-	ASP	Linearized aspect of point ranging from NE (low values) to SW (high values)
Slope	%	SLP	Slope of point
Terrain shape index*	-	TSI	Measure of surface shape of point, where TSI <-0.05 is convex and TSI >0.05 is concave
Geology type	-	GEO	Limestone, shale, shale/sandstone mix, or sandstone parent geology of point
Historical fire regime	-	FIR	0-35 year frequency - low severity, 35-100+ year frequency - mixed severity, or 200+ year frequency - stand-replacement severity historical fire regime of point
Distance to water	m	DWT	Distance from point to nearest edge of water body or stream
Average max temp*	°C	MXT	Annual average maximum temperature (1961-1990) of point
Average min temp*	°C	MNT	Annual average minimum temperature (1961-1990) of point
Average annual precipitation	cm	PCP	Average annual total precipitation (1961-1990) of point
1910 land cover	-	HIS	Primary forest, second or third-growth forest, or agricultural land cover of point in 1910
Current land cover	-	VEG	Mixed mesophytic, northern hardwood, red spruce-montane, or non-forest current land cover of point
Potential natural community type	-	PNC	Mixed mesophytic, northern hardwood, red spruce-montane, or non-forest potential natural community type of point

* Variable was not used in logistic regression or discriminant function modeling because of high redundancy (Spearman's $r \geq 0.70$), but was used in CART modeling.

TABLE 2. Logistic regression models explaining influence of biotic and abiotic habitat attributes on landscape-level occurrence of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Model ^a	K ^b	AIC_c ^c	ΔAIC_c ^d	w_i ^e
Landform/geology {ELV, ASP, SLP, GEO}	7	257.54	0.00	0.91
Landform/geology/vegetation {ELV, ASP, SLP, GEO, VEG}	10	262.19	4.65	0.09
Global {ELV, ASP, SLP, GEO, FIR, DWT, PCP, HIS, VEG, PNC}	18	269.53	11.99	0.00
Geology {GEO}	4	273.22	15.68	0.00
Desiccation {ELV, ASP, SLP, DWT, PCP}	6	318.88	61.34	0.00
Niche partitioning {ELV, DWT}	3	319.83	62.29	0.00
Landform {ELV, ASP, SLP}	4	321.29	63.75	0.00
Elevation {ELV}	2	326.29	68.75	0.00
Landform/vegetation {ELV, ASP, SLP, VEG, PNC}	10	330.20	72.66	0.00
All vegetation {HIS, VEG, PNC}	9	339.44	81.90	0.00
Succession {PNC, FIR}	5	347.81	90.27	0.00
Potential natural cover {PNC}	4	348.24	90.70	0.00
Current vegetation {VEG}	4	361.00	103.46	0.00

^a Abbreviations in parentheses correspond to model parameters in Table 1.

^b Number of estimable parameters in approximating model.

^c Akaike's Information Criterion corrected for small sample size.

^d Difference in value between AIC_c of the current model versus the best-approximating model (AIC_{cmin}).

^e Akaike weight. Probability that the current model (i) is the best-approximating model among those considered.

TABLE 3. Parameter estimates (β) and standard errors (SE) from the best-approximating models explaining influence of habitat attributes on landscape-level presence of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Coefficients of the categorical variables “geology type” and “current land cover” were calculated relative to sandstone and northern hardwoods, respectively.

Model	β	SE	R^{2a}
Landform/geology			0.532
Constant	-2.414	1.573	
Limestone	-22.126	28008.449	
Shale	-2.893	0.411	
Shale/Sandstone Mix	-1.201	0.614	
Elevation	0.004	0.001	
Slope	-0.027	0.013	
Aspect	-0.288	0.171	
Landform/geology/vegetation			0.537
Constant	-2.143	1.683	
Limestone	-21.576	28203.641	
Shale	-2.903	0.416	
Shale/Sandstone Mix	-1.211	0.621	
Elevation	0.004	0.001	
Slope	-0.027	0.014	
Aspect	-0.263	0.173	
Mixed Mesophytic	-0.422	0.718	
Non-Forest	-0.736	0.715	
Red Spruce-Montane	0.288	0.589	

^a Nagelkerke’s rescaled R^2



FIGURE 1. Cheat Mountain salamander (*Plethodon nettingi*), Monongahela National Forest, West Virginia, USA. Photo credit: Lester Dillard.

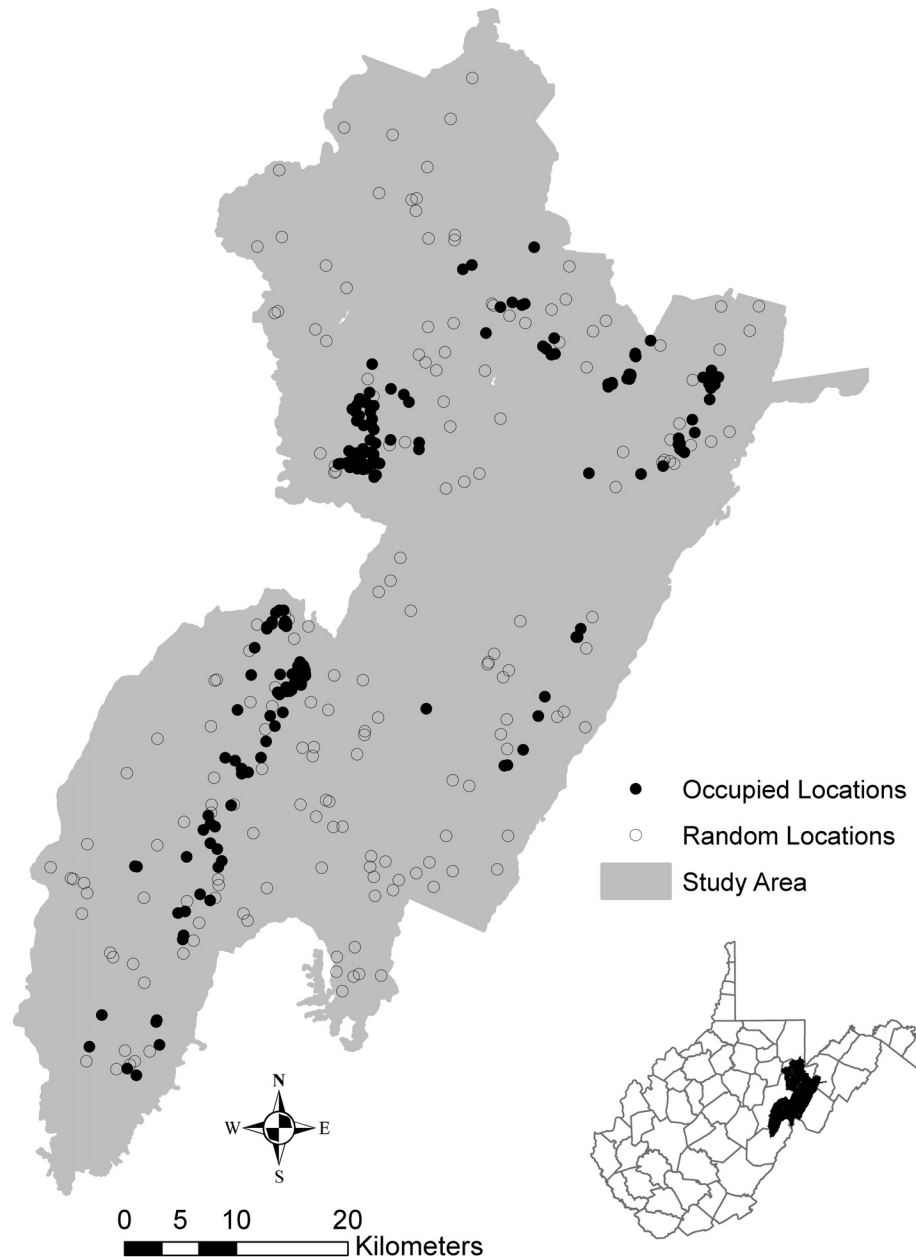
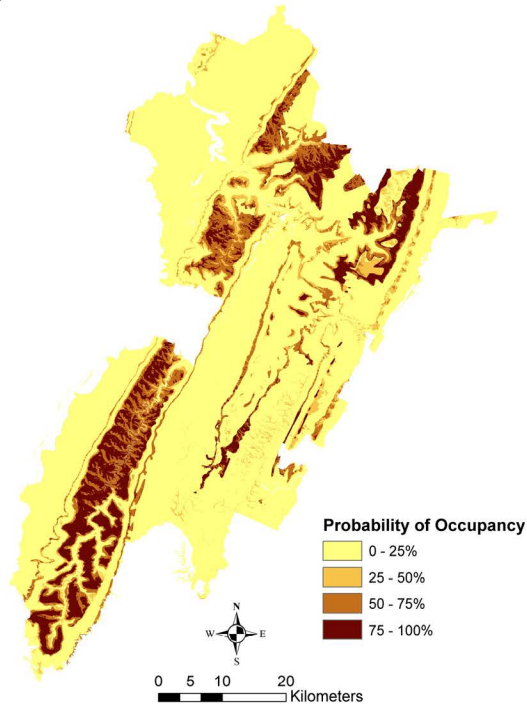
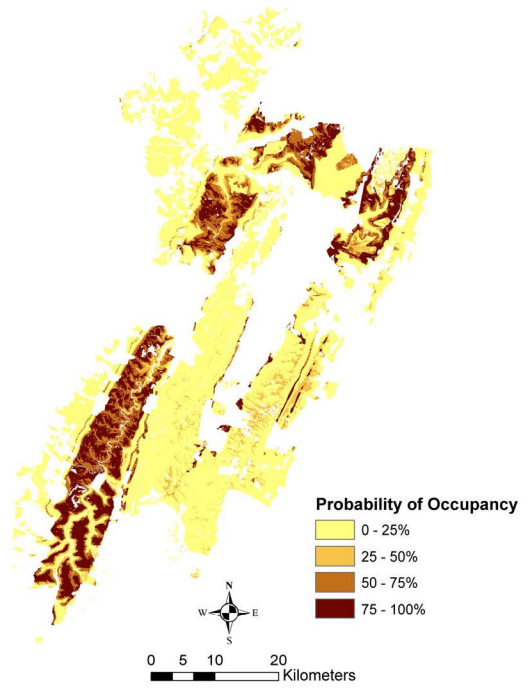


FIGURE 2. Map of study area showing locations of occupied ($n = 180$) and random ($n = 180$) points selected for landscape-level habitat modeling of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Occupied and random points are not to scale. See text for selection criteria.

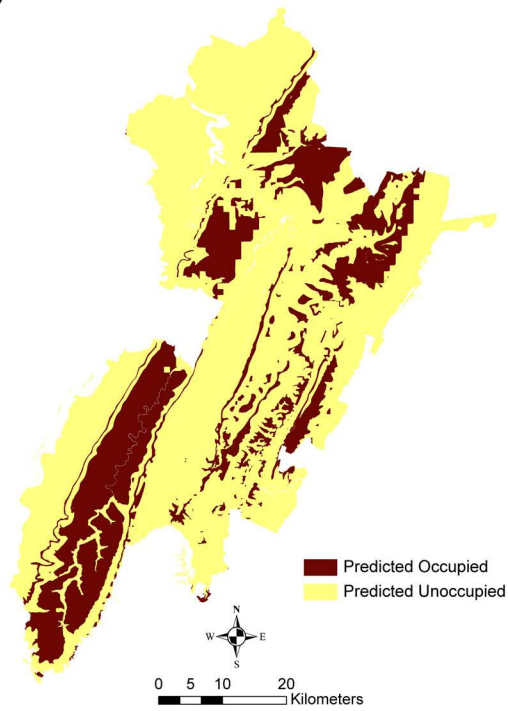
a)



b)



c)



d)

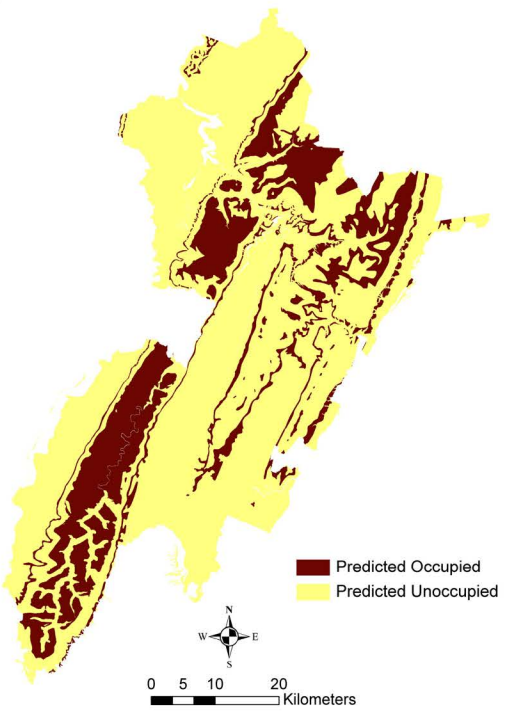


FIGURE 3. (*Previous page*) Predicted occupancy maps of Cheat Mountain salamanders within the Allegheny Mountains of West Virginia, USA, 2006 determined from *a*) landform/geology logistic regression model, *b*) landform/geology/vegetation logistic regression model, *c*) optimal CART model, and *d*) forward stepwise discriminant function model. See text for description of modeling methods and parameters.

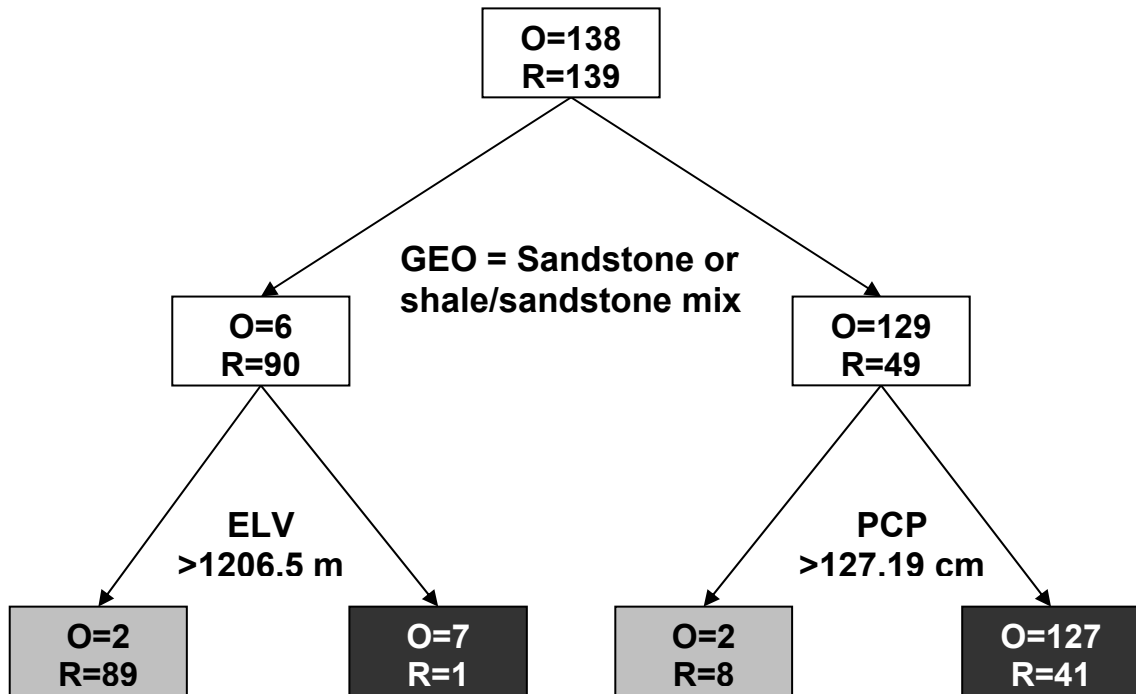


FIGURE 4. Tree diagram of optimal CART model used for explaining landscape-level occupancy of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Decision rules at splits apply to the right branch, while the opposite rule applies to the left branch. Numbers inside nodes indicate total number of occupied (O) and random (R) data points and shading indicates majority classification of each terminal node (black = occupied, grey = random points).

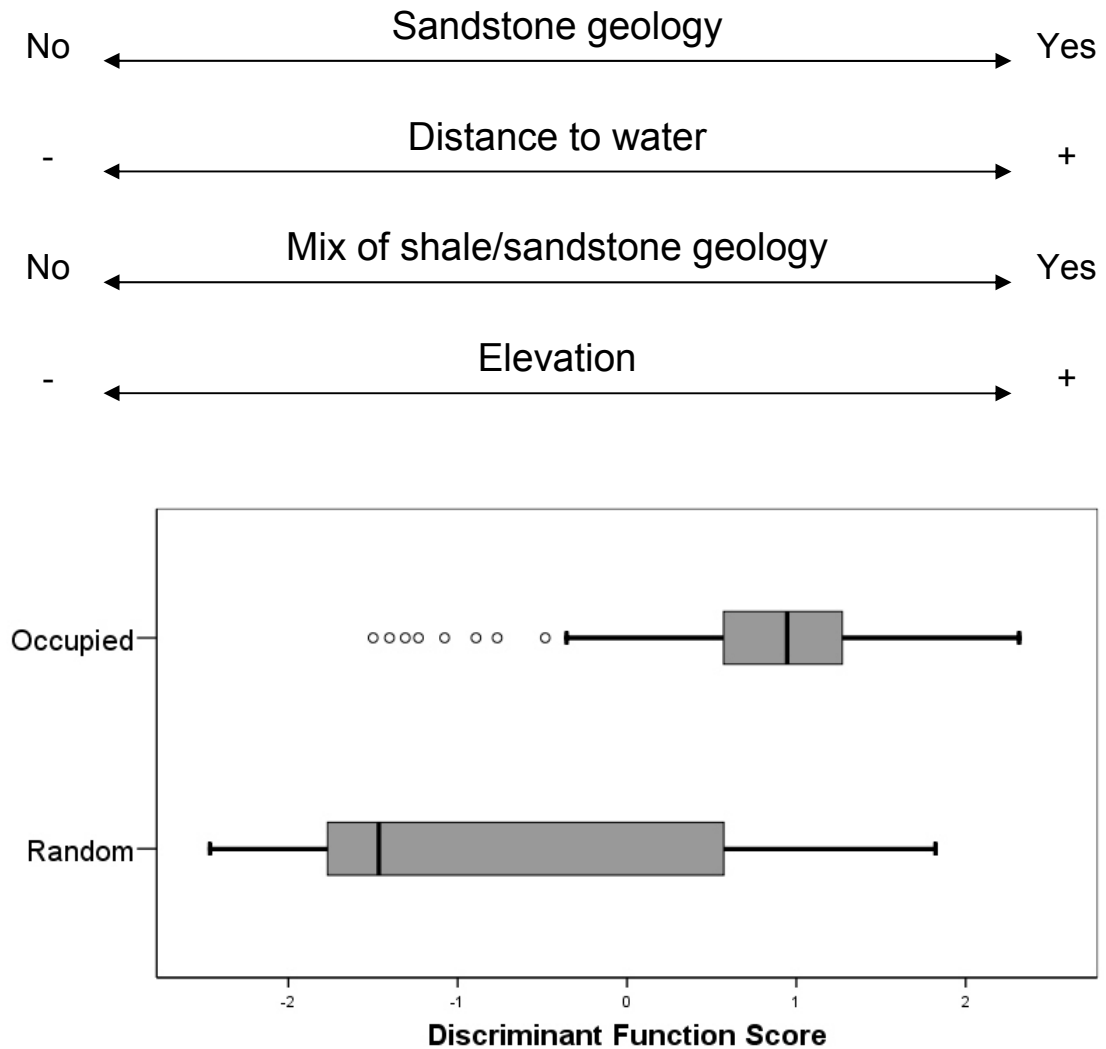


FIGURE 5. Graphical output of forward stepwise discriminant function model used for explaining landscape-level occupancy of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Variables above box plot are listed in the order of importance. The shaded box represents the interquartile (IQ) range, whiskers indicate the highest and lowest values which are no greater than 1.5 times the IQ range, the line across the box indicates the median, and circles represent outliers (between 1.5 and 3 times the IQ range).

CHAPTER II:
SITE-LEVEL HABITAT MODELS FOR THE ENDEMIC,
THREATENED CHEAT MOUNTAIN SALAMANDER (*PLETHODON*
***NETTINGI*): THE IMPORTANCE OF GEOPHYSICAL AND BIOTIC**
ATTRIBUTES FOR PREDICTING OCCURRENCE

Abstract: The federally threatened Cheat Mountain salamander (*Plethodon nettingi*; hereafter CMS) is known to occur in approximately 70 small, scattered populations in the Allegheny Mountains of eastern West Virginia, USA. Current conservation and management efforts on federal, state, and private lands involving CMS must largely rely on small scale, largely descriptive studies of habitat associations from a few sample sites. To address the critical need for quantitative data, I used an information-theoretic approach to elucidate site-level habitat relationships of CMS relative to a suite of biotic and abiotic habitat variables measured across the species' range. I collected data on 18 explanatory habitat variables at CMS-occupied ($n = 67$) and random ($n = 37$) sites in the summer of 2006 and examined CMS habitat relationships using *a priori*, logistic regression models with information-theoretic model selection. Among 16 specified models, a model containing the variable depth to rock received the strongest empirical support, although five competing models containing additional abiotic variables (emergent rock ground cover, rocky outcrops, seeps) and biotic variables (canopy closure, conifer density, bryophyte ground cover) received limited support. Overall, results of model selection indicated that the probability of CMS occurrence at the site-level increased in areas with shallower depth to rock, areas proximal to rocky outcrops

but distal to seeps, areas with higher densities of bryophytes, and areas with high densities of red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). Within the Allegheny Mountains, associations between CMS and abiotic habitat features appear to be important predictors of site-level occurrence, although vegetation associations interact to form more precise habitat relationships within forested landscapes. The information gained from my study should increase the capacity of managers to plan for the continued persistence and conservation of Cheat Mountain salamanders in this landscape.

INTRODUCTION

Woodland salamanders of the family Plethodontidae are among the most abundant vertebrates in the moist temperate forests of North America (Burton and Likens 1975, Hairston 1987, Mathis 1991, Petranka 1998). Despite this abundance, many woodland salamander species generally are restricted to a relatively narrow range of environmental conditions. Because plethodontids are lungless and rely entirely on cutaneous respiration, their skin must remain moist to permit efficient gas exchange (Feder 1983). Accordingly, the moist and permeable skin of woodland salamanders makes them vulnerable to desiccation and limits surface activity to periods when humidity and soil moisture are high (Spotila 1972). Even when environmental conditions are favorable, terrestrial salamanders risk desiccation during periods of surface activity and must periodically retreat to moist microhabitats for rehydration (Feder 1983).

Presence and abundance of woodland salamanders have been positively correlated with the volume of coarse woody debris (Petranka et al. 1994, Brooks 1999, Grover and

Wilbur 2002), stand age (Petranka et al. 1993, 1994, Ford et al. 2002, Hicks and Pearson 2003), canopy closure (DeGraaf and Yamasaki 2002, Duguay and Wood 2002, Morneault et al. 2004), depth and quality of leaf litter (Pough et al. 1987, deMaynadier and Hunter 1998), organic soil layer thickness and moisture (DeGraaf and Yamasaki 2002), and understory vegetation density (Pough et al. 1987, Brooks 1999, DeGraaf and Yamasaki 2002, Morneault et al. 2004). Consequently, cool, moist microhabitat conditions characteristic of mature or late successional forests are thought to best meet the habitat requirements of many woodland salamanders (deMaynadier and Hunter 1995, Petranka 1998).

The Cheat Mountain salamander (*Plethodon nettingi*; hereafter CMS) is a small terrestrial plethodontid endemic to high-elevation forests of the Allegheny Mountains in Tucker, Randolph, Pocahontas, Grant, and Pendleton counties of eastern West Virginia (Green 1938, Green and Pauley 1987). The species is believed to consist of approximately 70 isolated populations distributed across an area of approximately 1800 km² (U.S. Fish and Wildlife Service 1991, Pauley and Pauley 1997, Petranka 1998). Most (75%) known CMS populations reportedly consist of ≤ 10 individuals (U.S. Fish and Wildlife Service 1991), and $\geq 80\%$ of those populations occur on the Monongahela National Forest (MNF; U.S. Fish and Wildlife Service 1991).

Cheat Mountain salamanders were listed as a threatened species in 1989 by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1991). Historically, the range of CMS was possibly more extensive than the current restricted distribution (U.S. Fish and Wildlife Service 1991). However, exploitative logging and large wildfires in the region eliminated $>93\%$ of red spruce (*Picea rubens*) forests by 1920 (Clarkson 1964,

Clovis 1979, Mielke et al. 1986). Accordingly, many CMS populations were thought to have been extirpated during this period. Although no published studies have directly assessed effects of forest disturbance on CMS, presumably this species responds in a manner similar to other woodland salamanders to the microclimatic, vegetational, and structural changes that occur after timber harvest (deMaynadier and Hunter 1995, Russell et al. 2004a). Pauley and Watson (2003) found that CMS abundance increased with distance from forest opening edge created by forest regeneration areas, ski trails, and roads. In addition to legacy habitat disturbance, recent or ongoing forest management, surface mining, road building, and recreational development activities, as well as competition with sympatric red-backed salamanders (*P. cinereus*) and Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*) have been hypothesized to continue limiting CMS distribution and abundance (Highton 1972, Pauley 1980a, Pauley 1998). Because extant CMS populations are small and geographically isolated, loss of genetic diversity also is thought to possibly threaten the species (U.S. Fish and Wildlife Service 1991, Kramer et al. 1993).

Despite the threatened status of CMS, required protection under the Endangered Species Act, along with continued concerns about habitat disturbance effects and an identified recovery plan task of conducting quantitative habitat assessments (U.S. Fish and Wildlife Service 1991), relatively little has been published regarding CMS habitat relationships. In Chapter I, the distribution of CMS was modeled relative to landscape-level habitat characteristics. Results of this study indicated that the probability of CMS occurrence was primarily related to coarse-scale geophysical characteristics, including elevation, geology type, topography, and distance to water.

However, existing reports of site-level CMS habitat associations typically describe only general cover type associations or microhabitat relationships from limited descriptive observations. Cheat mountain salamanders have been reported to occur in coniferous and mixed conifer-deciduous forest stands with a bryophyte (*Bizzania* spp.)-dominated forest floor ranging in elevation from 805-1482 m (Green and Pauley 1987, Pauley and Pauley 1997). Brooks (1945, 1948) indicated that CMS were restricted to pure stands of red spruce or mixed red spruce-yellow birch (*Betula alleghaniensis*) forests and that CMS were more abundant in newly regenerating red spruce stands, although this observation may be related to the scarcity of mature spruce forests in the area at the time (Clarkson 1964). Though without reference to stand age, I also found a positive landscape-level association between CMS occurrence and presence of red spruce cover (Chapter I). In contrast, Clovis (1979) found CMS in a wider range of stand types, including those dominated by red spruce, red maple (*Acer rubrum*), yellow birch, and black cherry (*Prunus serotina*). Pauley (1980b) also detected CMS populations in northern hardwood stands with both a small or wholly absent red spruce component.

In addition to forest stand composition, surface microhabitats that retain moisture also may be important site-level habitat elements for CMS. Brooks (1948) described typical CMS habitat as a forest floor with decaying red spruce logs covered with mosses and lichens or moss-covered emergent rock. Surface-active CMS have been observed under emergent rocks, within and under decaying logs, on the trunks and lower limbs of trees (≤ 2 m high), on sandstone cliff faces, and along road banks (Brooks 1945, 1948, Green and Pauley 1987, Pauley 1998). Brooks (1948) found CMS on both gentle and steep slopes, nor did he observe any discernable association between CMS presence and

riparian habitats. Although Pauley and Pauley (1997) described bryophyte ground cover as an important habitat element for CMS, Calise (1978) found no differences in bryophyte species composition at CMS sites when compared to unoccupied sites. Pauley (1980b) noted that CMS occupied sites had higher relative humidities and lower temperatures than those of sympatric *P. cinereus* or *D. ochrophaeus*. Moreover, he noted that soil moisture and temperature, relative humidity, and insolation were similar at CMS sites regardless if the overstory was red spruce or hardwood-dominated. When two CMS-occupied sites were compared with two unoccupied sites, soil and litter moisture, relative humidity, and litter mass were higher, but soil temperatures lower, at occupied sites (Pauley 1998). Additionally, Pauley (1998) hypothesized that favorable temperature and moisture regimes at occupied sites were associated with the presence of emergent rock microhabitats. Similarly, Santiago (1999) found that sites occupied by CMS also were associated with high relative humidity, but found no correlations between presence of CMS and either air or soil temperatures. Still, CMS appeared to have the most restrictive humidity requirements of four sympatric woodland salamanders (*D. ochrophaeus*, *P. cinereus*, *P. glutinosus*, *P. wehrlei*) examined by Santiago (1999).

Because the distribution of CMS within the Allegheny Mountains of West Virginia is discontinuous and important fine scale habitat features are poorly quantified, extensive surveys for occupancy must be conducted prior to most forest management or other land-disturbing activities on both public and private lands. However, current information to guide site-level conservation and management efforts for CMS is limited to largely descriptive observations made at a small number of locations (Brooks 1948, Pauley 1980b, 1998, Pauley and Pauley 1997). Accordingly, research is needed that

quantitatively models how abiotic habitat features interact with vegetation characteristics at a fine scale to influence CMS occupancy across the range of the species. Quantitative models that can reliably describe sites known to be occupied by CMS should increase the efficacy of future survey and monitoring efforts, more effectively evaluate potential impacts of proposed management activities on CMS, and aid in recovery of the species (U.S. Fish and Wildlife Service 1991). Therefore, my goal was to develop site-level habitat models of CMS occurrence across the predicted distribution of the species in West Virginia (Chapter I). Specifically, I (1) examined if logistic regression modeling of site-level habitat characteristics with information-theoretic model selection could reliably differentiate between CMS-occupied and random locations; (2) evaluated the relative importance of biotic and abiotic habitat features for describing CMS habitat relationships; and (3) compared these findings to both recent landscape-scale habitat modeling results (Chapter I) and to previous, qualitative descriptions of CMS habitat associations.

STUDY AREA

The known distribution of CMS lies entirely within the northern high Allegheny Mountains ecological subsection (M221Ba; Keys et al. 1995) in eastern West Virginia, USA (Fig. 6). Therefore, I constrained my modeling to this area. This 320,081-ha landscape included portions of the MNF, Canaan Valley National Wildlife Refuge (CVNWR), Canaan Valley Resort State Park, Blackwater Falls State Park, as well as large areas of corporate and non-industrial private forest ownership. Geoclimatic conditions include steep slopes, broad mountaintops and ridges, narrow valleys with small, high-gradient streams, high precipitation, and cool temperatures. Elevation ranges

from 291 to 1482 m with an average of 951.7 ± 210.1 m. Geologic formations are of sedimentary origin and include sandstone, shale, and limestone. Area soils have high moisture content with thick humus, while soil fertility and pH vary depending upon parent material (Kochenderfer 2006). Over a 30-year period (1961-1990), average annual minimum temperature was 2.6 ± 0.3 °C, average annual maximum temperature was 13.5 ± 1.4 °C, and average annual precipitation was 131.3 ± 11.0 cm/year.

Mountains and some higher valleys within the study area generally are wholly forested whereas lower elevation valleys have been converted in part to pasture (McCay et al. 1997). At middle elevations, covering most of the region, the forest cover was an Allegheny hardwood-northern hardwood type dominated by American beech (*Fagus grandifolia*), yellow birch, sugar maple (*A. saccharum*), red maple, and black cherry. Remnant stands of red spruce and eastern hemlock (*Tsuga canadensis*) were present at the higher elevations and along sheltered riparian areas. Species from mixed mesophytic forest associations such as yellow poplar (*Liriodendron tulipifera*), basswood (*Tilia americana*), sweet birch (*B. lenta*), and northern red oak (*Quercus rubra*) occurred at lower elevations (Ford et al. 2002). Although relatively rare locally, on some xeric exposures oak (*Q. spp.*)-dominated or oak-pine (*Pinus spp.*) cover types occurred (McCay et al. 1997, Ford et al. 2002, Kochenderfer 2006).

METHODS

Salamander occurrence and random point locations

To determine CMS presence, I acquired locations from Geographic Information System (GIS) databases maintained by MNF ($n = 204$) and CVNWR ($n = 49$) where ≥ 1 CMS was found during previous field surveys. I specified that locations must (1) be accessible for collection of habitat data and (2) be separated by ≥ 60 m to increase the likelihood of independence for CMS detections and reduce the potential for spatial autocorrelation of habitat data (Legendre 1993). Although CMS occurrence data were available from private lands within the study area, restricted access precluded collection of habitat data. Therefore, only data from public lands were used for analyses. Using these criteria, 180 occupied CMS points were retained for model development.

To represent habitats currently “unoccupied” by CMS, I selected an equal number ($n = 180$) of random points from the study area. Because true absence of CMS at these points was unknown, I used the term “pseudo-absence” in conjunction with random sites. Prior to selecting random points, I buffered all occupied points with a 60-m radius area using ArcView 3.3 (ESRI 2002). I assumed these buffers prevented overlap of occupied and random sites. Terrestrial plethodontid salamanders are relatively sedentary, with small home ranges (e.g., $<1\text{-}25\text{ m}^2$) and limited dispersal abilities (citations in Petranka 1998). Moreover, the apparent rarity of CMS across the landscape increased the likelihood of salamander absence outside the 60-m buffers. Within my defined pseudo-absence area, I generated random points using a random point generator (Jenness 2005). I required that random points met land ownership and minimum distance criteria as described above for occupied locations.

Previous landscape-level modeling of CMS distribution delineated broad areas of probable CMS occurrence across the range of the species (Chapter I). To create more informative habitat models within the predicted range of CMS, I constrained my site-level analyses to areas with $\geq 50\%$ probability of CMS occupancy as identified by the best-approximating logistic regression model from the landscape study (Chapter I, Fig. 3a). This selection criterion limited my modeling efforts to a pool of 155 occupied and 47 random sites.

Habitat measurements

During the summer of 2006, I was able to survey 67 occupied and 37 random points selected by my criteria within the predicted range of CMS (Fig. 6). At the center of each location, identified with a handheld GPS unit, I established a 10×10 -m sampling plot and measured biotic and abiotic habitat variables thought to be potential correlates of CMS presence (Brooks 1948, Green and Pauley 1987, Pauley 1998, Petranka 1998). I recorded the species and diameter at breast height (dbh) of all trees ≥ 10 cm dbh within each plot. Overstory composition was classified as one of three broad forest cover types appropriate for these central Appalachian systems in the higher elevations of the Allegheny Mountains (Braun 1950, McNab and Avers 1994, Mueller 1996): red spruce-montane, northern hardwood, and mixed mesophytic. I estimated overhead canopy closure at each plot center with a spherical densiometer (Lemmon 1956). Densiometer readings from each cardinal direction were averaged. I measured visual obscurity using a 2.5×150 -cm cover pole (after Robel et al. 1970), marked in 10-cm sections. The pole was placed in the center of the plot and I recorded the total number of sections $\geq 0.75\%$ obscured from each corner of the plot, measured at eye level. The mean of the four

readings was used to estimate percent shrub obscuring the cover pole. I also recorded the dominant type of shrub vegetation obscuring the cover pole. Shrub type was grouped into four categories appropriate for my study area and included red spruce / eastern hemlock, rhododendron (*Rhododendron maximum*) / mountain laurel (*Kalmia latifolia*), deciduous shrubs, or mixed. I recorded the presence of large rocky outcrops and seeps (depressed, moist patches) within 30 m of each plot center.

I sampled ground cover within five, 1-m² quadrats located at the center of the 10 × 10-m plot and 2.5 m from the plot center in each cardinal direction. I visually estimated percent ground cover of ferns, herbs, bryophytes, coniferous and deciduous litter, emergent rock, woody debris, and bare ground in each quadrat using categories defined by Daubenmire (1959). The midpoint of each Daubenmire category was used to average ground cover estimates for each plot. At the center of each quadrat, I measured litter depth and depth to rock with a graduated metal probe. Depth measurements were averaged for the plot. I partitioned average depth to rock into four ordinal categories (≤ 10.0 cm, 10.1-20 cm, 20.1-30 cm, ≥ 30 cm).

Model specification and analyses

I used logistic regression to determine the probability of CMS occurrence in relation to habitat characteristics measured at each occupied and random site. I specified a set of *a priori*, candidate models based on (1) available biological information on CMS and other woodland salamanders, and (2) my previous experience with these species (Burnham and Anderson 2002). Prior to model specification, I eliminated redundant variables (Spearman's $r \geq 0.70$) and retained 18 variables for inclusion in models (Table 4). I specified 16 models: a global model containing all 18 variables and subset models

representing potential influences of biotic and abiotic attributes on CMS presence (Table 5). Each model in my set represented a competing hypothesis of the determinants of CMS occurrence. I specified six univariate models including an “outcrop” model, representing the reported association between CMS and rocky outcrops (Pauley 1998). Additionally, I constructed nine multivariate models including a “literature habitat” model, representing a combination of recent descriptions of CMS habitat (i.e., associations with red spruce, canopy closure, and bryophytes; Pauley 1980*b*, Pauley and Pauley 1997) and my own work (i.e., associations with eastern hemlock and colluvial rock; Chapter I). I did not consider all possible combinations of variables, as this approach typically inflates the number of models beyond the number that can be reliably analyzed (Burnham and Anderson 2002). Prior to model selection, I examined fit of global models following recommendations of Burnham and Anderson (2002) that included examining residuals, measures of fit (Nagelkerke’s rescaled $R^2 = 0.26$), classification tables (overall accuracy = 69.2%), and histograms of expected probabilities.

I used Akaike’s Information Criterion (AIC; Hurvich and Tsai 1989, Burnham and Anderson 2002) for model selection. Because the number of occupied and random sites ($n = 121$) was small relative to the number of variables (K) in several models (i.e., $n/K < 40$), I used AIC corrected for small sample size (AIC_c) for model selection (Hurvich and Tsai 1989, Burnham and Anderson 2002). I used the formulas presented in Burnham and Anderson (2002) to calculate AIC_c from the log-likelihoods for each model. I ranked all candidate models according to their AIC_c values and the best model (i.e., most parsimonious) was the model with the smallest AIC_c value (Burnham and Anderson 2002). I drew primary inference from models within 2 units of AIC_{cmin} , although models

within 4-5 units may have limited empirical support (Burnham and Anderson 2002). I calculated Akaike weights (w_i) to determine the weight of evidence in favor of each model (Burnham and Anderson 2002). To assess model fit of supported models, I calculated Nagelkerke's rescaled R^2 . All categorical variables were transformed into dummy variables (Cohen and Cohen 1983) and coefficients were calculated relative to the most frequently occurring category for each variable (Russell et al. 2004b, 2005). All analyses were performed using SPSS software (SPSS 2005).

RESULTS

Of 16 logistic regression models explaining the site-level occurrence of CMS, the single abiotic variable "depth to rock" was selected as the best-approximating model (Table 5). Salamander presence was negatively associated with increasing depth to subsurface rock (Table 6). My second-best model, "literature habitat," also received empirical support ($\Delta AIC_c = 2.49$; Table 5). This model also indicated that CMS occurrence was negatively associated with subsurface rock depth, but positively associated with red spruce and eastern hemlock density, percent canopy closure, and percent ground cover of bryophytes (Table 6). Weight of evidence ($w_{\text{best model}}/w_{\text{second-best model}}$) in favor of the "depth to rock" model was 3.5 times greater than that of the "literature habitat" model (Table 5), indicating some uncertainty in selection of the best candidate model (Burnham and Anderson 2002). However, evidence for a depth to rock effect was strong in that the sum of Akaike weights for the three empirically-supported models containing this variable was 0.66.

Four additional models received limited empirical support (i.e., within 5 ΔAIC_c units of AIC_{min} ; Table 5). My third-best model, “bryophytes,” ($\Delta AIC_c = 2.69$; Table 5) indicated that CMS occurrence was positively associated with percent ground cover of bryophytes (Table 6). My fourth-best model, “abiotic” ($\Delta AIC_c = 3.55$; Table 5) indicated that CMS occurrence was negatively associated with subsurface rock depth, percent ground cover of emergent rock and proximity to seeps, but positively associated with proximity to rock outcrops. My fifth-best model, “conifer density,” ($\Delta AIC_c = 3.96$; Table 5) indicated that CMS presence was positively associated with increasing tree density of red spruce and eastern hemlock (Table 6). My sixth-best model, “outcrop” ($\Delta AIC_c = 4.13$; Table 5) indicated that CMS occurrence was positively associated with the presence of rocky outcrops (Table 6). The remaining 10 models received marginal or no empirical support ($\Delta AIC_c \geq 5.29$, $w_i \leq 0.03$; Table 5).

DISCUSSION

My research provides a range-wide assessment of factors potentially influencing the probability of occupancy by CMS at a site-level. Site-level occurrence of CMS was primarily influenced by geophysical characteristics rather than by patterns of vegetation composition and structure. In particular, my best-approximating logistic regression model explaining occupancy of CMS included the single variable depth to rock. The probability of CMS occurrence was positively related to more shallow rock depths. I am unaware of any literature correlating rock depth with CMS occupancy, but soil depth was useful for describing the niche separation between Shenandoah salamanders (*P. shenandoah*), a high-elevation sister species of CMS (Duellman and Sweet 1999), and *P.*

cinereus (Jaeger 1970, Griffis and Jaeger 1998). In contrast, Ford et al. (2002) did not find a relationship between depth to rock or soil depth and the richness, diversity, or relative abundance of woodland salamanders in southern Appalachian forests. Most species of terrestrial plethodontid salamanders are believed to be largely subterranean, with only a small percentage of populations near the surface at a given time (Taub 1961, Heatwole 1962, Petranka and Murray 2001, Bailey et al. 2004). In my study area, rocks just below the surface often indicate the presence of extensive colluvium that contains abundant interstitial spaces. Other plethodontid salamanders, and presumably CMS, use such underground refugia to avoid dry, hot weather during summer and to overwinter (Petranka 1998). Individuals typically exit subterranean interstices for surficial activity (e.g., foraging) only when moist, cool microclimatic conditions exist that allow for cutaneous respiration by CMS and other lungless salamanders (Feder 1983, Owen 1989, Grover 1998, Petranka 1998, Welsh et al. 2006).

My “literature habitat” model also received empirical support and provided additional evidence of an association with rock depth. This model, as well as the empirically-supported model “conifer density” indicated a positive association between CMS occurrence and the stem densities of both red spruce and eastern hemlock. Previous, qualitative descriptions of CMS habitat suggested a strong association between the historic or current distribution of red spruce forests and the range of CMS (Brooks 1945, 1948, Pauley 1980*b*, U.S. Fish and Wildlife Service 1991, Pauley and Pauley 1997). My field-based results also corroborate the coarse scale, GIS-based data used in previous modeling of CMS landscape-level distribution (Chapter I) that indicated a correlation between CMS occurrence and the presence of red spruce forest cover. In

addition to red spruce, I suggest that presence of eastern hemlock should be added to currently accepted habitat descriptions of CMS. Mature red spruce and eastern hemlock stands have dense canopies, resulting in shaded ground conditions that may provide cool, moist microclimates ideal for CMS (Petranka 1998).

The functional importance of red spruce and eastern hemlock for CMS remains unknown. However, densities of many plethodontid salamanders, including *P. cinereus*, appear to be lower in coniferous forests than deciduous forests (Petranka 1998, Brooks 2001). Soil and leaf litter pH is more acidic within stands with a large conifer component (Foote and Jones 1989, DeGraaf and Rudis 1990), which may limit terrestrial salamander distribution (Wyman and Hawksley-Lescault 1987, Wyman 1988, Wyman and Jancola 1992, Sugalski and Claussen 1997). Pauley (1980*b*) observed lower soil pH in occupied CMS locations ($n = 4$) than in non-occupied locations ($n = 3$), although differences were not statistically significant. I suggest that spatial variation in soil and leaf-litter pH, as influenced by the presence of red spruce and eastern hemlock, may be an important aspect of micro-niche segregation between CMS and competitively dominant sympatric salamanders such as *P. cinereus*.

My literature habitat model indicated a positive association between CMS occupancy and overstory canopy closure. My results are consistent with accepted relationships between canopy closure and other terrestrial salamanders (deMaynadier and Hunter 1995, Petranka 1998, Russell et al. 2004*a*). Pauley (1980*b*) reported that the percentage of light reaching the forest floor in CMS-occupied locations ($n = 4$; $\bar{x} = 26.42 \pm 14.91$) was less than in non-occupied locations ($n = 3$; $\bar{x} = 29.91 \pm 9.08$). However, my own analysis of his unpublished data did not reveal a significant difference (Mann-

Whitney *U*-test: $Z = -0.354$, $P = 0.724$). This model, as well as the single-variable model “bryophytes” which also received empirical support, indicated a positive association between percent ground cover of bryophytes and CMS occupancy. My results quantitatively corroborate CMS habitat descriptions by Brooks (1948) and Pauley and Pauley (1997). The presence and density of certain bryophyte species that I observed at occupied sites (e.g., *Bazzania* spp.) may be indicators of suitable microhabitat conditions for CMS including higher soil moisture and site-level humidity.

My “abiotic” model also received empirical support and provided additional evidence of an association with rock depth. This model, as well as the single-variable model “outcrop” which also received empirical support, indicated a positive association between CMS occupancy and the presence of rocky outcrops. Fracturing of exposed outcrops from intense freeze-thaw cycles in the High Alleghenies provides conduits to the underlying layers of rock and associated interstitial spaces. Moreover, during disturbance events such as wildfires, salamanders are known to migrate into underground retreats (Russell et al. 1999, Pilliod et al. 2003). Large rock outcrops and associated colluvium have been hypothesized to be important refugia for CMS, and may have allowed this species to persist during exploitative logging and widespread wildfires in the early 20th century (Pauley 1998).

My abiotic model suggested a potential influence of emergent rock ground cover on CMS occupancy. Throughout the Allegheny Mountain portion of the central Appalachians, high-elevation plateaus are capped by resistant sandstone parent materials (Fenneman 1938). Recent landscape-level modeling (Chapter I) indicated a strong association between CMS distribution and sandstone, most likely reflecting the surface

and subsurface habitats produced by this geology type. In my study area, sandstone parent materials generally weather to produce large outcrops, emergent rocks, and colluvial materials. Emergent rocks and other cover objects are used during the day by surface-active CMS and other terrestrial salamanders to avoid desiccation and predation (Green and Pauley 1987, Pauley 1998, Petranka 1998). However, my results indicated a negative association between CMS occupancy and the percent cover of emergent rock. I think this counterintuitive relationship may indicate that modest amounts of emergent rock are favorable for CMS and other terrestrial salamanders, as evidenced by a positive association between CMS and isolated rock outcrops, but extensive coverage of surface rock within sites may reflect generally poor site conditions for salamanders (e.g., low soil moisture, limited vegetation coverage and growth). Petranka (1998) provided evidence that populations of *P. cinereus* usually reach their greatest numbers in forested habitats with deep soils, but are absent or occur at low densities in shallow, rocky soils.

Finally, my abiotic model indicated a negative correlation between CMS occurrence and the presence of seeps. My results corroborate early CMS habitat descriptions by Brooks (1948) and recent research on CMS landscape-level distribution (Chapter I), indicating that CMS-occupied sites were farther from water sources when compared to random locations. My findings may provide some support to the prevailing hypothesis that both *P. cinereus* and *D. ochrophaeus* competitively dominate CMS and potentially restrict its local distribution (Highton 1972, Pauley 1980a, Adams et al. 2007). Grover and Wilbur (2002) found that *P. cinereus* abundance increased in artificially created seeps in upland forest habitats in the Allegheny Mountains. Throughout high elevation forests in my study area, *D. ochrophaeus* are ubiquitous because of abundant

precipitation, but may congregate near seeps and other water sources for breeding and during periods of drought (Petranka 1998).

My results indicated that CMS occupancy was most strongly associated with abiotic variables than with overstory, shrub, or ground cover vegetation type and structure. More precisely, an association with vegetation was only detected in three logistic regression models with limited empirical support. Both Clovis (1979) and Pauley (1980*b*) failed to detect meaningful differences in overstory, shrub, or ground cover vegetation composition and structure between CMS-occupied ($n = 4$) and non-occupied sites ($n = 4$). I do not suggest that CMS are insensitive to vegetation composition and other biotic attributes. Rather, associations between CMS and abiotic habitat features may be primary predictors of site-level occurrence, although vegetation associations interact with these features to form more precise habitat relationships within forested landscapes. Additional quantitative site-level and microhabitat studies that explicitly examine CMS presence and population densities in relation to structural, physiochemical, and other abiotic attributes as well as occupancy and density of competitive sympatric salamanders (i.e., *P. cinereus* and *D. ochrophaeus*) within high-elevation conifer stands will be necessary to further evaluate critical habitat requirements.

Despite showing considerable agreement or complementary information with existing observations of CMS, I urge caution in extending my modeling results beyond this first quantitative general description of CMS site-level habitat relationships, as my study contained several limitations and assumptions. Because my research relied on previous ground surveys to determine occupancy, I assumed that CMS was still present and that habitat conditions had not changed dramatically between the original surveys

and my modeling effort. Given that at least some occupied sites I incorporated into my analyses appear to have been surveyed ≥ 15 -20 years ago, it is possible that subsequent human or natural disturbances to these sites significantly altered habitat conditions. In addition, available CMS data were restricted to occurrence. Therefore, my modeling effort did not address site-level influences on CMS abundance, densities, or range-wide population viability.

I also assumed that random locations were currently unoccupied but potentially available to CMS (Manly et al. 1993). I chose to compare CMS-occupied sites with random locations rather than with historic survey sites where CMS previously was deemed to be absent. Detection probabilities of surface-active plethodontid salamanders vary considerably with temporal and environmental conditions (Bailey et al. 2004). Failure to account for detection probabilities can significantly increase the likelihood of false absences, particularly for inherently rare species (Bailey et al. 2004). Consequently, false absences may introduce considerable bias in the use of logistic regression modeling to understand distribution and habitat association patterns (Royle et al. 2005, Ford et al. 2006, Haan et al. 2007). In addition, I detected considerable potential biases in the distribution of historic CMS-“absent” sites, including spatial autocorrelation with existing roads and trails in the region. Therefore, I think the use of random sites represents a conservative but suitable approach. Unfortunately, current scientific collecting permit restrictions for CMS research (Adams et al. 2007) will likely preclude estimation of detection probabilities for this species, as well as collection of other critically needed data in the foreseeable future.

Although my best-approximating model and other supporting models defined the “fundamental niche” (Zaniewski et al. 2002, Ford et al. 2006) of CMS, my models failed to account for much of the variation in the site-level occurrence of the species. In contrast, my landscape-level assessment of CMS distribution resulted in a set of models with relatively high predictive power and classification accuracy (Chapter I). My models may indicate that fine-scale habitat relationships of CMS may be considerably more complicated than can be described by the site-level and microhabitat variables I measured. Because I avoided specification of all potential models (Burnham and Anderson 2002), it is possible that combinations of variables I did not consider may have provided better predictive power, for which this type of model specification and selection has been criticized (Guthery et al. 2005). Therefore, comparisons of habitat characteristics at CMS-occupied sites with those at sites where salamanders have been reliably determined to be absent (Bailey et al. 2004), in combination with refined model specification incorporating new data (Burnham and Anderson 2002) may improve the predictive power of my models. Conversely, my inability to definitively discriminate between CMS-occupied and random locations may indicate that this species is somewhat more general in its habitat associations than is currently accepted.

Nonetheless, all variables associated with the presence of CMS in my study are those that have support in previous observations of the species (Brooks 1945, 1948, Clovis 1979, Green and Pauley 1987, Pauley and Pauley 1997). Low explanatory power does not necessarily indicate that a model fails to capture important ecological information (Whitaker and Stauffer 2006). Some data sets will have an inherently low “signal-to-noise” ratio, which may occur when variables are difficult to measure

accurately or are subject to inherent random variation (Whitaker and Stauffer 2006). In such cases, even good models that offer important ecological insights may have only limited explanatory power.

IMPLICATIONS FOR CONSERVATION

Natural resource managers working in areas occupied or potentially occupied by threatened, endangered or sensitive species such as the Cheat Mountain salamander need readily available information on site-specific habitat associations. This first attempt to model the habitat relationships of CMS across its distribution indicates that field-based efforts to identify occupied habitat should move beyond the traditional focus on vegetation composition and explicitly integrate important geophysical factors such as surficial geology and proximity to water (Russell et al. 2004*b*, 2005). Furthermore, I suggest that future research studies include a more defined focus on occurrence and abundance of competitor sympatric salamander species. Even with limited explanatory power, my models identified previously unreported interactions of site-level variables that potentially influence the distribution of CMS. As such, I view my modeling efforts as an exploratory but critical first step in quantitatively elucidating habitat relationships of CMS across the range of the species, which addresses a key but heretofore uncompleted task in the CMS recovery plan (U.S. Fish and Wildlife Service 1991).

I think my effort should be useful to land managers as it describes areas where potentially critical or optimal locations from an occupancy perspective exist on the MNF and CVNWR. Because the distribution of CMS is discontinuous and important habitat features are poorly quantified, extensive surveys for occupancy must be conducted prior

to most land-disturbing activities (e.g., timber harvesting, road building, and recreational development). Combined with landscape-level distribution models (Chapter I), my site-level habitat models could reduce the time and effort associated with future field-based CMS surveys, and may assist the identification of new populations. Lastly, these multi-scale efforts provide potential guidelines for future management efforts designed to restore red spruce ecosystems to benefit CMS and other high elevation obligates in the region (Shuler et al. 2002). My combined results suggest such efforts may be more effective if situated in areas with existing abiotic features associated with CMS occurrence, including 1) high elevation sites with sandstone geology, 2) areas with northeasterly aspects, gentler slopes, high annual precipitation, 3) areas with shallower depth to rock, and 4) areas proximal to rocky outcrops but distal from seeps and other surface water. Accordingly, the information gained from this study will increase the capacity of managers to plan for the continued persistence and conservation of Cheat Mountain salamanders, as well as their associated habitats.

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LITERATURE CITED

- Adams, D. C., M. E. West, and M. L. Collyer. 2007. Location-specific sympatric morphological divergence as a possible responses to species interactions in West Virginia *Plethodon* salamander communities. *Journal of Animal Ecology* 76:289-295.
- Bailey, L. L., T. R. Simons, and K. H. Pollock. 2004. Estimating detection probability parameters for *Plethodon* salamanders using the robust capture-recapture design. *Journal of Wildlife Management* 68:1-13.
- Braun, E. L. 1950. *Deciduous forests of eastern North America*. Hafner Press, New York, New York, USA.
- Brooks, M. 1945. Notes on amphibians from Brickle's Knob, West Virginia. *Copeia* 1945:231.
- Brooks, M. 1948. Notes on the Cheat Mountain salamander. *Copeia* 1948:239-244.
- Brooks, R. T. 1999. Residual effects of thinning and high white-tailed deer densities of northern redback salamanders in southern New England oak forests. *Journal of Wildlife Management* 63:1172-1180.
- Brooks, R. T. 2001. Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. *Forest Ecology and Management* 149:197-204.

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Burton, T. M., and G. E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook experimental forest, New Hampshire. *Copeia* 1975:541-546.
- Calise, C. 1978. Bryophyte ecology in high elevation forest of West Virginia. Thesis, West Virginia University, Morgantown, West Virginia, USA.
- Clarkson, R. B. 1964. Tumult on the mountains. McClain Printing, Parsons, West Virginia, USA.
- Clovis, J. F. 1979. Tree importance values in West Virginia red spruce forests inhabited by the Cheat Mountain salamander. *Proceedings of the West Virginia Academy of Science* 54:58-64.
- Cohen, J., and P. Cohen. 1983. Applied multiple regression–correlation analysis for the behavioral sciences. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.
- Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. *Northwest Science* 33:43-64.
- DeGraaf, R. M., and D. D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. *Forest Ecology and Management* 32:155-165.
- DeGraaf, R. M., and M. Yamasaki. 2002. Effects of edge contrast on redback salamander distribution in even-aged northern hardwoods. *Forest Science* 48:351-363.

- deMaynadier, P. G., and M. L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* 3:230-261.
- deMaynadier, P. G., and M. L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340-352.
- Duellman, W. E., and S. S. Sweet. 1999. Distributional patterns of amphibians in the Nearctic Region of North America. Pages 31-109 *in* W. E. Duellman, editor. *Patterns of Distributions of Amphibians: A Global Perspective*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Duguay, J. P., and P. B. Wood. 2002. Salamander abundance in regenerating forest stands on the Monongahela National Forest, West Virginia. *Forest Science* 48:331-335.
- ESRI (Environmental Systems Research Institute, Inc.). 2002. ArcView 3.3. ESRI, Redlands, California, USA.
- Feder, M. E. 1983. Integrating the ecology and physiology of Plethodontid salamanders. *Herpetologica* 39:291-310.
- Fenneman, N. E. 1938. *Physiography of eastern United States*. McGraw-Hill, New York, New York, USA.
- Foote, L. W., and S. B. Jones. 1989. *Native shrubs and woody vines of the southeast*. Timber Press, Portland, Oregon, USA.

- Ford, W. M., B. R. Chapman, M. A. Menzel, and R. H. Odom. 2002. Stand age and habitat influences on salamanders in Appalachian cove hardwood forests. *Forest Ecology and Management* 155:131-141.
- Ford, W. M., J. M. Menzel, M. A. Menzel, J. W. Edwards, and J. C. Kilgo. 2006. Presence and absence of bats across habitat scales in the upper Coastal Plain of South Carolina. *Journal of Wildlife Management* 70:1200-1209.
- Green, N. 1938. A new salamander, *Plethodon nettingi*, from West Virginia. *Annals of the Carnegie Museum* 27:295-299.
- Green, N. B., and T. K. Pauley. 1987. *Amphibians and reptiles in West Virginia*. University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.
- Griffis, M. R., and R. G. Jaeger. 1998. Competition leads to an extinction-prone species of salamander: interspecific territoriality in a metapopulation. *Ecology* 79:2494-2502.
- Grover, M. C. 1998. Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. *Journal of Herpetology* 32:489-497.
- Grover, M. C., and H. M. Wilbur. 2002. Ecology of ecotones: interactions between salamanders on a complex environmental gradient. *Ecology* 83:2112-2123.
- Guthery, F. S., L. A. Brennan, M. J. Peterson, and J. J. Lusk. 2005. Information theory in wildlife science: critique and viewpoint. *Journal of Wildlife Management* 69:457-465.
- Haan, S. S., M. J. Desmond, W. R. Gould, and J. P. Ward, Jr. 2007. Influence of habitat characteristics on detected site occupancy of the New Mexico endemic

- Sacramento Mountains salamander, *Aneides hardii*. *Journal of Herpetology* 41:1-8.
- Hairston, N. G. 1987. *Community ecology and salamander guilds*. Cambridge University Press, Cambridge, England. 230 pp.
- Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. *Ecology* 43:460-472.
- Hicks, N. G., and S. M. Pearson. 2003. Salamander diversity and abundance in forests with alternative land use histories in the Southern Blue Ridge Mountains. *Forest Ecology and Management* 177:117-130.
- Highton, R. 1972. Distributional interactions among eastern North American salamanders of the genus *Plethodon*. Pages 139-188 in P. C. Holt, editor. *The distributional history of the biota of the Southern Appalachians. Part III: vertebrates*. Research Division Monograph 4. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
- Hurvich, C., and C. L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297-307.
- Jaeger, R. G. 1970. Potential extinction through competition between two species of terrestrial salamanders. *Evolution* 24:632-642.
- Jenness, J. 2005. *Random point generator extension for ArcView 3.x, version 1.3*. Jenness Enterprises, Flagstaff, Arizona, USA.
- Keys, J. E., Jr., C. A. Carpenter, S. L. Hooks, F. G. Koenig, W. H. McNab, W. E. Russell, and M. L. Smith. 1995. *Ecological units of the eastern United States: first approximation*. USDA Forest Service, Atlanta, Georgia, USA.

- Kochenderfer, J. N. 2006. Fernow and the Appalachian hardwood region. Pages 17-39 in M. B. Adams, D. R. DeWalle, and J. L. Hon, editors. The Fernow Watershed Acidification Study. Springer Press, Dordrecht, Netherlands.
- Kramer, P. N., N. Reichenbach, M. Hayslett, and P. Sattler. 1993. Population dynamics and conservation of the peaks of otter salamander, *Plethodon hubrichti*. Journal of Herpetology 27:431-135.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314-320.
- Manly, B. F. J., L. McDonald, and D. Thomas. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London, UK.
- Mathis, A. 1991. Territories of male and female terrestrial salamanders: costs, benefits and intersexual spatial associations. Oecologia 86:433-440.
- McCay, D. H., M. D. Abrams, and T. E. Demeo. 1997. Gradient analysis of secondary forests of eastern West Virginia. Journal of the Torrey Botanical Society 124:160–173.
- McNab, W. H., and P. E. Avers, compilers. 1994. Ecological subregions of the United States: section descriptions. USDA Forest Service Administrative Publication WOWSA-5. USDA Forest Service, Washington, D.C., USA.

- Mielke, M. E., D. G. Soctomah, M. A. Marsden, and W. M. Ciesla. 1986. Decline and mortality of red spruce in West Virginia. USDA Forest Service Report 86-4. USDA Forest Service, Fort Collins, Colorado, USA.
- Morneault, A. E., B. J. Naylor, L. W. Schaeffer, and D. C. Othmer. 2004. The effect of shelterwood harvesting and site preparation on eastern red-backed salamanders in white pine stands. *Forest Ecology and Management* 199:1-10.
- Mueller, R. F. 1996. Biodiversity: central Appalachian plant distributions and forest types. *Wild Earth* 6:37-43.
- Owen, J. G. 1989. Patterns of herpetofaunal species richness: relation to temperature, precipitation, and variance in elevation. *Journal of Biogeography* 2:141-150.
- Pauley, B. A. 1998. The use of emergent rocks as refugia for the Cheat Mountain salamander, *Plethodon nettingi* Green. Thesis. Marshall University, Huntington, West Virginia, USA.
- Pauley, B. A., and T. K. Pauley. 1997. Range and distribution of the Cheat Mountain salamander, *Plethodon nettingi*: an update. *Proceedings of the West Virginia Academy of Science* 69:3.
- Pauley, T. K. 1980a. Field notes on the distribution of terrestrial amphibians and reptiles of the West Virginia mountains above 975 meters. *Proceedings of the West Virginia Academy of Science* 52:84-92.
- Pauley, T. K. 1980b. The ecological status of the Cheat Mountain Salamander (*Plethodon nettingi*). Unpublished report to the U.S. Forest Service, Elkins, West Virginia, USA.

- Pauley, T. K., and M. B. Watson. 2003. Determination of the size of buffer zones to prevent detrimental effects on the Cheat Mountain Salamander (*Plethadon nettingi*). Unpublished report to the U.S. Fish and Wildlife Service, Elkins, West Virginia, USA.
- Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.
- Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* 67:135-147.
- Petranka, J. W., M. E. Eldridge, and K. F. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363-370.
- Petranka, J. W. and S. M. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. *Journal of Herpetology* 35:36-44.
- Pilliod, D. S., R. B. Bury, E. J. Hyde, C. A. Pearl, and P. S. Corn. 2003. Fire and amphibians in North America. *Forest Ecology and Management* 178:163-181.
- Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. *Forest Ecology and Management* 20:1-9.
- Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Journal of Range Management* 23:295-297.

- Royle, J. A., J. D. Nichols, and M. Kery. 2005. Modeling occurrence and abundance of species when detection is imperfect. *Oikos* 110:353-359.
- Russell, K. R., T. J. Mabee, M. B. Cole, and M. J. Rochelle. 2005. Evaluating biotic and abiotic influences on torrent salamanders in managed forests of western Oregon. *Wildlife Society Bulletin* 33:1413-1424.
- Russell, K. R., T. J. Mabee, and M. B. Cole. 2004a. Distribution and habitat of Columbia torrent salamanders at multiple spatial scales in managed forests of northwestern Oregon. *Journal of Wildlife Management* 68:405-417.
- Russell, K. R., T. B. Wigley, W. M. Baughman, H. G. Hanlin, and W. M. Ford. 2004b. Responses of southeastern amphibians and reptiles to forest management: a review. Pages 319-334 *in* H. M. Rauscher and K. Johnsen, editors. *Southern forest science: past, present, and future*. USDA Forest Service General Technical Report. USDA Forest Service, Southern Research Station, Asheville, NC., USA.
- Russell, K. R., D. H. Van Lear, and D. C. Guynn, Jr. 1999. Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Society Bulletin* 27:374-384.
- Santiago, J. 1999. Influences of relative humidity, soil and air temperatures, and lunar phase on occurrences of terrestrial Plethodontid salamanders at high elevation sites. Thesis. Marshall University, Huntington, West Virginia, USA.
- Shuler, T. M., W. M. Ford, and R. J. Collins. 2002. Successional dynamics and restoration implication of a montane coniferous forest in the central Appalachians, USA. *Natural Areas Journal* 22:88-98.

- Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs* 42:95-125.
- SPSS. 2005. SPSS Version 14.0 for Windows. SPSS, Inc., Chicago, Illinois, USA.
- Straughnsbaugh, P. D., and E. L. Core. 1977. *Flora of West Virginia*. Seneca Books, Grantsville, West Virginia, USA.
- Sugalski, M. T., and D. L. Claussen. 1997. Preference for soil moisture, soil pH, and light intensity by the salamander, *Plethodon cinereus*. *Journal of Herpetology* 31:245-250.
- Taub, F. B. 1961. The distribution of red-backed salamanders, *Plethodon c. cinereus*, within the soil. *Ecology* 42:681-698.
- U.S. Fish and Wildlife Service. 1991. Cheat Mountain salamander recovery plan. U.S. Fish and Wildlife Service, Newton Corner, Massachusetts, USA.
- Welsh, Jr., H. H., J. R. Dunk, and W. J. Zielinski. 2006. Developing and applying habitat models using forest inventory data: an example using a terrestrial salamander. *Journal of Wildlife Management* 70:671-681.
- Whitaker, D. M., and D. F. Stauffer. 2006. Letters to the editor. *Journal of Wildlife Management* 70:1490-1491.
- Wyman, R. L. 1988. Soil acidity and moisture and the distribution of amphibians in five forests of southcentral New York. *Copeia* 1988:394-399.
- Wyman, R. L., and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. *Ecology* 68:1819-1827.

Wyman, R. L., and J. Jancola. 1992. Degree and scale of terrestrial acidification and amphibian community structure. *Journal of Herpetology*. 26:392-401.

Zaniewski, A. E., A. Lehman, and J. Overton. 2002. Predicting species spatial distributions using presence-only data: a case study of native New Zealand ferns. *Ecological Modeling* 157:261-280.

TABLE 4. Biotic and abiotic habitat variables measured from occupied ($n = 67$) and random ($n = 37$) sites, included in logistic regression models explaining site-level habitat relationships of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006.

Variable	Units	Abbreviation	Additional description
Hardwood density	#	HWDN	Total # of hardwood stems ≥ 10 cm dbh in 100-m ² plot
Hardwood average diameter	cm	HWDI	Average DBH of hardwoods ≥ 10 cm dbh in 100-m ² plot
Red spruce density	#	SPDN	Total # of red spruce stems ≥ 10 cm dbh in 100-m ² plot
Eastern hemlock density	#	HEDN	Total # of eastern hemlock stems ≥ 10 cm dbh in 100-m ² plot
Overstory type	-	OVST	Cover type within 100-m ² plot (red spruce-montane, northern hardwood, mixed mesophytic)
Canopy closure	%	CANP	Average % canopy closure at plot center
Shrub obscurity	%	SHOB	Average % vertical shrub obscurity from 0-1.5 m
Shrub type	-	SHTY	Majority shrub type within 100-m ² plot (red spruce/eastern hemlock, rhododendron/mountain laurel, other deciduous, mixed)
Rock outcrop proximal	Y/N	RKOC	Rocky outcrop present within 30 m of plot center
Seep proximal	Y/N	SEEP	Seep present within 30 m of plot center
Fern ground cover	%	GCFN	Average % fern in 5 1-m ² plots
Herbaceous ground cover	%	GCHB	Average % herbaceous vegetation in 5 1-m ² plots
Bryophyte ground cover	%	GCBR	Average % bryophytes in 5 1-m ² plots
Emergent rock ground cover	%	GCRK	Average % emergent rock in 5 1-m ² plots
Woody debris ground cover	%	GCWD	Average % woody debris in 5 1-m ² plots
Bare ground cover	%	GCSL	Average % bare soil in 5 1-m ² plots
Leaf litter depth	cm	LLDP	Average leaf litter depth in 5 1-m ² plots
Depth to rock	-	RKDP	Average depth to rock depth in 5 1-m ² plots portioned into 4 ordinal categories (≤ 10.0 cm, 10.1-20 cm, 20.1-30 cm, ≥ 30 cm)

TABLE 5. Logistic regression models explaining influence of biotic and abiotic habitat attributes on site-level occurrence of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Model ^a	K ^b	AIC_c ^c	ΔAIC_c ^d	w_i ^e
Depth to rock {RKDP}	2	133.87	0.00	0.45
Literature habitat {SPDN, HEDN, CANP, RKDP, GCBR}	6	136.37	2.49	0.13
Bryophytes {GCBR}	2	136.56	2.69	0.12
Abiotic {RKDP, GCRK, RKOC, SEEP}	5	137.42	3.55	0.08
Conifer density {SPDN, HEDN}	3	137.84	3.96	0.06
Outcrop {RKOC}	2	138.00	4.13	0.06
Herbaceous vegetation {GCHB}	2	139.17	5.29	0.03
Cover objects {GCRK, GCWD}	3	139.37	5.49	0.03
Overstory canopy {CANP}	2	139.39	5.52	0.03
Cover type {OVST}	3	140.84	6.97	0.01
Ground cover vegetation {GCFN, GCHB, GCBR}	4	143.24	9.37	0.00
Shrub vegetation {SHOB, SHTY}	5	143.83	9.96	0.00
Overstory vegetation {HWDN, SPDN, HEDN, HWDI, OVST, CANP}	8	146.31	12.44	0.00
Ground cover {GCFN, GCHB, GCBR, GCRK, GCWD, GCSL}	7	146.89	13.02	0.00
All vegetation {HWDN, SPDN, HEDN, HWDI, OVST, CANP, SHOB, SHTY, GCFN, GCHB, GCBR}	15	159.89	26.02	0.00
Global {HWDN, SPDN, HEDN, HWDI, OVST, CANP, SHOB, SHTY, RKOC, SEEP, GCFN, GCHB, GCBR, GCRK, GCWD, GCSL, LLDP, RKDP}	22	170.20	36.33	0.00

a Abbreviations in parentheses correspond to model parameters in Table 1.

b Number of estimable parameters in approximating model.

c Akaike's Information Criterion corrected for small sample size.

d Difference in value between AIC_c of the current model versus the best-approximating model (AIC_{cmin}).

e Akaike weight. Probability that the current model (w_i) is the best-approximating model among those considered.

TABLE 6. Parameter estimates (β) and standard errors (SE) from the best-approximating models explaining influence of habitat attributes on site-level presence of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006.

Model	β	SE	R^{2a}
Depth to rock			0.073
Constant	1.606	0.490	
Depth to rock	-0.479	0.205	
Literature habitat			0.125
Constant	0.293	3.953	
Red spruce density	0.030	0.060	
Eastern hemlock density	0.596	0.365	
Canopy closure	1.227	4.127	
Depth to rock	-0.530	0.231	
Bryophyte ground cover	0.377	2.038	
Bryophytes			0.012
Constant	0.404	0.311	
Bryophyte ground cover	1.468	1.627	
Abiotic			0.109
Constant	1.914	0.641	
Depth to rock	-0.564	0.243	
Emergent rock ground cover	-1.987	1.845	
Rock outcrop proximal	0.900	0.713	
Seep proximal	-0.156	0.604	
Conifer density			0.049
Constant	0.420	0.235	
Red spruce density	0.019	0.048	
Eastern hemlock density	0.519	0.354	
Outcrop			0.020
Constant	0.499	0.217	
Rock outcrop proximal	0.800	0.687	

a Nagelkerke's rescaled R^2

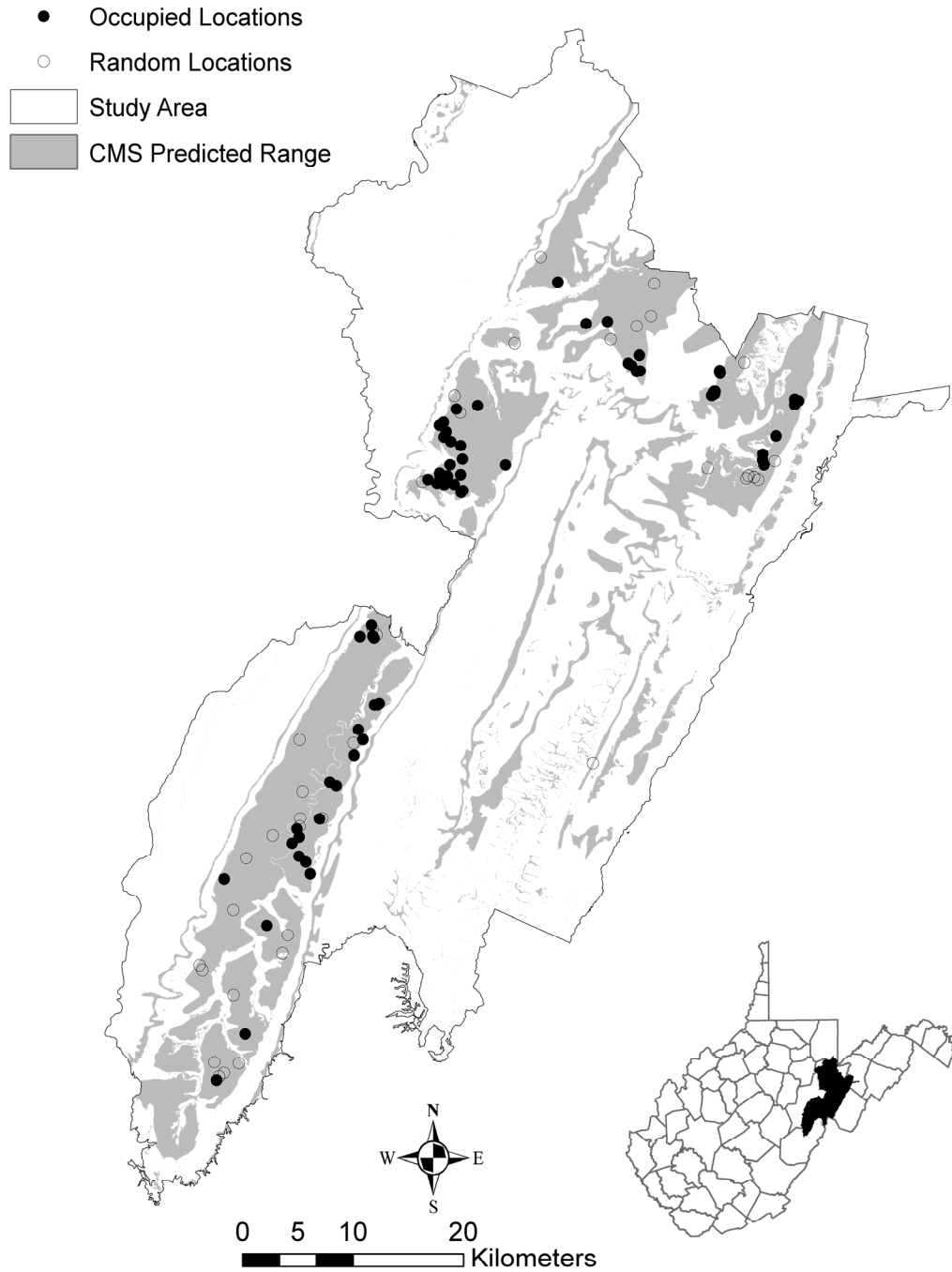


FIGURE 6. Map of study area, CMS predicted range (Chapter I, Fig. 3a), and locations of occupied ($n = 67$) and random ($n = 37$) points used for site-level habitat modeling of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Occupied and random points are not to scale.

CONCLUSIONS

At a landscape-level, common variables in all three modeling approaches indicated that the probability of predicting occurrence of Cheat Mountain salamanders (CMS; *Plethodon nettingi*) increased in areas with high elevations and sandstone geology. In addition, other abiotic variables including aspect, slope, and distance to water were potentially important variables for predicting CMS distribution. However, one logistic regression model with empirical support indicated that presence of red spruce (*Picea rubens*) cover types was potentially related to salamander occurrence. Therefore, the landscape-level distribution of CMS may not be solely tied to abiotic features. At a site-level, my modeling results also confirmed the importance of abiotic habitat features for influencing CMS occurrence. The probability of predicting CMS site occupancy increased in areas with shallower depth to rock, and areas proximal to rocky outcrops but distal from seeps. Results of site-level modeling also indicated that CMS-occupied sites were associated with higher bryophyte ground cover and higher densities of overstory red spruce and eastern hemlock (*Tsuga canadensis*), confirming the coarse-scale cover type association elucidated during landscape modeling. From a multi-scale perspective, my study suggests that geophysical habitat features may exert an overriding influence on the current distribution of CMS. However, CMS associations with high-elevation red spruce and eastern hemlock forests indicate that vegetation characteristics and other biotic attributes also are potentially important aspects of CMS habitat. Moreover, the results of my research indicate that the relative importance of individual variables for predicting CMS habitat relationships may be scale dependent.

Results of habitat modeling at fine spatial scales often reflect constraints on individuals, whereas those at broad scales may reflect biological constraints manifested at the population or species levels. Although several of the habitat variables I modeled may not be directly related to the survivorship of individual salamanders, but are useful as surrogate variables that indicate location-dependent site and microhabitat conditions more directly associated with woodland salamander life histories. For example, in my study area higher elevations generally have higher average annual precipitation and cooler average annual temperatures when compared to lower elevations. Therefore, high-elevation areas may best provide the moist, cool environments required for cutaneous respiration by CMS and other lungless salamanders. There is increasing evidence that amphibians respond to habitat features at multiple spatial scales, and that these relationships are often compatible across scales. The results of my study involving CMS, including the interrelatedness and congruence among habitat variables modeled at the landscape- and site levels, provides further evidence of these relationships.

At a landscape level, my set of models examining CMS distribution had relatively high predictive power and classification accuracy. Conversely, my fine-scale models failed to account for much of the variation in the site-level occurrence of the species. Therefore, fine-scale habitat relationships of CMS may be considerably more complicated than can be described by the site-level and microhabitat variables I measured.

My research represents the first attempt to quantitatively model the range-wide habitat relationships of CMS and is an important first step in elucidating critical habitat characteristics for this federally threatened species. Quantifying range-wide habitat

relationships of CMS has been a key but heretofore ignored task identified in the species' recovery plan. My landscape-level methodologies are easily adapted to predicting distributions of other imperiled amphibian species in regions where similar occupancy and spatial data exist. In addition, my effort should assist public resource managers as it delineates where potentially critical or optimal habitats from an occupancy perspective exist on the Monongahela National Forest and Canaan Valley National Wildlife Refuge. Combined with my landscape-level distribution maps, the site-level habitat models I developed should reduce the time and effort associated with future field-based CMS surveys, and may assist the identification of new populations. Therefore, information gained from this multi-scale study will increase the capacity of managers to plan for the continued persistence and conservation of CMS, as well as their associated habitats. I suggest that future research on CMS distribution and habitat relationships should focus on (1) more refined quantification of multi-scale abiotic and biotic habitat variables; (2) the relationship between habitat variables and CMS density or population viability; and (3) the potential influence of sympatric salamander species on CMS distribution.