Macrohabitat models of occurrence for the threatened Cheat Mountain salamander, *Plethodon nettingi*

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Abstract. The federally threatened Cheat Mountain salamander (*Plethodon nettingi*; hereafter CMS) is known to occur at approximately 70 small, scattered sites in the Allegheny Mountains of eastern West Virginia. We 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. We collected data on 13 explanatory macrohabitat variables at CMS-occupied ($n = 180$) and random ($n = 180$) sites. We then examined CMS-macrohabitat relationships using a priori, logistic regression models with information-theoretic model selection, classification tree modeling, and discriminant function analysis. Among logistic regression models, a model containing the variables elevation, aspect, slope, and lithology received the strongest empirical support, although a model containing these variables and current vegetation type also received limited support. Variable selection within our classification tree and discriminant function modeling was consistent with logistic regression results. Common variables in all three approaches indicated that the probability of finding CMS across the species' range increased in areas at higher elevations and underlain by sandstone. Validation of models with empirical support using reserved data indicated that classification accuracy was $\geqslant$80% for all three analytical methods. Finally, we linked model outputs from all three methods to GIS coverage maps that predicted CMS occupancy within the study area. Our 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.

Key words: Cheat Mountain salamander; classification tree; discriminant function; distribution; endangered species; GIS; habitat; information theory; landscape; macrohabitat models; *Plethodon nettingi*.

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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 (Petranka, 1998), 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 (Gustafson et al., 2001; Welsh et al., 2004; Stoddard and Hayes, 2005; Suzuki et al., 2008). 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., 2004a), recent research indicates that 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., 2004b, 2005).

The Cheat Mountain salamander (*Plethodon nettingi*; 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 sites distributed across an area of approximately 1800 km^2 (Pauley and Pauley, 1997; Petranka, 1998). Most (75%) known CMS populations reportedly consist of $\leqslant$10 individuals and $\geqslant$80% of populations occur on the Monongahela National Forest (MNF; USDI Fish and Wildlife Service, 1991).

Cheat Mountain salamanders were listed as a threatened species in 1989 (USDI Fish and Wildlife Service, 1991). Historically, its range possibly was more extensive than the current restricted distribution (USDI Fish and Wildlife Service, 1991). However, intensive logging combined with large wildfires in the region eliminated >93% of red spruce forests by 1920 (Clarkson, 1964; Clovis, 1979; Mielke et al., 1986), which 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., 2004a; Riedel et al., 2008). 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 (*Plethodon cinereus*) and dusky salamanders (*Desmognathus* spp.) 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 (USDI 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*)-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. Currently, only small scale, largely descriptive studies (Brooks, 1948; Pauley, 1980b; Pauley and Pauley, 1997; Pauley, 1998) of CMS-vegetation associations or microhabitat relationships (Dillard et al., 2008) 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 macrohabitats known to be occupied by CMS; (2) predict CMS distribution across the range of the species; 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.

Our objectives were to create macrohabitat 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, we (1) used three different statistical approaches to model macrohabitat associated with CMS-occupied and available random points using spatial data readily available to resource managers; (2) evaluated the classification accuracy of each modeling approach; (3) examined the relative role of biotic and abiotic habitat characteristics for predicting CMS

occurrence at a coarse, landscape level; and (4) examined the use and limitations of broad-scale modeling for amphibian conservation.

Methods

Study area

The known distribution of CMS lies entirely within the northern high Allegheny Mountains ecological subsection (Keys et al., 1995) in eastern West Virginia, USA (fig. 1). Therefore, we constrained our 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 $\pm$ 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$\pm$0.3°C, average annual maximum temperature was 13.5 $\pm$ 1.4°C, and average annual precipitation was 131.3 $\pm$ 11.0 cm/year.

Mountains and some higher valleys within the study area generally were forested, whereas lower elevation valleys had been converted in part to pasture. 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-dominated or oak-pine (*Pinus* spp.) cover types occurred (Ford et al., 2002a; Kochenderfer, 2006).

Salamander occurrence and random point data

To determine CMS presence, we acquired locations from GIS databases maintained by MNF ($n = 170$) and CVNWR ($n = 49$) where $\geqslant$1 CMS was found during previous field surveys on public lands. These occurrence data were collected by federal, state, and university biologists over the past several decades using transect, time-constrained, and area-constrained searches (for details of representative sampling methods see Pauley and Pauley, 1997; Pauley, 1998; Pauley and Watson, 2003),

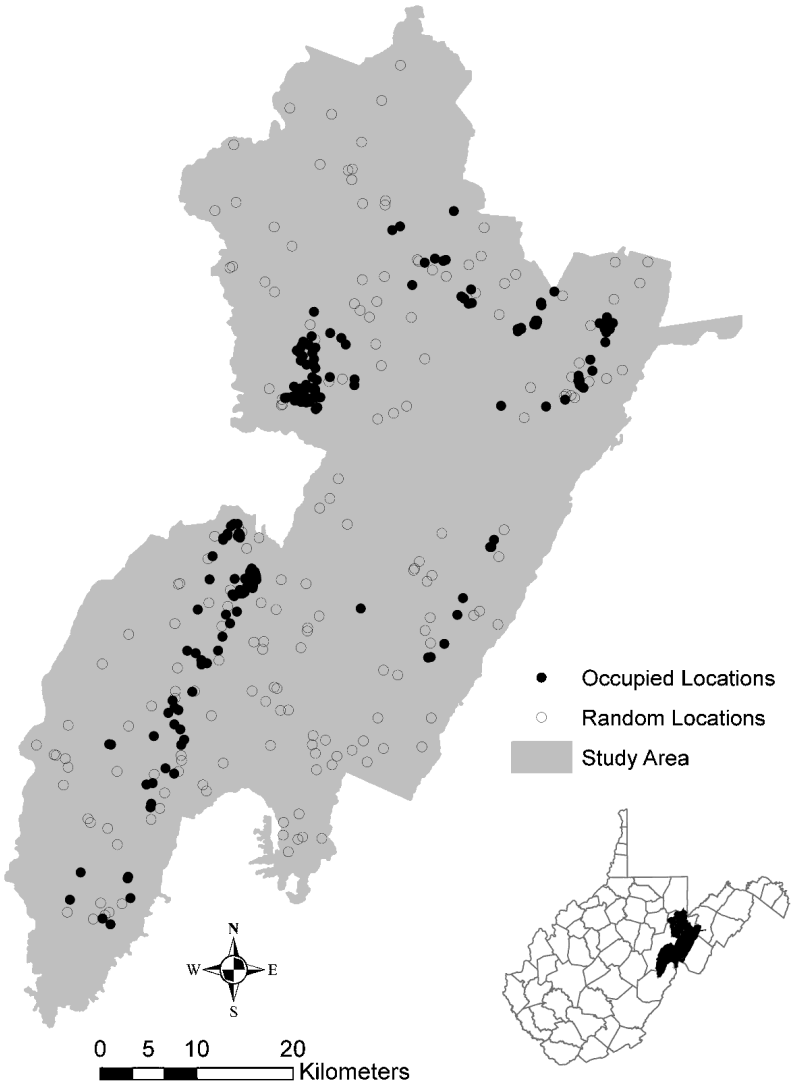

Figure 1. Map of study area showing locations of occupied ($n = 180$) and random ($n = 180$) points selected for macrohabitat modeling of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Occupied and random points are not to scale. See text for selection criteria.

although the majority were documented following federal listing of the species. Although recently documented locations were typically collected using a handheld GPS unit, historic locations were placed on topographic maps by researchers and later digitized for use in a GIS database. For our analytical use, we specified that locations must (1) be separated by $\geqslant$60 m to increase the likelihood of independence of CMS detections and reduce the potential for spatial autocorrelation of habitat data (Legendre, 1993), required to meet the assumptions of our statistical tests, and (2) have data available for all habitat variables (table 1). Although CMS occurrence

Table 1. Biotic and abiotic habitat variables measured from occupied ($n = 180$) and random ($n = 180$) sites, used for modeling the range-wide, macrohabitat 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
Lithology	-	LIT	Limestone, shale, shale/sandstone mix, or sandstone lithologic type 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 $r \geqslant 0.70$), but was used in CART modeling.

data were available from private lands within the study area, restricted access precluded collection of habitat data. Using these criteria, 180 occupied CMS points were retained for model development.

To represent habitats available to CMS, we selected an equal number ($n = 180$) of random points from the study area. We assumed that random locations were currently unoccupied but potentially available to CMS (Manly et al., 1993). We chose to compare CMS-occupied sites with random locations rather than with historic survey sites where CMS previously was deemed to be absent because 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 (Haan et al., 2007). In addition, during our previously study of CMS microhabitat relationships we detected considerable potential biases in the distribution of historic CMS-"absent" sites, including spatial

autocorrelation with existing roads and trails in the region (Dillard et al., 2008). Therefore, the use of random sites represents a conservative but suitable approach. Prior to selecting random points, we buffered all occupied points with a 60-m radius area using ArcView 3.3 (ESRI, Inc., Redlands, CA). We assumed these buffers prevented overlap of occupied and random sites. Terrestrial plethodontid salamanders are relatively sedentary, with small home ranges (e.g., <1-25 m^2) and 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 our defined available, but likely unoccupied area, we generated random points using a random point generator (Jenness, 2005). We required that random points met minimum distance and habitat data criteria as described above for occupied locations.

Habitat variables

For each occupied and random location, we characterized a set of biotic and abiotic macrohabitat variables that potentially explained CMS distribution. We 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., 2004a; Welsh et al., 2004), (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 macrohabitat variables (table 1). We 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:

$$[1 - \text{cosine}(\text{aspect in radians})] + [1 - \text{sine}(\text{aspect in radians})]$$

so that mesic, northeasterly aspects had low values and xeric, southwesterly aspects had high values (Ford et al., 2002b). Terrain shape index quantifies the surface shape of a plot, ranging from convex (TSI $< {}^{-}0.05$) to concave (TSI > 0.05). These broad-scale variables previously have been used to characterize landforms and related biological attributes of the central and southern Appalachian Mountains (McNab, 1989). We determined lithology 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 km^2.

Current land cover of the study area was characterized from MNF (1:24 000 scale) and CVNWR (1:12 000 scale) stand-level maps. We combined these data

sources and grouped land cover into three forested categories and one non-forest type appropriate for Appalachian systems (following Braun, 1950; McNab and Avers, 1994). 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. Historical fire regime (based on fire frequency and severity) and potential natural community type data were obtained from MNF GIS coverages at a scale of 1:24 000. Potential natural community data, representing climax community type given natural disturbances but excluding anthropogenic disturbances, were grouped into the same categories as current land cover. All data layers were incorporated into ArcView 3.3 (ESRI, Inc., Redlands, CA) and ArcGIS 9.1 (ESRI, Inc., Redlands, CA) for visualization and analyses.

Modeling overview

We used three comparative statistical methods to model CMS habitat relationships: a priori specification of logistic regression models using information-theoretic model selection (Burnham and Anderson, 2002), classification tree modeling (CART; Breiman et al., 1984), and discriminant function analysis (DFA; McGarigal et al., 2000). We used a comparative statistical approach because different multivariate techniques applied to the same data (e.g., known and random locations) may identify distinctly different suites of explanatory variables (Rexstad et al., 1988). Furthermore, although 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., 2004b, 2005; Stoddard and Hayes, 2005), a priori model specification and information-theoretic model selection have recently been criticized (Guthery et al., 2005). Therefore, we 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). Finally, we selected DFA as a third analysis approach because it also is frequently used to model species occurrence data (McGarigal et al., 2000). For all analyses, the dependent variable was site occupancy by CMS or site availability to CMS (as represented by random points).

Prior to modeling, all location data were subdivided based on a random Bernoulli variable, with approximately 75% used for model development and 25% used for model validation. Therefore, we were able to assess how well each model classified data not used in model development. We 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 for Windows version 14.0

(SPSS, Inc., Chicago, IL) and CART modeling was performed using CART 5.0 (Salford Systems, San Diego, CA).

Logistic regression modeling

Prior to model development, we eliminated redundant variables (Spearman's $r \geqslant 0.70$) and retained 10 variables for inclusion in models (table 1). We then specified a set of a priori, candidate logistic regression models (Burnham and Anderson, 2002) based on (1) a review of published literature on habitat relationships of CMS and other woodland salamanders, and (2) our previous experience with these species. We specified 13 models: a global model containing all 10 macrohabitat variables and subset models representing potential influences of biotic and abiotic attributes on CMS presence (table 2). We 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, we examined fit of the global model 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.

Table 2. Logistic regression models explaining influence of biotic and abiotic habitat attributes on 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/lithology {ELV, ASP, SLP, LIT}	7	257.54	0.00	0.91
Landform/lithology/vegetation {ELV, ASP, SLP, LIT, VEG}	10	262.19	4.65	0.09
Global {ELV, ASP, SLP, LIT, FIR, DWT, PCP, HIS, VEG, PNC}	18	269.53	11.99	0.00
Lithology {LIT}	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 ($AIC_{c\,\min}$).
[e] Akaike weight. Probability that the current model (i) is the best approximating model among those considered.

We used Akaike's Information Criterion (AIC; Hurvich and Tsai, 1989; Burnham and Anderson, 2002) for model selection as other authors (Boyce et al., 2002) have suggested that this method is appropriate to select the best model from a set of alternative models derived from use vs. availability data. Because the number of occupied and random sites ($n = 360$) was small relative to the number of variables (K) in several models (i.e., $n/K < 40$), we used AIC corrected for small sample size (AIC_c) and used the formulas presented in Burnham and Anderson (2002) to calculate AIC_c from the log-likelihoods for each model. We 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). We drew primary inference from models within 2 units of $AIC_{c\,\min}$, although models within 4-7 units may have limited empirical support (Burnham and Anderson, 2002). We 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, we 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. 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%.

Classification tree 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 continuous or categorical predictor variables. Each step in the tree-building process finds a rule, dependent on all previous steps and 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 occupied or random locations). Using these methods, CART can create a tree that will completely describe the data, and at extreme classification, terminal nodes may be occupied by a single case. Increasing tree size by adding more splits 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" to a large size, 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 our analysis was a classification tree (Breiman et al., 1984) because our response variable was categorical. To construct our original tree, we 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). We specified equal priors for our data because we sampled an equal number of CMS-occupied points and random points. After the initial classification tree was specified, we 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 $\times$ 30 m) was created from the optimal CART model, predicting areas as occupied or likely unoccupied by CMS.

Discriminant function analysis

Lastly, we used a multivariate DFA to evaluate which habitat variables were most useful for differentiating between CMS-occupied and random locations. As with our logistic regression analyses, we eliminated redundant variables (Spearman's $r \geqslant 0.70$) 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). We 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, we 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 $\leqslant 0.05$ was entered. We 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 likely unoccupied by CMS.

Results

Logistic regression modeling

Of 13 a priori logistic regression, macrohabitat models explaining the occurrence of CMS, "landform/lithology" was selected as our best approximating model (table 2). The presence of CMS was positively associated with increasing elevation, sandstone, and northeasterly aspects, but negatively associated with other lithologic

Table 3. Parameter estimates (B) and standard errors (SE) from the best approximating models explaining influence of habitat attributes on presence of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Coefficients of the categorical variables "lithology" and "current land cover" were calculated relative to sandstone and northern hardwoods, respectively.

Model	B	SE	R^{2a}
Landform/lithology			0.532
Constant	−2.414	1.573	
Limestone	−22.126	28008.449	
Shale	−2.893	0.411	
Shale/SS	−1.201	0.614	
Elevation	0.004	0.001	
Slope	−0.027	0.013	
Aspect	−0.288	0.171	
Landform/lithology/vegetation			0.537
Constant	−2.143	1.683	
Limestone	−21.576	28203.641	
Shale	−2.903	0.416	
Shale/SS	−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.

types and steep slopes (table 3). The second-best model, "landform/lithology/vegetation", received limited empirical support ($\Delta\text{AIC}_c = 4.65$; table 2). This model indicated that in addition to lithological and topographical features, CMS occurrence was positively associated with the presence of red spruce-montane forest cover (table 3). In both supported models, SEs associated with limestone were notably high (table 3), resulting from a low sample size ($n = 4$), but representative of the sparse geographic coverage of this lithologic type within our study area. Weight of evidence ($w_{\text{best model}}/w_{\text{second best model}}$) in favor of our "landform/lithology" model was about 10 times greater than that of our "landform/lithology/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 ($\Delta\text{AIC}_c \geqslant 11.99$, $w_i = 0.0$; table 2).

The "landform/lithology" 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/lithology" model was mapped across the study area (fig. 2a). The "landform/lithology/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/lithology" model (fig. 2b). Stand-level land cover data were not uniformly

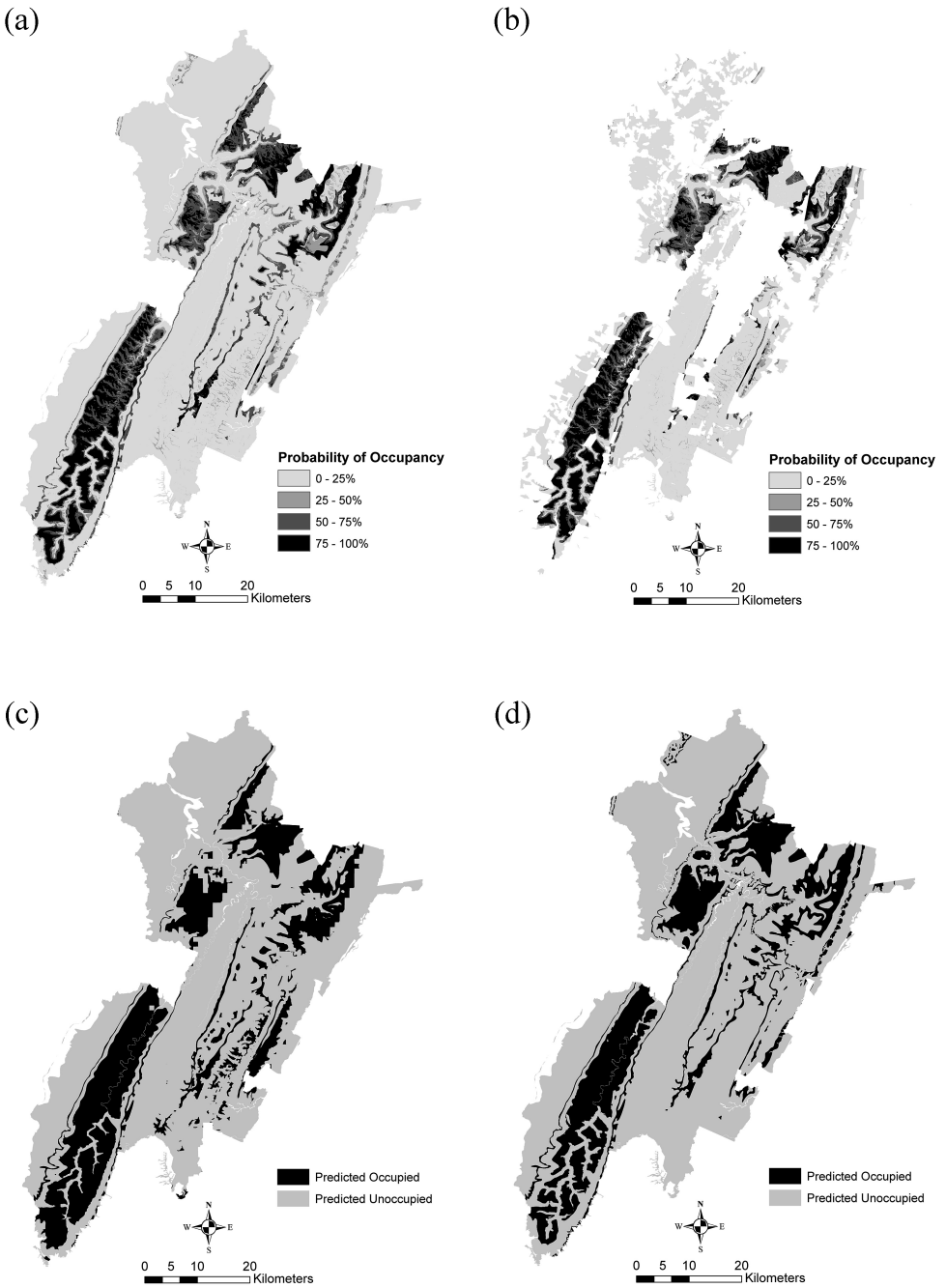

Figure 2. Predicted occupancy maps of Cheat Mountain salamanders within the Allegheny Mountains of West Virginia, USA, 2006 determined from (a) landform/lithology logistic regression model, (b) landform/lithology/vegetation logistic regression model, (c) optimal classification tree model and (d) forward stepwise discriminant function model. See text for description of modeling methods and parameters.

available throughout the study area because of private and industrial ownership, thus a subset of the study area was excluded from the "landform/lithology/vegetation" predictive map.

Classification tree modeling

Our initial CART model contained 22 splits and 23 terminal nodes, but we minimized misclassification error of the validation dataset at a tree size of four terminal nodes (fig. 3). Our optimum, pruned model contained three habitat variables and indicated that the majority of CMS occupied locations were best explained by the presence of sandstone or mixed shale-sandstone, and an average annual precipitation of >127.19 cm. Our model also indicated that some CMS locations were associated with limestone or shale when elevation was >1206.5 m. The final CART model did not include any biotic variables (i.e., vegetation). Our CART model had an overall classification accuracy of 84.1% and a validation accuracy of 85.5%. Areas predicted as occupied and likely unoccupied by CMS were mapped across the study area using model parameters (fig. 2c).

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, distance to water, mixed shale-sandstone, 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. 4) indicated that CMS occupancy

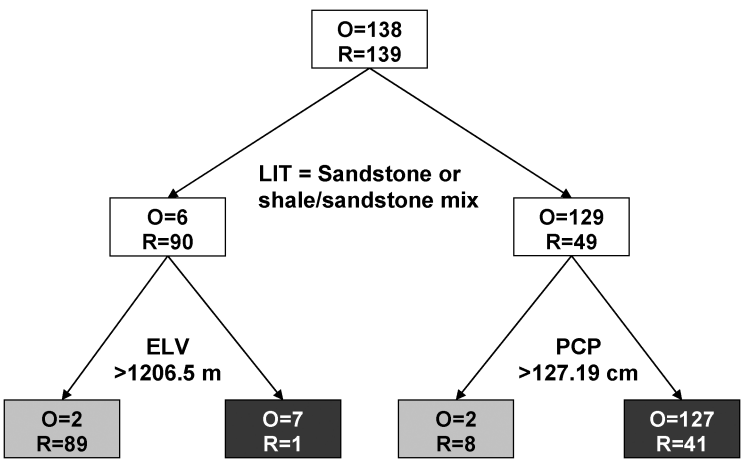

Figure 3. Tree diagram of optimal classification tree used for explaining occupancy of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Decision rules at splits apply to the right branch, while the opposite rule applies to the left branch. Numbers inside nodes indicate total number of occupied (O) and random (R) data points and shading indicates majority classification of each terminal node (black = occupied, grey = random points).

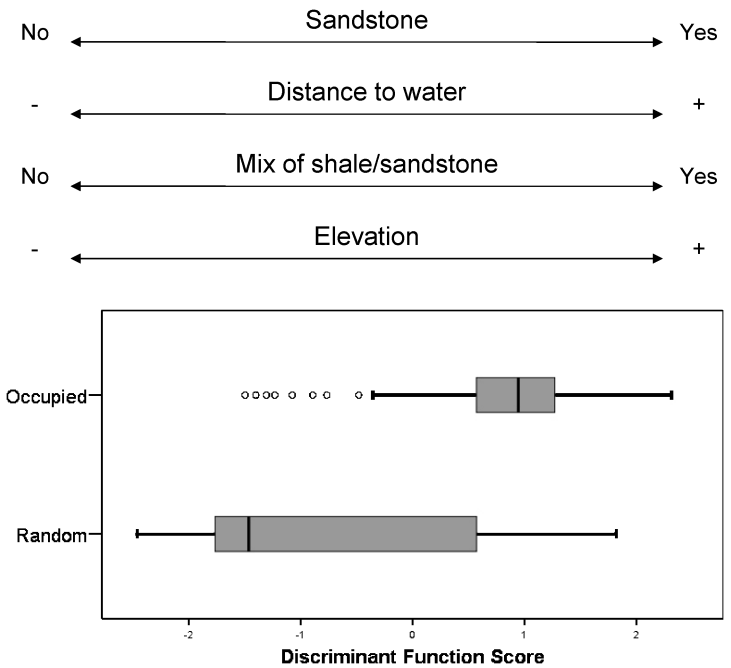

Figure 4. Graphical output of forward stepwise discriminant function model used for explaining occupancy of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Variables above box plot are listed in the order of importance. The shaded box represents the interquartile (IQ) 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).

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). Our DFA model produced an overall classification accuracy of 79.4% and a validation accuracy of 84.3%. Areas predicted as occupied and likely unoccupied by CMS were mapped across the study area using model parameters (fig. 2d).

Discussion

Models of CMS distribution

Our research provides the first quantitative assessment of factors potentially influencing the range-wide and macrohabitat-related 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 sand-

stone. Although earlier observations suggested the potential importance of elevation in defining CMS distribution (Pauley, 1980a; USDI Fish and Wildlife Service, 1991), our 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 (e.g., climate, vegetation composition) rather than a direct effect of elevation per se. For example, in our 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, our 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, our 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 lithology and the distribution of stream amphibians (e.g., Diller and Wallace, 1996; Sutherland and Bunnell, 2001; Russell et al., 2004b, 2005) and plethodontid salamanders (e.g., *Plethodon vandykei*; McIntyre et al., 2006). However, we are unaware of any literature identifying correlations between eastern plethodontids, including CMS, and specific lithologic types. All of our macrohabitat models with empirical support indicated an association between CMS occupancy and the presence of sandstone. 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 lithology could represent an inherent intercorrelation with elevation. However, at high elevations (i.e., $>$1200 m) in our study area, 43.5% of the total land area consists of sandstone, whereas 40.2% is shale and 15.6% is mixed shale-sandstone. Accordingly, it is plausible that the independent combination of these two geophysical features best predict CMS occupancy at the landscape level.

The strong association between CMS distribution and sandstone reflects the surface and subsurface habitats produced by this lithologic type. In our study area, sandstone parent materials generally weather to produce abundant emergent rocks

and colluvial accumulations. 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 may have served as important refugia for CMS that allowed this species to persist during intensive 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, we speculate that the association between sandstone 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 plethondontid 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, we 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 limited 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; USDI Fish and Wildlife Service, 1991). Because of historic timber harvest, >93% of the original red spruce acreage in our 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) and are often underlain by sandstone. Therefore, it is unclear whether coarse-scale associations between the current distribution of CMS and red spruce forest cover reflect an intercorrelation with geophysical features (i.e., elevation and lithology), 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). However, recent modeling of CMS microhabitat relationships also suggested that red spruce cover was an important correlate of CMS occurrence (Dillard et al., 2008). Regardless, quantitative studies that explicitly examine CMS demography and population viability 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.

Our findings indicate that geophysical features exert an overriding influence on the range-wide occurrence of CMS, supporting Highton's (1972, 1995) description of *P. nettingi* as a relictual species tied to higher elevations. However, we 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; Suzuki et al., 2008; Dillard et al., 2008). 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., 2004b, 2005; Stoddard and Hayes, 2005). For example, lithology, elevation, and aspect are indirect predictor variables (Guisan and Zimmermann, 2000) that may have no direct physiological relevance for survivorship or fecundity 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 intensive timber harvest or subsequent wildfire as well as the presence of other salamander species to shape the current distribution of CMS (Highton, 1972; Pauley, 1980a; Pauley, 1998). We think that variation in these site-level habitat attributes may be a source of much of the unexplained variation in our 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 we 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. We think the congruent results obtained from three disparate analysis techniques is particularly important in the context of accurately modeling habitat relationships of a federally-threatened species. 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. 3) that may be easily interpreted by natural resource managers. Additionally, results of CART analyses are not affected by interactions among predictor variables, or by nonlinear relationships between predictor variables and the response variable. A considerable limitation of CART and DFA models is that output maps (fig. 2c-d) only allow binary predictions of occupancy (i.e., present or likely unoccupied), whereas logistic regression provides a continuous level of predicted CMS occupancy across the study area (fig. 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 our consistently high percentage of correct classification, wildlife habitat modeling studies typically contain several limitations and assumptions. Because our research relied on previous ground surveys to determine occupancy, we assumed that CMS was still present at each location and that habitat conditions had not changed dramatically between the original surveys and our modeling effort. Given that at least some occupied sites we incorporated into our analyses were surveyed $\geqslant$15-20 years ago, it is possible that subsequent human or natural disturbances to these sites significantly altered habitat conditions. Because we avoided a priori specification of all potential models for logistic regression analyses (Burnham and Anderson, 2002), it is possible that combinations of variables we did not consider may have provided even better predictive power, for which this type of model specification and selection has been criticized (Guthery et al., 2005). We 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; our modeling effort does not address macrohabitat influences on CMS abundance, densities, or range-wide population viability. Finally, because we emphasized parsimony in each of our modeling approaches and used relatively coarse macrohabitat data, we recognize the potential for fine-scale errors in our occupancy maps. For example, one logistic regression model (fig. 2a) and the DFA model (fig. 2d) 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,

we urge a conservative approach when applying our 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 amphibian species. Our 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 lithology. We think our 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. With this spatially-explicit information, conservation planning efforts will be more informed and potentially more effective.

Our models generated predictions over very large areas and used spatial data that were readily available to many land managers. Therefore, our methodologies should be easily adapted to predicting distributions of other plethodontid salamander 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; Welsh et al., 2004). Our research provides an example of how integration of biological knowledge, habitat modeling, and GIS-based data can reveal important aspects of range-wide habitat associations of amphibians.

Secondly, if CMS depend on areas outlined by our 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. Our models should reduce the time and effort associated with future CMS surveys, including the identification of new populations.

Finally, our models provide a broad-scale 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). Our results suggest such efforts may be more effective if situated in areas of high predicted probability (e.g., $\geqslant 0.5$) of CMS occurrence, including (1) high elevation sites underlain by sandstone, (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; Menzel et al., 2006). For example, there is a high degree of congruence (including identification of specific predictor variables) between our occupancy maps for CMS and those developed for Virginia northern flying squirrels (Menzel et al., 2006). Accordingly, we think our 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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