

Site-level habitat models for the endemic, threatened Cheat Mountain salamander (*Plethodon nettingi*): the importance of geophysical and biotic attributes for predicting occurrence

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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 largely rely on small scale, largely descriptive studies of habitat associations from a few sample sites. To address the critical need for quantitative data, we 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. We 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. Overall, results indicated that the probability of CMS occurrence at a fine spatial scale 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 our study should increase the capacity of managers to plan for the continued persistence and conservation of Cheat Mountain salamanders in this landscape.

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Introduction

Woodland salamanders of the family Plethodontidae are perhaps the most abundant vertebrates in the moist temperate forests of North America, with the density of red-backed salamanders (*Plethodon cinereus*) and other terrestrial plethodontids often exceeding 1–2 individuals/m² (Burton and Likens 1975; Hairston 1987; Mathis 1991; Petranka 1998). Despite their often high densities, many woodland salamander species have small ranges and patchy distributions generally attributable to physiological restrictions to a relatively narrow range of past and present environmental conditions (Petranka 1998). 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 (CWD; 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 (*P. 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 1,800 km² (US Fish and Wildlife Service 1991; Pauley and Pauley 1997; Petranka 1998). Most (75%) known CMS populations reportedly consist of ≤10 individuals (US Fish and Wildlife Service 1991), and ≥80% of those populations occur on the Monongahela National Forest (MNF; US Fish and Wildlife Service 1991).

Cheat Mountain salamanders were listed as a threatened species in 1989 by the US Fish and Wildlife Service (US Fish and Wildlife Service 1991). Historically, the range of CMS was possibly more extensive than the current restricted distribution (US 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 by this date. 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). T. K. Pauley and M. B. Watson (unpublished report) 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, recreational development activities, as well as competition with sympatric red-backed salamanders and Allegheny Mountain dusky salamanders (*Desmognathus ochrophaeus*) have been hypothesized to continue limiting CMS distribution and abundance (Highton 1972; Pauley 1980, 1998). Because extant CMS populations are small and geographically isolated, loss of genetic diversity also is thought to possibly threaten the species (US 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 (US Fish and Wildlife Service 1991), relatively little has been published regarding CMS habitat relationships. Dillard (2007) modeled the distribution of CMS 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 [i.e., red spruce or red spruce-eastern hemlock (*Tsuga canadensis*)] and mixed conifer-deciduous forest stands with a bryophyte (*Bizzania* spp.)-dominated forest floor ranging in elevation from 805 to 1,482 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, Dillard (2007) also found a positive landscape-level association between CMS occurrence and presence of red spruce cover. 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*). T. K. Pauley (unpublished report) also detected CMS populations in northern hardwood stands with either 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, and did not 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 (1980) noted that CMS-occupied sites had higher relative humidities and lower temperatures than those of sympatric red-backed salamanders or Allegheny Mountain dusky salamanders. 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 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 4 sympatric woodland salamanders [Allegheny mountain dusky, red-backed, Northern slimy (*P. glutinosus*), Wehrle's (*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 1998; Pauley and Pauley 1997; T. K. Pauley, unpublished report). 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 (US Fish and Wildlife Service 1991). Therefore, our goal was to develop site-level habitat models of CMS occurrence across the range of the species in West Virginia. Specifically, we (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 (Dillard 2007) and to previous, qualitative descriptions of CMS habitat associations.

Methods

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. 1). Therefore, we constrained our modeling to this area. The 320,081-ha region 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. Steep slopes, broad mountaintops and ridges, and narrow valleys with small, high-gradient streams characterize topography of the region. Elevation ranges from 291 to 1,482 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, whereas soil fertility and pH vary depending upon parent material (Kochenderfer 2006). Over a 30-year period (1961–1990), average annual minimum temperature was $2.6 \pm 0.3^\circ\text{C}$, average annual maximum temperature was $13.5 \pm 1.4^\circ\text{C}$, and average annual precipitation was 131.3 ± 11.0 cm/year.

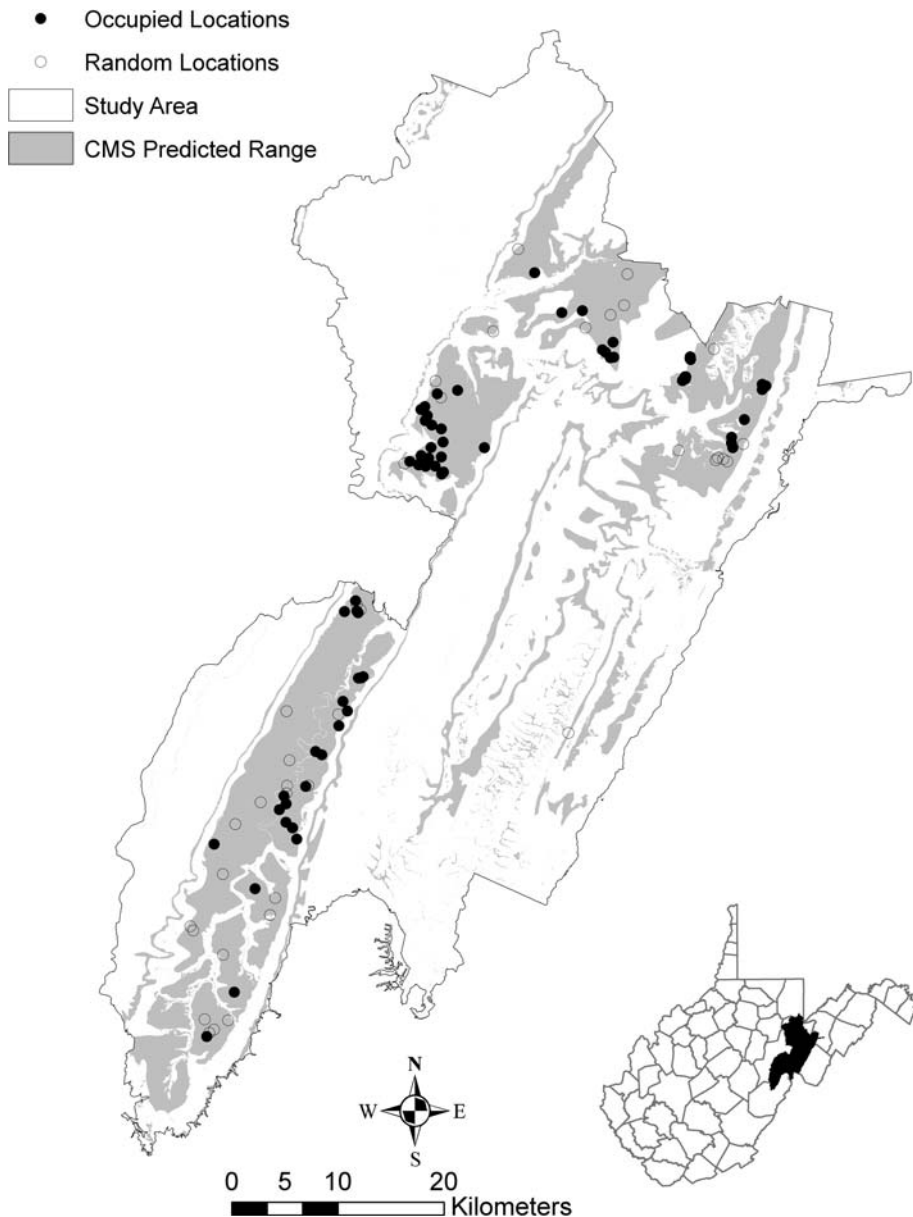


Fig. 1 Map of study area, CMS predicted range (Dillard 2007), and locations of occupied ($n = 67$) and random ($n = 37$) points used for site-level habitat modeling of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006. Occupied and random points are not to scale

Mountains and some higher valleys within the study area generally were forested, whereas lower elevation valleys had 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 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, oak (*Q. spp.*)-dominated or oak-pine (*Pinus spp.*) cover types occurred on some xeric exposures (McCay et al. 1997; Ford et al. 2002; Kochenderfer 2006).

Salamander occurrence and random point locations

To determine CMS presence, we 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. We 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 of 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, we selected an equal number ($n = 180$) of random points from the study area. Because true absence of CMS at these points was unknown, we used the term “pseudo-absence” in conjunction with random sites. Prior to selecting random points, we buffered all occupied points with a 60-m radius area using ArcView 3.3 (ESRI 2002). We 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 Petranks 1998). Moreover, the apparent rarity of CMS across the landscape increased the likelihood of salamander absence outside the 60-m buffers. Within our defined pseudo-absence area, we generated random points using a random point generator (Jenness 2005). We 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 (Dillard 2007). The best-approximating logistic regression model from this study indicated 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. To create more informative site-level habitat models within the predicted range of CMS, we constrained our 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 (Fig. 1; Dillard 2007). This selection criterion limited our modeling efforts to a pool of 155 occupied and 47 random sites.

Habitat measurements

During the summer of 2006, we were able to survey 67 occupied and 37 random points selected by our criteria within the predicted range of CMS (Fig. 1). At each point, identified with a handheld GPS unit, we established a $10 \times 10\text{-m}$ 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; Petranks 1998). We 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. We estimated overhead canopy closure at each plot center with a spherical densiometer (Lemmon 1956). Densiometer readings from each cardinal direction were averaged. We 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 we recorded the total number of sections $\geq 75\%$ obscured from each corner of the plot, measured at eye level. The mean of the four readings was used to estimate percent shrub/understory obscurity for each plot. We also recorded the dominant type of shrub/understory vegetation obscuring the cover pole. Shrub/understory type was grouped into four categories appropriate for our study area and included red spruce/eastern hemlock, rhododendron (*Rhododendron maximum*)/mountain laurel (*Kalmia latifolia*), deciduous shrubs, or mixed. We recorded the presence of large rocky outcrops and seeps (depressed, moist patches) within 30 m of each plot center.

We sampled ground cover within five, 1-m^2 quadrats located at the center of the 10×10 -m plot and 2.5 m from the plot center in each cardinal direction. We 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, we measured litter depth and depth to rock with a graduated metal probe. Depth measurements were averaged for the plot. We 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

We used logistic regression to determine the probability of CMS occurrence in relation to habitat characteristics measured at each occupied and random site. Prior to model specification, we eliminated redundant variables (Spearman's $r \geq 0.70$) and retained 18 variables for inclusion in models (Table 1).

We specified a set of a priori, candidate models based on (1) available biological information on CMS and other woodland salamanders, and (2) our previous experience with these species (Burnham and Anderson 2002). We 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 2). Each model in our set represented a competing hypothesis of the determinants of CMS occurrence. We specified six univariate models including an “outcrop” model, representing the reported association between CMS and rocky outcrops (Pauley 1998). Additionally, we constructed 9 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 and Pauley 1997; T. K. Pauley, unpublished report) and our own work (i.e., associations with eastern hemlock and colluvial rock; Dillard 2007). We 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, we examined fit of the global model following recommendations of Burnham

Table 1 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/understory obscenity	%	SHOB	Average % vertical shrub/understory obscenity from 0 to 1.5 m
Shrub/understory type	–	SHTY	Majority shrub/understory 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 five 1-m ² plots
Herbaceous ground cover	%	GCHB	Average % herbaceous vegetation in five 1-m ² plots
Bryophyte ground cover	%	GCBR	Average % bryophytes in five 1-m ² plots
Emergent rock ground cover	%	GCRK	Average % emergent rock in five 1-m ² plots
Woody debris ground cover	%	GCWD	Average % woody debris in five 1-m ² plots
Bare ground cover	%	GCSL	Average % bare soil in five 1-m ² plots
Leaf litter depth	cm	LLDP	Average leaf litter depth in five 1-m ² plots
Depth to rock	–	RKDP	Average depth to rock depth in five 1-m ² plots portioned into 4 ordinal categories (≤ 10.0 cm, 10.1–20 cm, 20.1–30 cm, ≥ 30 cm)

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.

We 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., $n/K < 40$), we used AIC corrected for small sample size (AIC_c) for model selection (Hurvich and Tsai 1989; Burnham and Anderson 2002). We 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 (AIC_{cmin}; Burnham and Anderson 2002). We drew primary inference from models within two units of AIC_{cmin}, although models within five 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

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 ^a	K^b	AIC ^c	ΔAIC^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/understory 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

Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c)

^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 is the best approximating model among those considered

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 (Russell et al. 2004b, 2005). All analyses were performed using SPSS software (SPSS 2005).

Results

The single abiotic variable "depth to rock" was selected as the best approximating model of 16 logistic regression models explaining the site-level occurrence of CMS (Table 2). Salamander presence was negatively associated with increasing depth to subsurface rock (Table 3). Our second-best model, "literature habitat," also received empirical support ($\Delta AIC_c = 2.49$; Table 2). 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 3). 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 2),

Table 3 Parameter estimates (B), standard errors (SE), and scaled coefficients of determination (R^2) from the six best-approximating models explaining influence of habitat attributes on presence of Cheat Mountain salamanders in the Allegheny Mountains of West Virginia, USA, 2006

Model	B	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

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_{cmin} ; Table 2). Our third-best model, “bryophytes,” ($\Delta\text{AIC}_c = 2.69$; Table 2) indicated that CMS occurrence was positively associated with percent ground cover of bryophytes (Table 3). Our fourth-best model, “abiotic” ($\Delta\text{AIC}_c = 3.55$; Table 2) 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. Our fifth-best model, “conifer density,” ($\Delta\text{AIC}_c = 3.96$; Table 2) indicated that CMS presence was positively associated with increasing tree density of red spruce and eastern hemlock (Table 3). Our sixth-best model, “outcrop” ($\Delta\text{AIC}_c = 4.13$; Table 2) indicated that CMS occurrence was positively associated with the presence of rocky outcrops (Table 3). The remaining 10 models received marginal or no empirical support ($\Delta\text{AIC}_c \geq 5.29$, $w_i \leq 0.03$; Table 2).

Discussion

Habitat models

Our research provides a range-wide assessment of factors potentially influencing the probability of occupancy by CMS at a fine spatial scale. Site-level occurrence of CMS was primarily influenced by geophysical characteristics rather than by patterns of vegetation composition and structure. In particular, our 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.

We are 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 red-backed salamanders (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 our 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 allow for cutaneous respiration by CMS and other lungless salamanders (Feder 1983; Owen 1989; Grover 1998; Petranka 1998; Welsh et al. 2006).

Our “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; US Fish and Wildlife Service 1991; Pauley and Pauley 1997; T. K. Pauley, unpublished report). Our field-based results also corroborate the coarse scale, GIS-based data used in previous modeling of CMS landscape-level distribution that indicated a correlation between CMS occurrence and the presence of red spruce forest cover (Dillard 2007). In addition to red spruce, we 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 red-backed salamanders, appear to be lower in coniferous forests than deciduous forests (Petranka 1998; Brooks 2001). Soil and leaf litter are 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). T. K. Pauley (unpublished report) observed lower soil pH in occupied CMS locations ($n = 4$) than in non-occupied locations ($n = 3$), although differences were not statistically significant. We suggest that 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 red-backed salamanders.

Our literature habitat model indicated a positive association between CMS occupancy and overstory canopy closure. Our results are consistent with accepted relationships between canopy closure and other terrestrial salamanders (deMaynadier and Hunter 1995; Petranks 1998; Russell et al. 2004a). T. K. Pauley (unpublished report) 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, our 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. Our results quantitatively corroborate CMS habitat descriptions by Brooks (1948) and Pauley and Pauley (1997). The presence and density of bryophytes including *Bazzania* spp., that we observed at occupied sites, may signify suitable microhabitat conditions for CMS by indicating higher soil moisture and site-level humidity.

Our “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 of the early 20th century (Pauley 1998).

Our 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 indicated a strong association between CMS distribution and sandstone (Dillard 2007), most likely reflecting the surface and subsurface habitats produced by this geology type. In our 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; Petranks 1998). However, our results indicated a negative association between CMS occupancy and the percent cover of emergent rock. We 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). Petranks (1998) provided evidence that populations of red-backed salamanders usually reach their greatest numbers in forested habitats with deep soils, but are absent or occur at low densities in shallow, rocky soils.

Finally, our abiotic model indicated a negative correlation between CMS occurrence and the presence of seeps, corroborating early CMS habitat descriptions by Brooks (1948) and recent research on CMS landscape-level distribution, indicating that CMS-occupied

sites were farther from water sources when compared to random locations (Dillard 2007). Our findings may provide some support to the prevailing hypothesis that both red-backed and Allegheny mountain dusky salamanders competitively dominate CMS and potentially restrict its local distribution (Highton 1972; Pauley 1980; Adams et al. 2007). Grover and Wilbur (2002) found that red-backed salamander abundance increased in artificially created seeps in upland forest habitats in the Allegheny Mountains. Throughout high elevation forests in our study area, Allegheny mountain dusky salamanders are ubiquitous because of abundant precipitation, but may congregate near seeps and other water sources for breeding and during periods of drought (Petranka 1998).

Our results indicated that CMS occupancy was most strongly associated with abiotic variables than with overstory, shrub/understory, 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 T. K. Pauley (unpublished report) failed to detect meaningful differences in overstory, shrub/understory, or ground cover vegetation composition and structure between CMS-occupied ($n = 4$) and non-occupied sites ($n = 4$). We 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 examine properties of CMS populations in relation to structural, physiochemical, and other abiotic attributes as well as occupancy and density of competitive sympatric salamanders (i.e., red-backed and Allegheny mountain dusky salamanders) 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, we urge caution in extending our modeling results beyond a general description of CMS site-level habitat relationships, as our study contained several limitations and assumptions. Because our research relied on previous ground surveys to determine occupancy, we assumed that CMS was still present 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 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, our modeling effort did not address site-level influences on CMS abundance, densities, or range-wide population viability.

We also 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. 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, we detected considerable potential biases in the distribution of historic CMS-“absent” sites, including spatial autocorrelation with existing roads and trails in the region. Therefore, we 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 our best approximating model and other supporting models defined the “fundamental niche” (Zaniewski et al. 2002; Ford et al. 2006) of CMS, our models failed to account for much of the variation in the site-level occurrence of the species (Table 3). In contrast, our landscape-level assessment of CMS distribution resulted in a set of models with relatively high predictive power and classification accuracy (Dillard 2007). Our 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 we measured. Because we avoided specification of all potential models (Burnham and Anderson 2002), it is possible that combinations of variables we 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 our models. Conversely, our 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 our 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 (Whitaker and Stauffer 2006), which may occur when variables are difficult to measure accurately (e.g., canopy closure, visual obscurity) or are subject to inherent random variation (e.g., ground cover estimates). 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. 2004b, 2005). Furthermore, we suggest that future research studies include a more defined focus on occurrence and abundance of competitor sympatric salamander species. Even with limited explanatory power, our models identified previously unreported interactions of site-level variables that potentially influence the distribution of CMS. As such, we view our 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 (US Fish and Wildlife Service 1991).

We think our 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). When combined with landscape-level distribution models (Dillard 2007), further refinements to our 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 eventually could provide 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). Although preliminary, our 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 may 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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