

Abiotic factors influencing abundance and microhabitat use of stream salamanders in southern Appalachian forests

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Abstract

In order to evaluate the effects of habitat loss and degradation on amphibian populations it is necessary to determine species-specific habitat use and how this influences abundance. While a number of studies have examined the influence of competition and predation in stream salamander assemblages in the southern Appalachian Mountains, there remains a relative lack of knowledge on the microhabitat use of these species. Using area-constrained daytime searches, we investigated microhabitat use and abundance for stream-breeding salamanders in mature forests in southern Appalachian streams from May to August 2004. We found that leaf litter depth, soil moisture, and canopy cover were all higher and soil temperature was lower in plots where stream salamanders were encountered compared to plots where salamanders were not encountered. A regression analysis using the information-theoretic approach (AIC) revealed that the model that included distance from stream, leaf litter depth, soil moisture, and soil temperature had the strongest support for predicting stream salamander abundance at the landscape level ($\omega_i = 0.99$). Microhabitat use in many species of stream salamanders is mediated by a number of complex factors including environmental variables, competition, and predation. Alteration of habitats likely results in increased competition and predation rates and subsequent local population declines, so it is imperative to mitigate the effects of practices such as even-aged timber harvesting in order to conserve amphibian biodiversity. © 2007 Elsevier B.V. All rights reserved.

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1. Introduction

The effects of habitat loss and degradation on amphibians are often pronounced because of their relatively low vagilities and narrow habitat tolerances (Gibbs, 1998; deMaynadier and Hunter, 2000; Semlitsch, 2000; Houlahan and Findlay, 2003). Many studies have shown a positive relationship between amount of forest cover and amphibian species occurrence and richness (Gibbs, 1998; Guerry and Hunter, 2002; Trenham and Shaffer, 2005). Despite this generalization, determination of species-specific habitat use is necessary to understand the effects of habitat loss and degradation on amphibian populations (Cushman, 2006), and develop conservation plans to mitigate the effects of habitat alteration.

Salamander communities make up an important ecological component of many forested ecosystems and often

exceed the combined biomass of other terrestrial vertebrates in the eastern United States (Burton and Likens, 1975; Hairston, 1987). In the southern Appalachian Mountains, headwater streams and associated riparian habitats contain high levels of salamander diversity and abundance (e.g., *Desmognathus*, *Eurycea*, *Gyrinophilus*, *Plethodon*, and *Pseudotriton*; Petranka and Murray, 2001; Peterman et al., 2008). These salamanders are members of Plethodontidae and lack lungs with which to breathe, but instead utilize dermal respiration to breathe across the surface of the skin (Petranka, 1998). Many genera of plethodontid salamanders inhabit streams and have biphasic life cycles that include an aquatic larval stage that is followed by a terrestrial adult stage (Petranka, 1998). While stream salamanders are dependent upon aquatic habitats for reproduction and larval development, terrestrial habitats are used for foraging and potentially overwintering (Barbour et al., 1969; Ashton and Ashton, 1978). Terrestrial woodland salamanders (*Plethodon* spp.) differ from stream salamanders in that they oviposit in terrestrial habitats and have direct development without an aquatic larval stage (Petranka, 1998).

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Although plethodontid salamanders have been the focus of demographic and behavioral studies in the southern Appalachian Mountains for more than five decades (e.g., Hairston, 1949, 1987; Organ, 1961; Peterman et al., 2008), information on habitat use is still lacking. More recently a few studies have begun to address how salamanders are distributed across the landscape and the environmental factors that affect their distribution (e.g., Grover, 2000; Moore et al., 2001; Petranka and Smith, 2005; Crawford and Semlitsch, 2007). In stream salamander assemblages in western North Carolina, Crawford and Semlitsch (2007) found four focal species that were spatially separated from one another. The majority of dusky salamanders (*Desmognathus quadramaculatus*, *D. monticola*, and *D. ocoee*) resided within 15 m of the stream's edge, whereas brook salamanders (*Eurycea wilderae*) occurred primarily beyond 15–20 m (and up to 100 m) from the stream's edge. This is most likely due to predation and competition pressures exerted by the larger dusky salamanders on the brook salamanders (Southerland, 1986a; Hairston, 1987). Both black-bellied salamanders (*D. quadramaculatus*) and seal salamanders (*D. monticola*) are large bodied and prey on juvenile and adult two-lined salamanders (Beachy, 1993; Crawford personal observation). Grover (2000) found that among both terrestrial and stream salamanders, larger species used wider cover objects, deeper retreats, and occupied cooler retreat sites than smaller species. Among the stream salamanders, larger species were found closer to water than smaller species and the rehydration rates of the smaller species that were found farther from the stream were higher than those of larger species found closer to the stream (Grover, 2000). The unique physiology of plethodontid salamanders makes them susceptible to dehydration and restricts their activity to periods when humidity and soil moisture are high (Spotila, 1972; Tracy, 1976). While several studies have documented the importance of soil moisture to stream salamanders, understanding what habitat features are associated with soil moisture and salamander abundance is essential in developing conservation strategies for these animals.

We sampled stream salamanders in the riparian areas along headwater streams to determine what environmental variables were most important for microhabitat use and their relationship to distance from the stream edge. We used regression analyses with an information-theoretic approach to select which environmental variables would best predict relative abundance of stream salamanders in riparian habitats.

2. Methods

2.1. Study area

To determine habitat use and stream salamander abundance, we sampled riparian forests adjacent to 14 headwater streams in the southern Appalachian Mountains, Nantahala National Forest, Macon County, North Carolina (U.S.A.). All sites were located between 718 and 1248 m in elevation, had not been subject to logging for at least 80 years and were located at least 1 km apart. Sites were sampled three times

each from May to August of 2004 using an area-constrained daytime search.

2.2. Sampling protocol

During sampling, we collected stream salamanders at paired transects that were separated by at least 1 m and extended perpendicular from the stream bank into the adjacent forest. Monitoring stations were established at 1, 3, 7, 10, 15, 25, 50, and 100 m from the stream bank, based on home range sizes and potential distances traveled by the target species of stream-breeding salamanders (Crawford and Semlitsch, 2007). At each stream, we conducted three collections by using area-constrained searches of each plot (2.25 m²) and sifting through leaf litter and coarse woody debris at each monitoring station for an average of 10 min. At each plot, data was collected on four environmental variables: (1) leaf litter depth—measured three times in each plot (six times per station) with a hand ruler for an average leaf litter depth value; (2) soil temperature—measured three times in each plot (six times per station) with an infrared Raytek[®] MT4 temperature gun for an average temperature value; (3) soil moisture—measured three times in each plot (six times per station) with an Aquaterr[®] M300 soil moisture meter for an average soil moisture value; and (4) canopy cover—measured one time in each plot (two times per station) with a spherical crown densiometer for an average canopy cover value. Additionally, slope and altitude were recorded for each of the 14 sites. Altitude was obtained with a Kestrel[®] 4000 Pocket Weather Tracker[™] and slope was obtained with a Haglöf[®] Electronic Clinometer.

We identified all salamanders to species, weighed (with a 20 g Pesola[®] LightLine Spring Scale) and measured for snout-vent length and total length (with a hand ruler), and recorded the distance from the stream. We released all salamanders at the site of capture. We determined size class (adult or juvenile) by comparing measured snout-vent lengths of each individual to published size classes for each species (Petranka, 1998).

2.3. Data analysis

To investigate the relationships between stream salamander abundance and environmental variables, we used an information-theoretic approach to model selection (Burnham and Anderson, 2002). The information-theoretic approach allows one to select a “best” model and to rank the remaining models (Burnham and Anderson, 2002). Burnham and Anderson (2002) suggest the information-theoretic approach should be used in observational studies where other hypothesis testing methods may lead to “data dredging” and over-fitted models. Using nine environmental variables, we built 16 *a priori* models to test hypotheses predicting stream salamander abundance. The environmental variables we selected (and subsequent models we built) were based on previous studies detailing their importance to plethodontid salamanders as well as pilot data collected during the 2003 field season. The predictive models are: (1) Null (intercept only); (2) Site (site); (3) Period (sampling period); (4) Distance (distance from stream); (5)

Table 1

Environmental variables^a for plots in which salamanders were not captured and plots in which salamanders were captured in riparian areas

Species	Litter depth (mm)	Temperature (°C)	Moisture (%)	Canopy (%)
Salamander absent	25.12 (0.28)	18.87 (0.11)	34.44 (0.50)	89.67 (0.29)
Salamander present	31.27 (0.43)	18.27 (0.15)	45.68 (0.85)	91.47 (0.24)
<i>Desmognathus monticola</i> present	30.15 (0.90)	18.35 (0.35)	43.35 (2.22)	91.70 (0.38)
<i>Desmognathus ocoee</i> present	30.48 (0.54)	17.70 (0.19)	46.45 (1.15)	91.47 (0.26)
<i>Eurycea wilderae</i> present	34.31 (1.01)	19.61 (0.28)	45.82 (1.38)	91.19 (0.76)

^a Mean and standard error values.

Leaf (leaf litter depth); (6) Temperature (surface soil temperature); (7) Moisture (soil moisture); (8) Canopy (canopy cover); (9) Slope (terrestrial slope); (10) Elevation (altitude of site); (11) Soil (soil moisture and soil temperature); (12) Forage (soil moisture and leaf litter depth); (13) Gradient (soil moisture and distance from stream); (14) Microhabitat (soil moisture, soil temperature, and leaf litter depth); (15) Macrohabitat (canopy cover, slope, and elevation); and (16) Global (site, period, distance from stream, leaf litter depth, soil temperature, soil moisture, canopy cover, slope, and elevation).

For each model, we calculated the AIC value corrected for small sample sizes (AIC_c), which is a measure of model fit adjusted for the number of parameters (Burnham and Anderson, 2002). AIC_c values were derived from loglinear regressions with a poisson distribution using the generalized linear model in SPSS (v. 15). We ranked all candidate models according to their AIC_c values, and the best model had the smallest AIC_c value (Burnham and Anderson, 2002). We also calculated ΔAIC_c, which is the difference in AIC between each model and the best model in the set. AIC differences less than two are considered to indicate little difference between models, while differences of 4–7 indicate considerably less support for the model with the higher AIC value although it may have some empirical support (Burnham and Anderson, 2002). Last, we calculated Akaike weights (ω_i) to determine the weight of evidence in favor of each model and to estimate the relative importance of each individual parameter (Burnham and Anderson, 2002). Based on these results we also generated six post hoc models using subsets of the variables included in each of the 16 *a priori* models. The post hoc predictive models are: (1) DistLeaf (distance from stream and leaf litter depth); (2) DistLeafMois (distance from stream, leaf litter depth, and soil moisture); (3) DistLeafMoisTemp (distance from stream, leaf litter depth, soil moisture, and soil temperature); (4) DistLeafTemp (distance from stream, leaf litter depth, and soil temperature); (5) DistTemp (distance from stream and soil temperature); and (6) TempLeaf (soil temperature and leaf litter depth).

3. Results

In 2004, stream salamanders were found in 149 of the 672 plots ($N = 16$ plots \times 14 sites \times 3 collections) that were searched. A total of 204 stream salamanders were captured in the 149 plots, including 107 Ocoee salamanders (*Desmognathus ocoee*), 42 seal salamanders (*D. monticola*), 4 black-bellied salamanders (*D. quadramaculatus*), 49 Blue Ridge two-lined salamanders (*E. wilderae*), and 2 three-lined salamanders

(*E. guttolineata*). Average leaf litter depth, average soil moisture, and average canopy cover were all lower and average soil temperature was higher in plots without a stream salamander of any species compared to plots where each stream salamander was captured (Table 1). For seal salamanders the average leaf litter depth, average soil moisture, and average canopy cover were all lower and average soil temperature was higher in plots without a seal salamander compared to plots where each seal salamander was captured (Table 1); for Ocoee salamanders the average leaf litter depth, average soil moisture, and average canopy cover were all lower and average soil temperature was higher in plots without an Ocoee salamander compared to plots where each Ocoee salamander was captured (Table 1); for two-lined salamanders the average leaf litter depth, average soil moisture, average canopy cover, and average soil temperature were all lower in plots without a two-lined salamander compared to plots where each two-lined salamander was captured (Table 1). We excluded plot data for black-bellied salamanders and three-lined salamanders due to low capture numbers.

Of the 16 *a priori* models, the Global model best predicted the abundance of stream salamanders ($\omega_i = 1.00$). This model included all nine variables, however, distance from stream, leaf litter depth, soil moisture, and soil temperature were the only variables for which the estimate of beta had a confidence interval that did not overlap zero (Table 2). One of the six post hoc models described the data as well or better than the *a priori* Global model (Table 3). A model including only the variables: distance from stream, leaf litter depth, soil moisture, and soil temperature ranked highest. The best *a priori* models for predicting seal salamander abundance were the Gradient model ($\omega_i = 0.60$) that included both distance from the stream and soil

Table 2

 β estimates and 95% confidence intervals for parameters in the *a priori* Global model for stream salamander abundance

Parameter	β	Lower 95% C.I.	Upper 95% C.I.
Intercept	-0.075	-4.130	3.979
Site	0.005	-0.051	0.060
Period	-0.051	-0.357	0.255
Distance	-0.043	-0.059	-0.027
Leaf	0.082	0.054	0.109
Temperature	-0.147	-0.254	-0.040
Moisture	0.038	0.025	0.051
Canopy	-0.002	-0.041	0.037
Slope	-0.010	-0.040	0.019
Elevation	-0.001	-0.002	0.001

The Global model includes nine environmental variables.

Table 3

Post hoc regression models (including the four best *a priori* models) explaining the influence of environmental variables on stream salamander abundance in headwater streams in the Nantahala National Forest, North Carolina

Model ^a	(−2Loglike)	K ^b	AIC _c	ΔAIC _c ^c	ω _i ^d
DistLeafMoisTemp	557.76	5	567.94	0.00	0.99
Global	556.05	10	576.73	8.78	0.01
DistLeafMois	573.41	4	581.53	13.58	0.00
DistLeafTemp	592.74	4	600.86	32.91	0.00
DistLeaf	597.18	3	603.26	35.31	0.00
Gradient	605.87	3	611.94	44.00	0.00
Microhabitat	611.01	4	619.13	51.19	0.00
Distance	636.52	2	640.56	72.62	0.00
DistTemp	635.92	3	642.00	74.05	0.00
TempLeaf	686.26	3	692.33	124.39	0.00

Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c). The global model fits the data ($\chi^2 = 213.107$, d.f. = 9, $P < 0.001$, $n = 336$).

^a Model names correspond to models given in Section 2.

^b Number of estimable parameters in approximating model.

^c Difference in value between AIC_c of the current model vs. the best-approximating model.

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

moisture and the Distance model ($\omega_i = 0.35$) that included only distance from the stream. The only variables for which the estimate of beta had a confidence interval that did not overlap zero were distance from the stream and leaf litter depth (although soil moisture was also close; Table 4). Four of the six post hoc models described the data as well or better than the *a priori* Gradient model (Table 5). A model including only the variables: distance from the stream and leaf litter depth ranked highest. The best *a priori* model for predicting Ocoee salamander abundance was the Global model ($\omega_i = 1.00$). This model included all nine variables, however, distance from stream, leaf litter depth, soil moisture, and soil temperature were the only variables for which the estimate of beta had a confidence interval that did not overlap zero (Table 6). One of the six post hoc models described the data as well or better than the *a priori* Global model (Table 7). A model including only the variables: distance from stream, leaf litter depth, soil moisture, and soil temperature ranked highest. The best *a priori* models

Table 4

β estimates and 95% confidence intervals for parameters in the *a priori* Global model for seal salamander abundance

Parameter	β	Lower 95% C.I.	Upper 95% C.I.
Intercept	−3.157	−12.385	6.070
Site	0.071	−0.035	0.177
Period	−0.152	−0.859	0.555
Distance	−0.150	−0.225	−0.076
Leaf	0.062	0.003	0.122
Temperature	−0.050	−0.290	0.190
Moisture	0.027	−0.005	0.059
Canopy	0.021	−0.067	0.110
Slope	0.022	−0.042	0.086
Elevation	−0.002	−0.005	0.001

The Global model includes nine environmental variables.

Table 5

Post hoc regression models (including the four best *a priori* models) explaining the influence of environmental variables on seal salamander abundance in headwater streams in the Nantahala National Forest, North Carolina

Model ^a	(−2Loglike)	K ^b	AIC _c	ΔAIC _c ^c	ω _i ^d
DistLeaf	210.17	3	216.25	0.00	0.32
DistLeafMois	208.20	4	216.32	0.08	0.31
DistLeafMoisTemp	208.07	5	218.26	2.01	0.12
DistLeafTemp	210.16	4	218.28	2.04	0.12
Gradient	213.22	3	219.29	3.02	0.07
Distance	216.35	2	220.39	4.14	0.04
DistTemp	216.24	3	222.31	6.06	0.02
Global	203.46	10	224.14	7.89	0.01
Microhabitat	246.36	4	254.48	38.24	0.00
TempLeaf	259.46	3	265.46	49.22	0.00

Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c). The global model fits the data ($\chi^2 = 69.888$, d.f. = 9, $P < 0.001$, $n = 336$).

^a Model names correspond to models given in Section 2.

^b Number of estimable parameters in approximating model.

^c Difference in value between AIC_c of the current model vs. the best-approximating model.

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

for predicting two-lined salamander abundance were the Forage model ($\omega_i = 0.51$) that included leaf litter depth and soil moisture and the Microhabitat model ($\omega_i = 0.41$) that included leaf litter depth, soil moisture, and soil temperature. The only variables for which the estimate of beta had a confidence interval that did not overlap zero were leaf litter depth and the intercept (Table 8). None of the six post hoc models described the data as well or better than the *a priori* Forage model (Table 9). Species-specific models were not tested for black-bellied salamanders and three-lined salamanders due to low capture numbers.

4. Discussion

Many stream-breeding salamanders are highly philopatric, long-lived, and usually exist in relatively stable populations (Hairston, 1987). These life history traits make them reliable indicators of potential biotic diversity in stream and riparian

Table 6

β estimates and 95% confidence intervals for parameters in the *a priori* Global model for Ocoee salamander abundance

Parameter	β	Lower 95% C.I.	Upper 95% C.I.
Intercept	1.784	−3.318	6.886
Site	−0.016	−0.108	0.076
Period	−0.087	−0.517	0.343
Distance	−0.123	−0.167	−0.079
Leaf	0.064	0.025	0.104
Temperature	−0.204	−0.371	−0.037
Moisture	0.047	0.030	0.065
Canopy	−0.014	−0.061	0.032
Slope	−0.043	−0.086	0.000
Elevation	0.000	−0.002	0.003

The Global model includes nine environmental variables.

Table 7

Post hoc regression models (including the four best *a priori* models) explaining the influence of environmental variables on Ocoee salamander abundance in headwater streams in the Nantahala National Forest, North Carolina

Model ^a	(−2Loglike)	K ^b	AIC _c	ΔAIC _c ^c	ω _i ^d
DistLeafMoisTemp	353.49	5	363.67	0.00	0.94
Global	348.54	10	369.22	5.55	0.06
DistLeafMois	372.38	4	380.50	16.83	0.00
DistLeafTemp	378.64	4	386.76	23.09	0.00
Gradient	381.15	3	387.23	23.55	0.00
DistLeaf	386.23	3	392.31	28.63	0.00
DistTemp	393.82	3	399.89	36.22	0.00
Distance	399.03	2	403.06	39.39	0.00
Microhabitat	419.36	4	427.48	63.81	0.00
TempLeaf	483.59	3	489.66	125.99	0.00

Model rankings were based on Akaike’s Information Criterion corrected for small sample size (AIC_c). The global model fits the data ($\chi^2 = 191.212$, d.f. = 9, $P < 0.001$, $n = 336$).

^a Model names correspond to models given in Section 2.

^b Number of estimable parameters in approximating model.

^c Difference in value between AIC_c of the current model vs. the best-approximating model.

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

ecosystems, and their relative abundance and core habitat use can be a critical indicator of stream and riparian ecosystem health (Welsh and Ollivier, 1998; Crawford and Semlitsch, 2007). In eastern United States forests, salamanders typically comprise the greatest biomass of any vertebrates (Burton and Likens, 1975; Petranka and Murray, 2001; Peterman et al., 2008) and serve a key role in the ecosystem because they consume invertebrates and serve as prey for other vertebrates. While numerous studies have documented the importance of competition and predation in structuring stream salamander assemblages and their distributions (e.g., Southerland, 1986b; Hairston, 1987; Roudebush and Taylor, 1987), relatively fewer studies have examined the importance of environmental factors in undisturbed habitats. Of these studies, Keen (1984) found that dusky salamanders (*Desmognathus fuscus*) were found under smaller rocks more frequently on high moisture than low moisture substrates. However, during times of low moisture, salamanders used larger rocks more frequently and were more

Table 8

β estimates and 95% confidence intervals for parameters in the *a priori* Global model for two-lined salamander abundance

Parameter	β	Lower 95% C.I.	Upper 95% C.I.
Intercept	−13.666	−23.529	−3.802
Site	−0.023	−0.136	0.090
Period	0.460	−0.190	1.111
Distance	−0.003	−0.017	0.012
Leaf	0.130	0.075	0.186
Temperature	0.063	−0.146	0.273
Moisture	0.009	−0.022	0.039
Canopy	0.060	−0.038	0.158
Slope	−0.010	−0.069	0.050
Elevation	0.000	−0.003	0.003

The Global model includes nine environmental variables.

Table 9

Post hoc regression models (including the four best *a priori* models) explaining the influence of environmental variables on two-lined salamander abundance in headwater streams in the Nantahala National Forest, North Carolina

Model ^a	(−2Loglike)	K ^b	AIC _c	ΔAIC _c ^c	ω _i ^d
Forage	246.55	3	252.62	0.00	0.32
Microhabitat	244.91	4	253.03	0.41	0.26
DistLeafMois	246.51	4	254.63	2.01	0.12
DistLeafMoisTemp	244.47	5	254.65	2.03	0.12
TempLeaf	250.07	3	256.14	3.52	0.06
DistLeafTemp	248.31	4	256.43	3.80	0.05
Leaf	252.70	2	256.74	4.12	0.04
DistLeaf	252.05	3	258.13	5.50	0.02
Global	239.60	10	260.27	7.65	0.01
DistTemp	271.83	3	277.90	25.28	0.00

Model rankings were based on Akaike’s Information Criterion corrected for small sample size (AIC_c). The global model fits the data ($\chi^2 = 44.598$, d.f. = 9, $P < 0.001$, $n = 336$).

^a Model names correspond to models given in Section 2.

^b Number of estimable parameters in approximating model.

^c Difference in value between AIC_c of the current model vs. the best-approximating model.

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

clumped in their dispersion pattern than on high moisture substrates (Keen, 1984).

We found that leaf litter depth, soil moisture, and canopy cover were all higher and soil temperature was lower in plots where stream salamanders were found. Additionally our regression analyses revealed that the model that included distance from the stream, leaf litter depth, soil moisture, and soil temperature had the strongest support for predicting stream salamander abundance. These were also the four variables whose beta estimates did not overlap zero (Table 2). For each of the three individual species (seal salamanders, Ocoee salamanders, and two-lined salamanders) both leaf litter depth and soil moisture were higher in plots where these species were found. Leaf litter depth and soil moisture were also the only two variables that were consistently important in the highest ranked species-specific models from the regression analyses. Salamanders in the Plethodontidae, which is a lungless family of salamanders (Petranka, 1998), are even more dependent on moist habitats for dermal respiration than other families of amphibians. These salamanders forage for invertebrates in the leaf litter and when this leaf litter becomes thinner, the soil becomes drier, or a combination of both it is unlikely they will have the moisture necessary to carry on dermal respiration. Jaeger (1980) found that the percentage of red-backed salamanders (*Plethodon cinereus*) under rocks and logs increased and the percentage of salamanders in the leaf litter decreased with decreasing rainfall. Additionally, individuals cannot forage during dry periods because of the high rates of body water loss (Jaeger, 1972; Spotila, 1972).

Selection of microhabitats is further mediated by competition from conspecifics and heterospecifics as well as predator–prey interactions (Jaeger, 1972; Southerland, 1986a; Colley et al., 1989). Jaeger (1972) found that during periods of drought prey items for salamanders decreased due to decreases in soil

moisture and leaf litter moisture. Eastern red-backed salamanders (*P. cinereus*), which were presumably superior competitors, inhabited isolated pockets where soil moisture was higher and forced the Shenandoah salamanders (*P. shenandoah*) to reside in the much drier talus slopes. In the southern Appalachians, Southerland (1986b) found that the larger black-bellied salamanders (*D. quadramaculatus*) predation of juvenile seal salamanders (*D. monticola*) sharply reduced survival and caused shifts in activity and habitat selection. In the 149 plots that we encountered stream salamanders, only 11 of these plots had salamanders of two or more species. This further suggests that competition and predation may be important in microhabitat use.

In the southern Appalachian Mountains, clear-cutting of forests results in reduced litter dry mass (amount of leaf litter), leaf litter depth, and leaf litter moisture (Ash, 1995). Additionally, Covington (1981) found that “forest floor organic matter” declined 55% over the first 15 years after logging. Logging activities have been shown to cause dramatic salamander declines in a number of studies and return of salamander populations to pre-disturbance levels can take up to 70 years (e.g., Petranks et al., 1993; Ash, 1997; Crawford and Semlitsch, unpublished data). This habitat degradation and alteration most likely causes a reduction in the amount of microhabitat available and forces smaller salamanders into a choice of suboptimal microhabitat or increasing predation risk in more suitable microhabitats (Crawford and Semlitsch, 2007). Either of these choices likely results in decreased abundances and salamanders being found closer to streams (Crawford and Semlitsch, 2007; Crawford and Semlitsch, unpublished data).

Microhabitat selection in many species of stream salamanders is mediated by a number of complex factors including environmental variables, competition, and predation. Alteration of habitats likely results in increased competition and predation rates and subsequent population declines, so it is imperative to mitigate the effects of practices such as even-aged timber harvesting. Other studies have suggested that even-aged timber harvesting is not the most appropriate method to maintain viable amphibian populations and alternative uneven-aged harvesting techniques (e.g., selective harvesting) would conserve these populations (Grialou et al., 2000; Karraker and Welsh, 2006). However, these studies only address populations at the local level and do not discuss the implications at the landscape level. If only 5–10% of the landscape was logged using even-aged timber harvest methods versus the entire landscape being logged using uneven-aged timber harvest, it is likely that the even-aged timber harvest method would be more successful in conserving salamanders at the landscape level. Our results indicate that by reducing the loss of leaf litter, soil moisture and overall canopy cover, declines of stream salamander assemblages can be kept to a minimum.

5. Conclusions

In the southern Appalachian Mountains we found that leaf litter depth, soil moisture, and canopy cover were all higher and

soil temperature was lower in plots where stream salamanders were encountered compared to plots where salamanders were not encountered. A regression analysis using the information-theoretic approach (AIC) revealed that the model that included distance from stream, leaf litter depth, soil moisture, and soil temperature had the strongest support for predicting stream salamander abundance at the landscape level ($\omega_1 = 0.99$). More specifically, for each of the three individual species (seal salamanders, Ocoee salamanders, and two-lined salamanders) both leaf litter depth and soil moisture were higher in plots where these species were found. Leaf litter depth and soil moisture were also the only two variables that were consistently important in the highest ranked species-specific models from the regression analyses. In addition to investigating alternative harvesting techniques (and their impacts), we would recommend implementing more stringent buffer zone criteria around streams of all types. Current U.S. Forest Service guidelines for southern Appalachian streams require only an ~9 m (30 feet) buffer for headwater through second-order streams and an ~30 m (100 feet) buffer for streams third-order and above. Crawford and Semlitsch (2007) found that stream salamander assemblages require a core terrestrial habitat of 42.6 m and recommended a total buffer zone of 92.6 m (core terrestrial habitat plus a 50 m buffer to mitigate edge effects). While current USFS regulations are not adequate to protect stream salamander populations in clearcuts, these larger buffer zones would likely decrease the impact of timber harvesting on microhabitats within riparian areas of streams and help prevent local population declines.

Although research on microhabitat use in amphibians has increased in the past decade, there remains a gap in our knowledge on the microhabitat use in stream-breeding salamanders and how this influences overall abundance and diversity at the landscape level. In order to mitigate the impacts of habitat alteration, it is necessary to have a clear understanding of the role of both abiotic and biotic factors play in determining microhabitat use and abundance. We have identified important factors in structuring these assemblages and hope our work stimulates future research on the mechanisms of selection, costs and benefits, links to population declines, and conservation solutions.

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