

Reprinted from

Forest Ecology and M a n a g e m e n t

Forest Ecology and Management 114 (1999) 245-252

Factors affecting salamander density and distribution within
four forest **types** in the Southern Appalachian Mountains

Craig A. Harper^{a,*}, David C. Guynn, Jr.^b

^a*Department of forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN 37901, USA*

^b*Department of Forest Resources, Clemson University, Clemson, SC 29634, USA*



Forest Ecology and Management

Aims and scope. forest Ecology and Management publishes scientific articles concerned with forest management and conservation, and in particular the application of biological, ecological and social knowledge to the management of man-made and natural forests. The scope of the journal includes all forest ecosystems of the world. A refereeing process ensures the quality and international interest of the manuscripts accepted for publication. The journal aims to encourage communication between scientists in disparate fields who share a common interest in ecology and natural-resource management, and to bridge the gap between research workers and forest managers in the field to the benefit of both. The journal should be of interest to research workers, managers and policy makers in forestry, natural resources, ecological conservation and related fields.

FOUNDING EDITOR

Laurence L. **Roche**, Murroe, Ireland

EDITORS-IN-CHIEF

For the Americas, Australia, New Zealand and the Pacific:

R.F. Fisher

Department of Forest Science
Texas A&M University
College Station, TX **77843-2135**, USA

For the rest of the world:

G.M.J. Mohren

Forest Production Ecology Group
Department of Vegetation Ecology
DLO-Institute for Forestry and Nature Research
P.O. Box 23
6700 AA Wageningen, The Netherlands

BOOK REVIEWS EDITOR

Margaret **R. Gale**

School of Forestry and Wood Products
Michigan Technological University
1400 Townsend Drive
Houghton, MI **49931**, USA

EDITORIAL ADVISORY BOARD

G. Abrahamsen, Agricultural University of Norway, AS, Norway

R. Aifaro, Canadian Forestry Service, Victoria, B.C., Canada

F. Andersson, Swedish University of Agricultural Sciences, Uppsala Sweden

P.M.S. Ashton, Yale University, New Haven, USA

P. Attiwill, University of Melbourne, Parkville, **Vic.**, Australia

J. Boyle, Oregon State University, Corvallis, USA

S. Brown, US Environmental Protection Agency, Corvallis, USA

I. Burke, Colorado State University, Fort Collins, CO, USA

J.C. Calvo, Institute of Technology, **Cartago**, Costa Rica

R.-J. Chen, University of Hong Kong, Pokfulam Road, Hong Kong

J.D. Deans, **Institute** of Terrestrial Ecology, Penicuik, Midlothian, UK

R.M. DeGraaf, USDA Forest Service, University of Massachusetts, Amherst, MA, USA

S. Diamandis, Forest Research Institute, Thessaloniki, Greece

D.P. Dykstra, **CIFOR**, Jakarta, Indonesia

E.P. Farrell, University College Dublin, Dublin, Ireland

P.M. Fearnside, Instituto Nacional de Pesquisas da

Amazonia-INPA, Manaus-Amazonas, Brazil

P.H. Freer-Smith, Forestry Commission, Farnham, UK

O. Garcia, ENGREF, Nancy, France

D. Gilmore, Canadian Forest Product Ltd., Alberta, Canada

R.A. Goyer, Louisiana State University, Baton Rouge, LA, USA

J.B. Hall, University College of North Wales, Bangor, UK

F. Houliier, Campus International de Bailiarguet, Laboratoire Associe de Modellsatfon des **Plantes (AMAP)**, **Montpellier**, France

B.M. Kumar, Kerala Agricultural University, Kerala, India

J.P. Lassoie, Cornell University, **Ithaca**, NY, USA

J.N. Long, Utah State University, Logan, UT, USA

A.E. Lugo, International Institute of Tropical Forestry, Rio Piedras, PR, USA

J.A. Maghembe, SADCC / **ICRAF** Agroforestry Project,

Zomba, Malawi

F. Makeschin, Institut für Bodenkunde und Standortslehre,

Tharandt, Germany

DC Malcolm, University of Edinburgh, Edinburgh, UK

E. Mälkönen, Finnish Forest Research Institute, Vantaa,

Finland

M.A.R. Nahuz, Instituto de Pesquisas Tecnológicas,

São Paula SP, Brazil

R. Päivinen, European Forestry Institute, Joensuu, Finland

S.G. Paillard, University of Missouri, Columbia, MO, USA

R.F. Powers, Pacific Southwest Research Station, **Redding**, **CA**, USA

T. Pukkala, University of Joensuu, Joensuu, Finland

FE. Putz, University of Florida, Gainesville, FL, USA

L Rasmussen, **RISQ**, Roskilde, Denmark

D.D. Reed, Michigan Technological University, Houghton, MI, USA

R. Sands, University of Canterbury, Christchurch, NZ

J.A. Stanturf, **Stoneville**, MS, USA

O. Sziklai, University of British Columbia Vancouver, B.C., Canada

J.R. Toliver, USDA Forest Service, Washington, DC, USA

K. von Weissenberg, University of Helsinki, Helsinki, Finland

D. Whitehead, Manaaki Whenua **Landacre** Research.

Lincoln, New Zealand

Publication information: forest Ecology and Management (ISSN 0378-1127). For 1999 volumes 111-122 are scheduled for publication. Subscription prices are available upon request from the Publisher. Subscriptions are accepted on a prepaid basis only and are entered on a calendar year basis. Issues are sent by surface mail except to the following countries where air delivery via SAL mail is ensured: Argentina, Australia, Brazil, Canada, Hong Kong, India, Israel, Japan, Malaysia, Mexico, New Zealand, Pakistan, PR China, Singapore, South Africa, South Korea, Taiwan, Thailand, USA. For all other countries airmail rates are available on request. Claims for missing issues should be made within six months of our publication (mailing) date.

Orders, claims, and product enquiries: please contact the Customer Support Department at the Regional Sales Office nearest you:

New York: Elsevier Science, PO Box 945, New York, NY 10159-0945, USA; Tel. (+1) (212) 833 3734 [toll free number for North American Customers: 1-888-4ES-INFO (437-4636)]; fax: (+1) (212) 833 3880; e-mail usinfo-f@elsevier.com

Amsterdam: Elsevier Science, PO Box 211, 1000 AE Amsterdam, The Netherlands; Tel.: (+31) 20 485-3757; fax: (+31) 20 485 3432; e-mail nlinfo-f@elsevier.nl

Tokyo: Elsevier Science, 9-15 Higashi-Axabu 1-chome, Minato-ku, Tokyo 108, Japan; Tel. (+81) (3) 5581 5033; fax (+81) (3) 5561 5047; e-mail: info@elsevier.co.jp

Singapore: Elsevier Science, No. 1 Temasek Avenue, #17-01 Millenia Tower, Singapore 039192; Tel. (+65) 434 3727; fax: (+65) 337 2230; e-mail: asiainfo@elsevier.com.sg

Rio de Janeiro: Elsevier Science, Rua Sete de Setembro 111/16 Andar, 20050-002 Centro, Rio de Janeiro - RJ, Brazil; phone: (+55) (21) 509 5340; fax: (+55) (21) 507 1991; e-mail: elsevier@campus.com.br [Note (Latin America): for orders, claims and help desk information, please contact the Regional Sales Office in New York as listed above]

Factors affecting salamander density and distribution within four forest types in the Southern Appalachian Mountains

Craig A. Harper^{a,*}, David C. Guynn, Jr.^b

^a*Department of forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN 37901, USA*

^b*Department of Forest Resources, Clemson University, Clemson, SC 29634, USA*

Abstract

We used a terrestrial vacuum to sample known area plots in order to obtain **density** estimates of salamanders and their primary prey, invertebrates of the forest floor. We sampled leaf litter and measured various vegetative and topographic parameters within four forest types (oak-pine, oak-hickory, mixed mesophytic and northern hardwoods) and three age classes (0–12, 13–39, and ≥ 40 years) over two field seasons within the **Wine** Spring Creek Ecosystem Management area in western North Carolina. We found salamanders preferred moist microsites across all forest types with the highest salamander densities **occurring** on sites with a northern and/or eastern exposure and within northern hardwood forests. Salamander densities were lowest on 0–12-year plots, yet were equal on 13–39 and ≥ 40 -year plots, suggesting a much quicker recovery from the impact of clearcutting than reported by previous researchers. Overall invertebrate densities did not influence salamander density or distribution although, plots in which salamanders were captured, harbored significantly higher numbers of snails than plots in which salamanders were not captured. We discuss the importance of calcium to salamanders and snails as a possible source thereof. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Salamander density; Invertebrate density; Southern Appalachian Mountains, Terrestrial vacuum

1. Introduction

Salamanders occur in many southern Appalachian habitats; however, factors influencing their density and spatial arrangement are not fully understood. Past research has looked at forest management (Pough et al., 1987; Ash, 1988; Petranka et al., 1993), soil pH (Wyman and Hawksley-Lescault, 1987; Wyman and Jancola, 1992), moisture and temperature of the forest floor (Heatwole, 1962; Jaeger, 1980; Wyman and Hawksley-Lescault, 1987), and vegetation and land-form characteristics (Heatwole, 1962; Pough et al.,

1987; DeGraaf and Rudis, 1990) as factors influencing salamander density and distribution within a variety of habitats. However, few researchers have examined the spatial relationship between salamanders and their primary prey – invertebrates of the forest floor.

Our study was initiated to examine abundance, biomass and diversity of macro-invertebrates of the forest floor and correlate that information with vegetation and topographic parameters. These data were collected as a part of study, investigating silvicultural strategies for improving wild turkey brood range. In addition to invertebrates, we incidentally captured salamanders in our leaf-litter samples. Consequently, we were able to look at the spatial relationship

*Corresponding author.

between salamanders and invertebrates of the forest floor, as well as surrounding vegetative and topographic parameters.

2. Methods and materials

This study was conducted on the **Wine** Spring Creek Ecosystem Management area (**35°1 1'00"N, 83°36'30"W**) and surrounding watersheds on the **Wayah** Ranger District in the Nantahala National Forest in western North Carolina. Mean annual precipitation for this area (≈ 4530 ha) during the study was 1917 mm and the mean annual temperature = **10.4°C**.

Based on continuous inventory stand conditions (CISC) silvicultural data obtained from the **Wayah** District **Office**, forests within the study area were placed into four broad types. These types were comprised of similar combined forest types, as designated by the USDA Forest Service: oak-pine (**chestnut-oak-scarlet-oak** & **chestnut-oak-scarlet-oak-yellow-pine**, upland-hardwoods-white-pine, **white-pine-upland-hardwoods**, and white-pine); oak-hickory (**white-oak-northern-red-oak-hickory**, northern red oak); mixed mesophytic (**cove-hardwoods-white-pine-hemlock**, hemlock-hardwoods, **yellow-poplar-white-oak-northern red oak**); and northern hardwoods (sugar-maple-beech-yellow birch). Forest types were divided into three age classes (O-12, 13-39, ≥ 40 years), thereby creating 12 strata. All stands had been subjected to even-aged forest management, using clearcutting as the regeneration method.

Vegetative characteristics and topographic parameters (i.e. aspect and elevation) were measured within each stratum using 0.04 ha circular plots. Plots were located randomly within each stratum, with the number of plots per stratum determined by the **amount** of the study area encompassed by age class. Percentage herbaceous cover by **lifeform** (i.e. forb, fern, grass, etc.) was determined by the line intercept method (Smith, 1990), using three transects (11.3 m) radiating from plot center to plot perimeter at 0°, 120° and 240°. In addition, litter depth was recorded with a metric rule at four locations within each plot, and canopy coverage was recorded with a densiometer (Lemmon, 1957) at the center, top and bottom (according to slope) of each plot. Understory

woody stem (< 1.4 m in height) density was recorded within a 40.0 m^2 circular plot nested at the center of each **0.04-ha** plot.

Five leaf-litter samples were collected 15 m from each plot center at 0°, 60°, 120°, 240° and 300°. These five samples per plot were treated as **subsamples** and averaged; thus, each **0.04-ha** plot was our sampling unit for invertebrates and salamanders. **Leaf-litter** samples were collected via vacuum using a 0.10 m^2 bottomless box with a lid (Harper and Guynn unpublished data). Each sub-sample was collected by a researcher, pacing 15 m out **from** the plot center and placing the box in front of him, thus capturing invertebrates within a known area. In order to avoid flushing flying invertebrates, the researcher would move slowly the last few paces, then quickly place the box on the forest floor. Next, the researcher would open the box lid while another worker would place the nozzle of the vacuum over the box. All vegetation, leaf litter, sticks and debris down to mineral soil, and fauna associated with those materials were vacuumed into cheesecloth sample bags.

The sample bags with content were oven-dried for 48 h at 60°C (Murkin et al., 1994). Content of sample bags was emptied into white trays under bright lighting, where salamanders and invertebrates were **separated** and picked from the litter using sieves and tweezers. Salamanders and invertebrates were then identified and weighed and the remaining litter content weighed. Sampling was conducted through June and July 1995 and 1996.

One hundred and twenty **0.04-ha** plots were used to collect vegetation and topographic data. Six-hundred leaf-litter sub-samples were collected within these plots. According to area represented within the study site, five plots were measured within each **0–12-year** forest stratum, 10 plots within each **13–39-year** forest stratum, and 15 plots within each ≥ 40 -year forest **stratum**.

Salamander density among all plots was tested for differences with respect to forest type and age class, using a **chi-square** test of independence, as well as, non-parametric **Kruskal-Wallis** procedure (SAS, 1990). Salamander density among all plots was tested for differences by aspect using **ANOVA** within the GLM procedure of SAS (1990). Because of **heterogeneity** of variances, salamander data were **transformed** by square root plus 0.5 (Steel and Torrie,

1980); however, results for transformed data were the same as for non-transformed data, therefore **non-transformed** densities are reported. Aspect was divided into four categories: **N (316–45°)**, **E (46–135°)**, **S (136–225°)**, and **W (226–315°)**. Pearson correlation coefficients were calculated for relationships between, salamander density, herbaceous cover, leaf-litter depth and weight and invertebrate density and weight using the **CORR** procedure within SAS. Also, plots in which we caught salamanders were tested against plots, where no salamanders were captured for differences in invertebrate abundance and biomass by invertebrate class using **MANOVA** within the GLM procedure. The **univariate** procedure within SAS was used to evaluate the distribution of invertebrate data, and Hartley's test was used to evaluate homogeneity of invertebrate variances. All invertebrate classes were distributed normally, except **Isopoda** (which was skewed low because of an absence from many plots); and all invertebrate classes displayed homogeneity of variances, except Isopoda and Gastropoda (which were slightly heterogeneous). Because of these cases of non-normality and unequal variances, all invertebrate data were transformed by square root plus 0.5 (Steel and Torrie, 1980), in order to meet the assumptions for **MANOVA**. Since the test results were identical for the non-transformed and transformed data, we present the non-transformed data for the clarification reasons. The significance level for all tests was **p=0.05**.

3. Results

A total of 48 salamanders were captured within the leaf-litter samples. Salamanders captured included, jordan's (*Plethodon jordani* **n=32**), mountain dusky (*Desmognathus ochmphaeus* **n=8**), seepage (*Desmognathus aeneus* **n=7**), and Blue Ridge two-lined (*Eurycea wilderae* **n=1**). Six classes of invertebrates were collected: Arachnida (including **Acari**, **Amblypygi**, Araneae, Gpiliones, and Pseudoscorpiones); Chilopoda (including Geophilomorpha, **Lithobiomorpha**, and Scolopendromorpha); Diplopoda (including Glomerida, Julida, Polydesmida, and Spirobolida); Gastropoda (including Pulmonata); Hexapoda (including Coleoptera, Collembola, Diptera, **Hemiptera**, Homoptera, Hymenoptera, Lepidoptera,

Table 1
Salamander densities (SE) on the Wme Spring Creek Ecosystem Management area

	Mean density per m ²
Forest type (# of plots)	
oak-pine (n=30)	0.4 (0.2)
oak-hickory (n=30)	0.9 (0.3)
mixed mesophytic (n=30)	0.7 (0.2)
northern hardwoods (n=30)	1.2 (0.3)
Age class	
0-12 (mean=5.8 years; range 3-12; n=20)	0.3 (0.2)
13-39 (mean=21.5 years; range 13-30 ; n=40)	0.9 (0.2)
≥40 (mean=78.8 years; range 40-135; n=60)	0.9 (0.2)
Aspect^a	
north (n=27)	1.3 (0.4) A
east (n=25)	1.2 (0.4) A
south (n=36)	0.3 (0.1) B
west (n=32)	0.6 (0.2) A,B
overall (n=120)	0.8 (0.1)

*Densities with the same letter **are** not significantly different (**p>0.05**).

Mecoptera, Neuroptera, Grthoptera, Plecoptera, **Pso-coptera**, and Siphonaptera); and Malacostraca (including Isopoda).

Estimated density of salamanders was the highest in northern hardwood stands and lowest in oak-pine stands (Table 1); however, there were no significant (**p=0.140**) differences between forest types. Among age classes, estimated density within **13–39-year** stands was equal to that in the **≥40-year** stands (Table 1). The **0–12-year** stands contained lower densities of salamanders, though not significantly (**p=0.257**) lower. The overall estimated density within the **Wine** Spring Creek Ecosystem Management area was 0.8 **salamanders/m²**. Considering aspectwise mean salamander density decreased from areas with expected high moisture to areas with expected lower moisture (Table 1). A **significantly (p=0.049)** higher number of salamanders was found on north- and **east-facing** plots, as opposed to those with a southern aspect. There was no significant correlation between salamander density and leaf-litter depth (**r=0.136**; **p=0.140**; **n=120**), litter weight (**r=0.088**; **p=0.341**; **n=120**), percent herbaceous cover (**r=0.133**; **p=0.146**; **n=120**), understory woody-stem density (**r=0.137**; **p=0.138**; **n=120**), or canopy coverage (**r=0.075**; **p=0.416**; **n=120**).

Table 2

Invertebrate densities (SE) and biomass(g) (SE) per m² within the four forest types on the Wine Spring Creek Ecosystem Management area

Invertebrate class ^a	Oak-pine	Oak-hickory	Mixed mesophytic	No. hardwoods
Arachnida				
density	6.0 (0.8)A	6.5 (0.9)A	6.3 (0.8)A	6.8 (0.9)A
biomass	0.0300 (0.0062)A	0.0373 (0.0056)A	0.0305 (0.0060)A	0.0393 (0.0075)A
Chilopoda				
density	7.5 (1.0)A,B	6.6 (1.1)A,B	4.7 (0.8)B	8.5 (1.2)A
biomass	0.0279 (0.0061)A	0.0317 (0.0074)A	0.0213 (0.0049)A	0.0283 (0.0050)A
Diplopoda				
density	21.1 (2.9)B	32.3 (6.1)B	44.6 (7.1)A	29.3 (4.3)B
biomass	0.4742 (0.0816)B	0.6067 (0.1232)A,B	0.9144 (0.1506)A	0.5663 (0.1090)B
Gastropoda				
density	54.6 (7.0)A	35.7 (5.9)B	59.5 (5.1)A	55.1 (6.9)A
biomass	0.9201 (0.2184)A	0.8266 (0.1787)A	1.2106 (0.2156)A	1.0539 (0.1907)A
Hexapoda				
density	26.3 (7.0)A	18.1 (2.4)A	15.6 (2.6)A	17.8 (1.6)A
biomass	0.1180 (0.0174)A	0.1262 (0.0196)A	0.1016 (0.0180)A	0.1536 (0.0273)A
Malacostmca				
density	4.3 (1.4)B,C	1.4 (0.5)C	5.2 (1.4)B	11.0 (2.9)A
biomass	0.0109 (0.0035)B	0.0040 (0.0015)B	0.0164 (0.0041)B	0.0310 (0.0092)A
Overall				
density	119.9 (10.3)A,B	110.6 (11.1)B	135.9 (9.8)A	128.5 (11.2)A,B
biomass	1.5811 (0.2571)A	1.6326 (0.2387)A	2.2947 (0.2345)A	1.8726 (0.2279)A

^a Densities and biomass within each invertebrate class with the same letter are not significantly different ($p > 0.05$).

Overall estimated invertebrate density was the highest within mixed mesophytic stands, though only significantly higher ($p = 0.020$) than that in oak-hickory stands (Table 2). Various differences in invertebrate density and biomass were discovered among invertebrate classes according to forest type. Invertebrate density decreased with stand age (Table 3). Overall invertebrate abundance was significantly higher ($p = 0.035$) within 0-12 vs. ≥ 40 -age stands. Also, estimated invertebrate biomass was higher in the 0-12 than 13-39 or ≥ 40 -year stands however, the difference was not significant ($p = 0.299$). Significant differences among invertebrate classes by forest-stand age included higher densities of gastropods ($p = 0.0001$) in 0-12 and 13-39-age stands than ≥ 40 -age stands; and higher densities of isopods ($p = 0.014$) in 0-12 than ≥ 40 -age stands (Table 3).

Among all strata, there was a significant positive correlation between salamander density and invertebrate density ($r = 0.224$; $p = 0.014$; $n = 120$). There was however, no significant relationship between salamander density and invertebrate biomass ($r = 0.138$; $p = 0.134$; $n = 120$). By invertebrate class, there was a significant positive correlation between salamander

density and arachnids ($r = -0.194$; $p = 0.033$; $n = 120$) and gastropods ($r = 0.189$; $p = 0.039$; $n = 120$). When plots in which salamanders were captured ($n = 33$) were compared to plots in which we did not capture salamanders ($n = 87$), plots with salamanders contained significantly ($p = 0.0058$) higher densities of invertebrates (Table 4). Among invertebrate classes, plots in which invertebrates were caught had a higher estimated density of all six invertebrate classes, including significantly ($p = 0.0053$) higher densities of Gastropods.

4. Discussion

Our data show a preference by salamanders for moist site conditions. This should be expected as terrestrial salamanders require moist skin for gas exchange (Duellman and Trueb, 1986), and search-out moist micro-habitats along the litter-soil interface during dry conditions (Heatwole, 1962; Jaeger, 1980). Moist site conditions are common on northeastern exposures and lower portions of slopes in the higher elevations of the southern Appalachians. Accordingly, we found salamander densities to be the highest on

Table 3

Invertebrate densities (SE) and biomass (g) (SE) per m² within the three forest age classes on the Wine Spring Creek Ecosystem Management area

Invertebrate class ^a	Forest-age class		
	0-12	13-39	>40
Arachnida			
density	4.8 (0.9)A	6.5 (0.6)A	6.9 (0.7)A
biomass	0.0202 (0.0050)A	0.0371 (0.0059)A	0.0371 (0.0046)A
Chilopoda			
density	6.6 (1.3)A	7.4 (1.0)A	6.5 (0.7)A
biomass	0.0170 (0.0046)A	0.0325 (0.0053)A	0.0273 (0.0044)A
Diplopoda			
density	42.0 (9.9)A	24.0 (2.7)B	33.6 (3.9)A,B
biomass	0.5338 (0.0962)A	0.4886 (0.0880)A	0.7771 (0.0987)A
Gastropoda			
density	57.6 (7.4)A	67.1 (6.0)A	38.5 (3.7)B
biomass	0.6873 (0.3011)A	1.2640 (0.1978)A	0.6873 (0.1009)B
Hexapoda			
density	19.7 (3.5)A	19.9 (4.4)A	19.1 (2.6)A
biomass	0.0995 (0.0143)A	0.1369 (0.0171)A	0.1253 (0.0170)A
Malacostraca			
density	9.8 (2.5)A	6.3 (2.2)A,B	3.5 (0.7)B
biomass	0.0286 (0.0078)A	0.0167 (0.0068)A,B	0.0105 (0.0019)B
Overall			
density	140.5 (14.3)A	131.1 (9.1)A,B	108.2 (7.2)B
biomass	2.1261 (0.3569)A	1.9758 (0.2316)A	1.6646 (0.1436)A

^a Densities and biomass within each invertebrate class with the same letter are not significantly different ($p > 0.05$).

plots (across forest types) with northern and eastern exposures (Table 1).

Slopes with a southern aspect receive more direct sunlight annually are therefore, hotter and the litter layer drier. On our study site, oak-pine stands are predominant on these drier slopes and present additional adverse conditions for salamanders. Soil and leaf-litter pH is generally lower within stands with a large conifer and/or ericaceous shrub (e.g. *Kalmia latifolia*, which is abundant within oak-pine stands on our study site) component (Foote and Jones, 1989, DeGraaf and Rudis, 1990). Soil pH, between 3.5 and 4.0 may limit salamander distribution and continued exposure can be lethal (Wyman and Jancola, 1992). In addition, the litter layer in coniferous stands usually is thinner (DeGraaf and Rudis, 1990), and thus, dries more rapidly than deeper deciduous litter layers. In South Carolina, considerably fewer salamanders were captured within pine stands than in oak-hickory stands (Bennett et al., 1980), and Wyman and Jancola (1992) reported higher densities of amphibians in a beech (*Fagus grandifolia*) than in coniferous forests in New

York. This factor also may influence salamander densities within the mixed mesophytic stands, we sampled, as hemlock (*Tsuga canadensis*) was common in the overstory (present in 19 out of 30 plots).

Salamanders were abundant, particularly, within northern hardwood forests on our study area. Northern hardwood stands in our study area averaged 1391 m in elevation and occurred on broad, north-facing slopes. Soil moisture was not measured on our plots, yet from our leaf-litter samples, it was evident that the litter layer within northern hardwood stands was never 'dry', providing salamanders with a hospitable environment. Pough et al. (1987) discovered above-ground activity of salamanders was positively correlated with leaf-litter depth in upland forests of New York. A deeper litter layer may retain moisture longer, especially when facilitated by microtopographical features, and can influence the horizontal distribution of salamanders (Heatwole, 1962). We did not find a significant positive correlation between salamander density and leaf-litter depth, however, we did not have an oak-coniferous stratum as did Pough et al. (1987).

Table 4

Invertebrate densities (SE) and biomass (g) (SE) per m² within the plots where salamanders were caught and plots where no salamanders were caught on the Wine Spring Creek Ecosystem Management area

Invertebrate class ^a	Plots with salamanders	Plots without salamanders
Arachnida		
density	7.5 (0.8)A	5.9 (0.5)A
biomass (g)	0.0356 (0.0060)A	0.0337 (0.0037)A
Chilopoda		
density	7.6 (1.0)A	6.6 (0.6)A
biomass (g)	0.0357 (0.0056)A	0.0241 (0.0034)A
Diplopoda		
density	37.5 (5.2)A	29.7 (3.2)A
biomass (g)	0.6709 (0.1159)A	0.6288 (0.0714)A
Gastropoda		
density	65.6 (5.9)A	45.8 (3.7)B
biomass (g)	1.1360 (0.1917)A	0.9523 (0.1181)A
Hexapoda		
density	20.1 (3.9)A	19.3 (2.4)A
biomass (g)	0.1210 (0.0201)A	0.1264 (0.0123)A
Malacostraca		
density	6.9 (1.8)A	4.9 (1.1)A
biomass (g)	0.0203 (0.0054)A	0.0138 (0.0033)A
Overall		
density	145.1 (9.9)A	112.2 (6.1)B
biomass (g)	2.0196 (0.2313)A	1.7791 (0.1424)A

^a Densities and biomass within each invertebrate class with the same letter are not significantly different ($p > 0.05$).

Within the leaf-litter layer, salamanders play a crucial role in the food web and nutrient cycles of many forest communities (Burton and Likens, 1975). Detritivores are the main prey for salamanders, thus salamanders help to maintain diversity within invertebrate populations of the forest floor and thereby facilitate litter decomposition. On our study area, overall invertebrate densities were high in all forest types and forest-age classes, with few significant differences. Because of this, we do not believe salamanders are limited by invertebrate abundance, or that salamanders inhabit particular forest types because of invertebrate populations. However, we do believe that abundance of certain invertebrates (e.g. snails) may be an influencing factor on salamander distribution within otherwise suitable habitats in the Wine Spring area.

As ectotherms, salamanders are particularly efficient at converting nutrients and biomass of low-order detritivores into a package for larger animals. As much

as 60% of the energy ingested by salamanders is converted into new biomass. Average protein concentration of terrestrial salamanders is 50%, making salamanders a highquality energy source for predators (Burton and Likens, 1975).

Our data suggest terrestrial salamanders on the Wine Spring area search out microsites with a high density of gastropods. Burton and Likens (1975) provide evidence supporting the notion snails are an important constituent in the diet of salamanders. Burton and Likens (1975) reported average calcium (Ca) content in salamanders is higher than that of all their prey except for gastropoda, diplopoda, and oribatid mites. Percentage Ca in gastropods was higher than any other prey item for salamanders at 25%; diplopods consisted of 15% Ca; and oribatid mites, 3%. No other invertebrate prey of terrestrial salamanders even approached 1% Ca. In order to reach a high Ca level, salamanders would have to consume a certain amount of prey with even higher Ca levels. This could explain why, across all forest types and age classes, plots on which we captured salamanders contained significantly higher numbers of snails than plots where salamanders were not caught. Burton (1976) studied feeding habits of four species of Plethodontidae and the land stage of *Notophthalmus viridescens* (Salamandridae), and found all five species preyed upon snails.

Diplopods were not as abundant in the diets of salamanders studied by Burton (1976) as gastropods or oribatid mites. This may be because of prey size. If the size of prey dictates what is eaten by salamanders, then prey density is a more important parameter than prey biomass in terms of habitat quality for salamanders. The majority of diplopods, we collected, were considerably larger (on the order of 4–5x) than the gastropods collected. Roughly, average diameter of snails, we collected, was <10 mm. All mites (order Acari) captured were grouped into arachnida. Although estimated densities of arachnida and diplopoda were higher within plots on which we caught salamanders, as opposed to plots where salamanders were not caught, the relationship was not significant (Table 4).

When compared with studies conducted in similar stand types, our salamander density estimates are fairly consistent with estimates from area-constrained searches (Heatwole, 1962, 0.4/m²; Jaeger, 1980, 2.2/

m^2 ; Wyman and Jancola, 1992, $0.37/\text{m}^2$) and slightly higher than those of surface-count estimates (Burton and Likens, 1975, $0.30/\text{m}^2$; Ash, 1988, $0.18/\text{m}^2$; Petranka et al., 1993, $0.33/\text{m}^2$). Although definitive conclusions cannot be made regarding salamander density and habitat use, our data suggest that salamander populations recover quickly from stand disturbance (i.e. clearcutting). Estimated salamander density in stands 13–39-year old was equal to that in older (≥ 40 years) stands (Table 1). The average age of stands sampled in the 13-39 age class was 21.5 years ($\text{SE}=0.7$). This recovery rate is much faster than 50-70 years indicated by Petranka et al. (1993).

Ash (1988) searched two recently **clearcut** (year following) and two mature forest plots in western North Carolina and found significantly fewer salamanders on recently **clearcut** plots. Litter abundance, soil moisture and changes in prey abundance were listed as possible factors contributing to lower salamander populations on recently harvested areas. Average litter depth in 0-12-year plots (2.3 cm) was significantly less ($p=0.0001$) than that of 13-39 and ≥ 40 -year plots (3.1 and 3.4 cm, respectively). This could lead to reduced litter moisture which would affect the density and distribution of terrestrial salamanders. Prey, however, was not a limiting factor for salamanders within 0-12-year plots (Table 3).

5. Conclusions

Collecting leaf-litter samples via vacuum was an efficient sampling method, as it permitted us to collect a large number of samples and sift through the contents after drying when time permitted. We used a 0.10 m^2 box for sampling, because our intention was to capture and obtain density estimates for invertebrates **only**. With this size box and number of samples taken, we were able to achieve reasonable bounds for our invertebrate density estimates. However, if sampling was conducted solely to obtain density estimates for salamanders, a larger box (e.g. 0.5 m^2) could be used **and** more samples taken to achieve smaller standard errors associated with mean density estimates. Live salamanders could be pulled from the leaf-litter samples within the sample bags quickly and easily. Salamanders captured with our vacuum were not harmed when sucked into the sample bag, thus

future researchers using this method for sampling salamander populations could count and measure the animals, either in a field or in the lab before releasing them.

Results of our study concur with previous studies concerning the apparent preference for moist microhabitats by terrestrial salamanders. Sites with northern and eastern exposures provided a more hospitable environment for salamanders. These sites were exemplified within northern hardwood stands. While, invertebrates of the forest floor were quite numerous in all available habitats, salamanders seemed to be situated in microsites with higher densities of prey, especially snails. A physiological need for Ca may make snails a necessary component in the terrestrial salamanders' diet. Our data support the notion that, microsite conditions have a greater influence on salamander density and distribution, than overall invertebrate density or biomass; however, density of certain invertebrates (e.g. snails) may have a bigger impact on salamander distribution than others.

Although, we cannot make definitive conclusions, the impact of clearcutting may not be as severe or long-lived in certain areas as some researchers believe. Future research should investigate, impacts of forest management practices with respect to stand type and aspect. Salamander populations may rebound post harvest more rapidly in areas with more suitable habitat (i.e. moist conditions) than on dry southern slopes where conditions already may be less than marginal (see Diller and Wallace, 1994).

Acknowledgements

We thank Dr. Wayne Swank, Bill Culpepper, Dr. Katherine Elliott, and Dr. Larry Nix for their input concerning study design. The USDA Forest Service and the Department of Forest Resources, Clemson University, provided financial support. Mr. James Williams, Department of Forest Resources, and Dr. Hoke Hill, Department of Experimental Statistics, Clemson University, provided help with statistical analyses. Also, we thank, Scott Langley and Chadd Hamrick for help in collecting data, as well as Chuck Still, Daniel Jones, Buck Howell, Jack Burwell, Eric Shuler, and Clint Nalley for helping sort leaf-litter samples. Theresa Harper sewed the vacuum sample

bags, and Kevin Russell aided in identifying the salamanders and provided helpful comments regarding the manuscript. Dr. Bently Wigley, Department of Aquaculture, Fisheries and Wildlife, Clemson University, and two anonymous reviewers provided several insightful suggestions on a previous copy of the manuscript.

References

- Ash, A.N., 1988. Disappearance of salamanders from clear-cut plots. J. Elisha Mitchell Scientific Society **104(3)**, 116-122.
- Bennett, S.H., Gibbons, J.W., Glanville, J., 1980. Terrestrial activity, abundance and diversity of amphibians in differently managed forest types. Am. Mid. Nat. **103(2)**, 412-416.
- Burton, T.M., 1976. An analysis of the feeding ecology of the salamanders (*Amphibia*, *Urodela*) of the Hubbard Brook Experimental Forest, New Hampshire. J. Herpetol. **10(3)**, 187-204.
- Burton, T.M., Likens, G.E., 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology **56**, 1068-1080.
- DeGraaf, R.M., Rudis, D.D., 1990. Herpetofaunal species composition and relative abundance among three New England forest types. For. Ecol. Manage. **32**, 155-165.
- Diller, L.V., Wallace, R.L., 1994. Distribution and habitat of *Plethodon elongatus* on managed, young growth forests in north coastal California. J. Herpetol. **28(3)**, 310-318.
- Duellman, W.E., Trueb, L., 1986. Biology of Amphibians. McGraw-Hill, New York, NY, 670 pp.
- Foote, L.E., Jones, Jr., S.B., 1989. Native Shrubs and Woody Vines of the Southeast. Timber Press, Portland, Oregon, 199 pp.
- Heatwole, H., 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. Ecology **43(3)**, 460-472.
- Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. Copeia **1980(2)**, 265-268.
- Lemmon, P.E., 1957. A new instrument for measuring forest overstory density. J. Forestry **55**, 667-669.
- Murkin, H.R., Wrubleski, D.A., Reid, E.A., 1994. Sampling invertebrates in aquatic and terrestrial habitats. In: Bookhout, T.A. (Ed), Research and Management Techniques For Wildlife and Habitats. Lawrence, Kansas, pp. 349-369.
- Petranka, J.W., Eldridge, M.E., Haley, K.E., 1993. Effects of timber harvesting on Southern Appalachian salamanders. Conserv. Biol. **7(2)**, 363-370.
- Pough, F.H., Smith, E.M., Rhodes, D.H., Collazo, A., 1987. The abundance of salamanders in forest stands with different histories of disturbance. For. Ecol. Manage. **20**, 1-9.
- SAS, 1990. SAS Institute, Inc., SAS Procedures Guide, Version 6, 3rd ed. Cary, North Carolina, 864 pp.
- Smith, R.L., 1990. Student Resource Manual to Accompany Ecology and Field Biology, 4th ed. Harper-Collins, New York, NY, 114 pp.
- Steel, R.G.D., Torrie, J.H., 1980. Principles of Statistics, 2nd ed. McGraw-Hill, New York, NY, 633 pp.
- Wyman, R.L., Hawksley-Lescault, D.S., 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. Ecology **68(6)**, 1819-1827.
- Wyman, R.L., Jancola, J., 1992. Degree and scale of terrestrial acidification and amphibian community structure. J. Herpetol. **26(4)**, 392-401.

Forest Ecology and Management

Submission of manuscripts.

Manuscripts should be submitted in triplicate. Authors from the Americas, Australia, New Zealand and the Pacific are requested to send their manuscripts to **Forest Ecology and Management**, Dr. Richard F. Fisher, Department of Forest Science, Texas A&M University, College Station, TX77843-2135, USA; all other authors are requested to send their manuscripts to the Editorial Office, *Forest Ecology and Management*, P.O. Box 181.1000 AD **Amsterdam**, The Netherlands.

Authors in Japan please note: Upon request, Elsevier Science Japan will provide authors with a list of people who can check and improve the English of their paper (*before submission*). Please contact our Tokyo **office:** Elsevier Science Japan, 1-9-15 Higashi-Azabu, Minato-ku, Tokyo **106-0044**, Japan: tel. **(+81)-3-5561-5033**; fax **(+81)-3-5561-5047**.

Electronic manuscripts: Electronic manuscripts have the advantage that there is no need for the rekeying of text, thereby avoiding the possibility of introducing errors and resulting in reliable and fast delivery of proofs.

For the initial submission of manuscripts for consideration, hardcopies are sufficient. For the processing of accepted *papers*, electronic versions are preferred. After *final acceptance*, your disk plus two, final and exactly matching printed versions should be submitted together. Double density (DD) or high density (HD) diskettes (3.5 or 5.25 inch) are acceptable. It is important that the file saved is in the native format of the wordprocessor program used. Label the disk with the name of the computer and wordprocessing package used, your name, and the name of the **file** on the disk. Further information may be obtained from the Publisher.

Enquiries concerning manuscripts and proofs: questions arising after acceptance of the manuscript, especially those relating to proofs, should be directed to Elsevier Science Ireland Ltd., Bay **15K**, Shannon Industrial Estate, Shannon, Co. **Clare**, Ireland. tel. **(+353-61) 471944**; fax **(+353-61) 472144**.

Advertising information: Advertising orders and enquiries can be sent to: **USA, Canada and South America:** Mr Tino de Carlo, The Advertising Department, Elsevier Science Inc., 855 Avenue of the Americas, New York, NY **10010-5107**, USA; phone: **(+1) (212) 633 3815**; fax: **(1) (212) 633 3820**; e-mail: **t.decarlo@elsevier.com** **Japan:** The Advertising Department, Elsevier Science K.K., 9-15 Higashi-Azabu 1-chome, Minato-ku, Tokyo 106, Japan; phone: **(+81) (3) 5561 5033**; fax: **(+81) (3) 5561 5047**. Europe and ROW Rachel Gresle-Farthing. **The Advertising Department, Elsevier Science Ltd., The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, UK;** phone: **(+44) (1865) 843565**; fax: **(+44) (1865) 843976**; e-mail: **r.gresle-farthing@elsevier.co.uk**

Orders, claims, and product enquiries: please contact the Customer Support Department at the Regional Sales Office nearest you:

New York: Elsevier Science, PO Box 945, New York, NY 10159-0945, USA; Tel.: **(+1) (212) 633 3730** [toll free number for North American customers: **1-888-4ES-INFO (437-4636)**]; Fax: **(+1) (212) 633 3680**; E-mail: **usinfo-f@elsevier.com**

Amsterdam: Elsevier Science, PO Box 211, 1000 AE **Amsterdam**, The Netherlands: Tel.: **(+31) 20 4853757**; Fax: **(+31) 20 4853432**; E-mail: **nlinfo-f@elsevier.nl**

Tokyo: Elsevier Science, 9-15, Higashi-Azabu 1-chome, Minato-ku, Tokyo 106-0044, Japan; Tel.: **(+81) (3) 55815033**; Fax: **(+81) (3) 5581 5047**; E-mail: **info@elsevier.co.jp**

Singapore: Elsevier Science, No. 1 Temasek Avenue, **#17-01 Millenia Tower**, Singapore 039192; Tel.: **(+65) 434 3727**; Fax: **(+65) 337 2230**; E-mail: **asiainfo@elsevier.com.sg**

Rio de Janeiro: Elsevier Science, Rua Sete de **Setembro 111/16** Andar, 20050-002 Centro, Rio de Janeiro - **RJ**, Brazil: Tel.: **(+55) (21) 509 5340**; Fax: **(+55) (21) 507 1991**; E-mail: **elsevier@campus.com.br** [Note (Latin America): for orders, claims and help desk information, please contact the Regional **Sales Office** in New York as listed above]

US mailing info: *Forest Ecology and Management* (**0378-1121**) is published monthly by Elsevier Science **B.V.** (Molenwerf 1, **Postbus 211, 1000 AE Amsterdam**). Annual subscription price in the **USA** is US\$ 2307.00 (valid in North, Central and South America), including air speed delivery. Second class postage rate is paid at Jamaica, NY 11431.

USA POSTMASTERS: Send address changes to *Forest Ecology and Management* Publications Expediting, Inc., 200 Meacham Avenue, Elmont, NY 11003.

AIRFREIGHT AND MAILING in the USA by Publications Expediting Inc., 200 Meacham Avenue, Elmont, NY 11003.

Forest Ecology and Management has no page charges

For a full and complete Guide for Authors, please refer to *Forest Ecology and Management*, Vol. 113, No. 1, pp. 105-108. The instructions can also be found on the World Wide Web: access under <http://www.elsevier.nl> or <http://www.elsevier.com>

LANDSCAPE AND URBAN PLANNING

An International Journal of Landscape Ecology,
Landscape Planning and Landscape design

Editor-in-Chief:

J.E. Rodiek, *College of Architecture, Texas A & M University, College Station, TX 77843-3137, USA*

AIMS AND SCOPE

A journal concerned with conceptual, scientific and design approaches to landscape. By emphasizing ecological understanding and a multi-disciplinary approach to analysis and planning and design, it attempts to draw attention to the interrelated nature of problems posed by nature and human use of land. In addition, papers dealing with ecological processes and interactions within urban areas, and between these areas and the surrounding natural systems which support them, will be considered. Papers in which specific problems are examined are welcome. Topics might include but are not limited to landscape ecology, landscape planning and landscape design. Landscape ecology examines how heterogeneous combinations of ecosystems are structured, how they function and how they change. Landscape planning examines the various ways humans structure their land use changes. Landscape design involves the physical strategies and forms by which land use change is actually directed. *Landscape and Urban Planning* is based on

the premise that research linked to practice will ultimately improve the human made landscape.

Editorial Advisory Board:

D. Bishop, Parkville, Vic., Australia,
G. Bolen, Wilmington, NC, USA,
D. Bruns, Schorndorf, Germany,
I.B. Byrom, Edinburgh, UK,
F.C. Daniel, Tucson, AZ, USA,
J.M. DeGraaf, Amherst, MA, USA
I.G. Fabos, Amherst, MA, USA,
J. Gonzalez Alonso, Madrid, Spain,
M. Hough, Etobicoke, ON, Canada,
P. Jacobs, Montreal, PQ, Canada,
D.S. Jones, Melbourne, Kc., Australia,
H. Lavery, Milton, Qld., Australia,
W.M. Marsh, Flint, MI, USA,
D.L. Mitchell, Dallas, TX, USA,
D.G. Morrison, Athens, GA, USA,
J.J. Nassauer, St' Paul, MN, USA,
M. Nelischer, Guelph, ON, Canada
D.D. Paterson, Vancouver, BC, Canada,
A. Ramos, Madrid, Spain,
P. Shepard, Claremont, CA, USA,
O.R. Skage, Alnarp, Sweden,
R.C. Smardon, Syracuse, NY, USA,
G. Sorta, Alnarp, Sweden,
F. Stearns, Rhinelander, WI, USA,

R.C. Szaro, Wash&ton, DC, USA,
J.W. Thomas, la Grande, OR, USA,
P.J. Trowbridge, Ithaca, NY, USA,
T.H.D. Turner, London, UK,
M.J. Vroom, Wageningen,
The Netherlands,
W.V. Wendler, College Station, TX,
USA,
B.-E. Yang, Seoul, Korea,
E.H. Zube, Tucson, AZ, USA

ABSTRACTED/INDEXED IN

Applied Ecology Abstracts,
Biological Abstracts,
Current Contents B & S,
Environmental Periodicals
Bibliography, Geobase,
Geographical Abstracts,
and Search.

1994 SUBSCRIPTION DATA

Volumes 28-30 (in 9 issues)
Subscription price:
Dfl. 1080.00 (US \$ 584.00)
Incl. Postage
ISSN 0169-2046



ELSEVIER
SCIENCE PUBLISHERS

Elsevier Science Publishers,
P.O. Box 211, 1000 AE Amsterdam,
The Netherlands
Fax: (020) 5803-203

Customers in the USA and Canada:
Elsevier Science Publishers
P.O. Box 945, Madison Square station,
New York, NY 10160-0757, USA
Fax: (212) 633-3680

The Dutch Guilder price quoted applies worldwide, except in the Americas (North, Central and South America). The US Dollar price quoted applies in the Americas only. Non VAT registered customers in the European Community should add the appropriate VAT rate applicable in their country to the price.