

# Habitat relationships of eastern red-backed salamanders (*Plethodon cinereus*) in Appalachian agroforestry and grazing systems

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Received 16 February 2007; received in revised form 3 October 2007; accepted 4 October 2007

Available online 19 November 2007

## Abstract

Woodland salamander responses to either traditional grazing or silvopasture systems are virtually unknown. An information-theoretic modelling approach was used to evaluate responses of red-backed salamanders (*Plethodon cinereus*) to silvopasture and meadow conversions in southern West Virginia. Searches of area-constrained plots and artificial coverboards that were distributed across a gradient of agricultural conversion and grazing intensity, including hardwood silvopastures, hay meadows, forest edges, and reference forests yielded 2823 salamanders between May 2004 and November 2005. Salamander presence and abundance were positively associated with increasing cover of herbaceous vegetation and negatively associated with the intensity of agricultural disturbance. Although salamander presence and abundance appeared to be negatively influenced by agricultural disturbance when compared to reference forest conditions, the occurrence of red-backed salamanders within agriculturally modified habitats indicates this species may be more resilient to forest conversion than previously thought. This study suggests that herbaceous vegetation retained within some agricultural treatments, in combination with artificial cover, may at least partially mitigate the loss of forest canopy for red-backed salamanders.

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**Keywords:** Appalachians; Agroforestry; Disturbance; Grazing; *Plethodon cinereus*; Red-backed salamanders

## 1. 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/m<sup>2</sup> (Petranka, 1998). However, many woodland salamander species are restricted to moist and cool environments under downed coarse woody debris and rocks, or in burrows (Grover, 1998; Petranka, 1998). Because of these requirements, many species are associated with microhabitat

characteristics indicative of mature and late-successional forests (deMaynadier and Hunter, 1995; Petranka, 1998). Multiple studies have suggested that clearcutting and other timber harvesting practices have caused long-term declines and localized extirpation of woodland salamanders from many southern Appalachian forests (citations in deMaynadier and Hunter, 1995; Russell et al., 2004a). However, there are data to indicate that salamander populations in both the southern and central Appalachians eventually recover from the effects of timber harvest, often within 5–24 years of cutting (citations in Russell et al., 2004a).

In the central Appalachian region, grassland management and pasture-based livestock production account for the majority of agricultural acreage and about 25% of the total regional land use (Buergler, 2004). If woodland salamander

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populations decline at least temporarily after timber harvest, conversion of forests to grasslands and pastures presumably represents a more severe and permanent disturbance. Silvopastures are gaining increased attention as viable multiple-use agricultural systems for the Appalachian forested region (Buergler, 2004). In existing forests, silvopastures are created by heavily thinning stands followed by removal of woody debris and emergent rock to promote growth of herbaceous forage and livestock safety (Buergler, 2004). In contrast with selective harvest methods, however, complete removal of surface cover and direct disturbance from livestock grazing in silvopastures may limit suitability of these habitats for woodland salamanders. Therefore, the objective of this study was to determine how red-backed salamanders responded to traditional pasture and silvopasture treatments within the central Appalachian Mountains of southern West Virginia. The *a priori* expectation was that red-backed salamander responses to forest conversion would reflect the degree to which these treatments resulted in alterations of required microclimates and microhabitats (deMaynadier and Hunter, 1995; Russell et al., 2004a).

## 2. Methods

The study was conducted at the USDA Agricultural Research Service's Appalachian Farming System Research Center (AFSRC) near Beckley, in Raleigh County, West Virginia. The AFSRC occurs within the Allegheny Mountain and Plateau physiographic province of the central Appalachians (Riedel, 2006). All work was carried out at three AFSRC experimental farms. Reba (51 ha; 884-m elevation) and School (22 ha; 884-m elevation) Farms included woodlands, ungrazed meadows, and traditional pastures. Reba Farm also included silvopasture plots that were rotationally grazed. The third site, Peters Farm (21 ha; 841-m elevation), was the least intensively managed farm, with no livestock grazing. Data were collected within 13 sites distributed across the three farms that represented a continuum of forest conversion and grazing intensity: reference woodlands ( $n = 3$ ), woodland edges ( $n = 3$ ), silvopastures ( $n = 3$ ), ungrazed hay meadows ( $n = 2$ ), and grazed pastures ( $n = 2$ ).

Reference woodland plots were  $\geq 40$  years old with no cutting for  $\geq 25$  years and no known history of grazing. Silvopastures were created from existing woodlands between 1997 and 2002 by reducing basal area (cross-sectional area of all overstory trees) from 19.1 m<sup>2</sup>/ha to 6.7 m<sup>2</sup>/ha. Ungrazed meadows and pastures had been converted from existing woodlands for  $\geq 25$  years, and pastures had been actively grazed for  $\geq 5$  years. Residual overstory trees on woodland and silvopasture plots primarily consisted of mixed mesophytic-Allegheny hardwoods (Riedel, 2006) dominated by sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and black cherry (*Prunus serotina*).

White oak (*Quercus alba*), black oak (*Q. velutina*), and blackgum (*Nyssa sylvatica*) occurred on the less mesic, somewhat drier aspects, whereas eastern hemlock (*Tsuga canadensis*) and rosebay rhododendron (*Rhododendron maximum*) dominated riparian areas. Ground cover of woodland plots consisted of herbaceous species, woody debris, and abundant emergent rock. However, essentially all woody debris and rocks were removed from silvopasture, meadow, and pasture plots. Common herbaceous or grassy species within pasture and silvopasture plots included cinquefoil (*Potentilla recta*), orchardgrass (*Dactylis glomerata*), ryegrass (*Lolium perenne*), tall fescue (*Festuca arundinacea*), and white clover (*Trifolium repens*).

Silvopastures were grazed by sheep at a density of 12–24 sheep/ha with a 5–7 day rotation and 25–35 day rest period. Traditional pastures at Reba farm were grazed by beef cattle at a density of 2.5 cattle/ha with a 3 day rotation and 27 day rest period, whereas pastures at School Farm were grazed by goats at a density of 7 goats/ha with a 2 week rotation and 30 day rest period. Ungrazed meadows and grazed pastures were mowed one and two times per year, respectively. Nitrogen–phosphate–potassium fertilizer (19–19–19) was applied to silvopastures and grazed meadows at a rate of 37 kg/ha/year. Ungrazed meadows were not fertilized during the study, although sulfur and lime historically had been applied to these sites for pH adjustment. Pesticide use was limited to applications of glyphosate herbicides along fence lines.

Between 2002 and 2004, arrays of 20 wood coverboards (Monti et al., 2000; Hyde and Simons, 2001) were established in each of the 13 sites. Because salamanders may avoid newly installed coverboards (Monti et al., 2000), arrays were established at least 1 month prior to data collection. Arrays at edge sites consisted of two rows of boards parallel to the woodland edge. One row was placed approximately 10 m inside and the other row an equal distance outside the woodland boundary. Each row consisted of 10 boards spaced approximately 15 m apart. A 4 × 5 grid of boards was established at each of the remaining 10 sites, with boards spaced approximately 15 m apart. Coverboards consisted of three white oak boards, with two boards on the bottom and one board placed on top for a total dimension of 30 cm × 46 cm × 5 cm. All surface debris was removed from under the boards so that each board lay flush against the topsoil.

Coverboards were checked weekly from 17 May to 10 August 2004, and then again 1–2 times monthly between September and December. In 2005, coverboards were checked once in March and April, weekly during 30 May–2 August, and then again monthly from September to November. Searches were performed during the day, and an attempt was made to check all boards over the course of 2 days to avoid time since rainfall effects. Salamanders were marked for individual recognition by toe-clipping or injecting a small amount of fluorescent elastomer (Northwest Marine Technology Inc., Shaw Island, WA, USA) at up

to four body locations (base of each limb; Riedel, 2006). After marking, salamanders were released next to the coverboard.

To provide an independent assessment of red-backed salamander populations and habitat characteristics, two area-constrained sampling methods were used: daytime searches for salamanders under natural cover objects along transects (Monti et al., 2000; Hyde and Simons, 2001) and opportunistic night-time surface counts (Hyde and Simons, 2001) within circular plots surrounding coverboards. Each transect and circular plot was sampled once during June–July of both 2004 and 2005. Three approximately 60 m × 3 m natural cover transects were established between and parallel to coverboard rows within each site. Each transect was searched for salamanders by turning and replacing all natural cover (e.g., logs, sticks, and rocks). Day transect surveys were conducted during 10 June–13 July 2004 and 6–14 July 2005. The type of cover object at each salamander location was recorded and a numbered flag placed at the location.

Night-time surveys for surface-active salamanders were conducted within a 3-m radius plot centered on each coverboard. Night-time surveys were initiated approximately 20 min after sunset and continued until all sites at a farm were sampled. Salamanders were hand-captured on the surface or climbing vegetation and their locations flagged, but potential cover objects or leaf litter were not disturbed. Surface counts were conducted on cool, humid nights within 24 h of precipitation when salamanders were likely to be foraging (Grover, 1998). Night surface surveys were conducted during the weeks of 11 July 2004 and 19 June 2005. Salamanders were marked and data recorded as previously described and released at the point of observation.

Habitat features within 3-m radius plots centered on each coverboard or flagged location were characterized. Within each plot the species and diameter at breast height (dbh) of all trees ≥10 cm were recorded. A spherical densiometer was used to estimate percent canopy closure above each coverboard (Lemmon, 1956). Percent cover of coarse woody debris (≥10 cm diameter), fine woody debris (<10 cm diameter), woody shrubs (≤1.5 m high), herbaceous plants, planted livestock forage, emergent rock, bare soil, and leaf litter was visually estimated in each plot. Soil samples were collected within 1 m of each coverboard for pH analyses. The humus layer was cleared away and soil samples were collected to 10 cm below the surface. Samples were placed in paper bags and air dried to a constant weight and then coarsely ground through a 2 mm sieve. Samples were then sent to the University of Wisconsin Soil and Forage Laboratory for pH measurement, which was determined by a 1:1 paste of air dried soil and deionized water using a digital ionanalyzer pH meter and combination electrode (Riedel, 2006). An electronic soil cone penetrometer was used to assess soil compaction (kPa) around each coverboard. Four readings (two each at depths of 5 and 10 cm) were taken within 1 m of each coverboard. Penetration resistance is

influenced by soil factors such as water content and bulk density. Therefore, all readings were collected within 24 h of a rain event to minimize variation in water content. The four values were averaged to determine mean soil penetrability immediately surrounding each coverboard. During salamander sampling, soil moisture and surface temperature were measured under each coverboard, natural cover object, or salamander surface location (night-time surveys). Soil temperature was measured with an IR 101 InfraScan Infrared Thermometer (La Crosse Technology, La Crescent, MN, USA). Soil moisture was measured to a depth of 12 cm with a HydroSense Portable Probe (Campbell Scientific Inc., Logan, UT, USA).

Logistic and linear regression combined with an information-theoretic approach for model selection (Burnham and Anderson, 2002; Russell et al., 2004b) were used to model habitat relationships of red-backed salamander presence and relative abundance across the continuum of forest disturbance and livestock grazing. Because few salamanders were captured during area-constrained searches, only coverboard data were used to model habitat relationships. Prior to model specification redundant variables (Spearman's  $r^2 \geq 0.70$ ) were eliminated, resulting in 16 variables for inclusion in models. Scatterplots and residual plots were examined to ensure that variables met assumptions of analyses (i.e., linearity, normality, colinearity). The square-root transformation was used on abundance data to approximate normality. Abundance was defined as the number of red-backed salamanders observed under a coverboard per year. A limited number of salamanders were not individually marked (e.g., small size), and some individuals were potentially counted more than once during a year. Recaptured individuals were excluded from analyses. Agroforestry and pasture management schemes were coded as a categorical variable representing a gradient of habitat disturbance type: woodland reference, edge, silvopasture, ungrazed meadow, and grazed meadow (i.e., least disturbed to most disturbed).

A set of 13 plausible *a priori* candidate models explaining salamander presence and abundance was developed. The constructed models were as follows: (1) ABIOTIC (%bare soil, %rock, mean soil compaction, pH), (2) CANOPY COVER (mean %canopy cover), (3) DISTURBANCE TYPE (woodland, edge, silvopasture, ungrazed meadow, grazed pasture), (4) GROUND DISTURBANCE (livestock presence, mean soil compaction + DISTURBANCE TYPE), (5) GROUND COVER (%coarse and fine woody debris, %rock, %leaf litter, %herbaceous vegetation), (6) MICROCLIMATE (%soil moisture, surface temperature), (7) OVERSTORY (tree dbh, %canopy cover, overstory tree type), (8) HERBACEOUS VEGETATION (%herbaceous vegetation), (9) SOIL (%soil moisture, pH, surface temperature), (10) VEGETATION (%herbaceous vegetation, %leaf litter, %woody shrubs + OVERSTORY), (11) HERBACEOUS DISTURBANCE (%herbaceous vegetation + DISTURBANCE TYPE), (12) MULTI-LEVEL

(%soil moisture, %canopy cover, %rock + HERBACEOUS DISTURBANCE), and (13) a global model (GLOBAL) containing all variables. The model set was analyzed separately for salamander presence and abundance using logistic and linear regression, respectively. Prior to model selection, the fit of global models was assessed by examining residuals, measures of fit, classification tables, and histograms of expected probabilities (Burnham and Anderson, 2002). Abundance of salamanders under coverboards was significantly higher in 2005 than in 2004 ( $t = -2.58$ ,  $P = 0.01$ ). Therefore, habitat relationships were modelled separately for each year.

Because the number of coverboards sampled ( $n = 260$ ) was small relative to the number of parameters ( $K$ ) in most models (i.e.,  $n/K < 40$ ), Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) was used for model selection (Burnham and Anderson, 2002). The formulas presented in Burnham and Anderson (2002) were used to calculate  $AIC_c$  for maximum likelihood (logistic regression) and least-squares (linear regression) methods. All candidate models were ranked according to their  $AIC_c$  values, and the best model (i.e., most parsimonious) was the model with the smallest  $AIC_c$  value (Burnham and Anderson, 2002). Other models were ranked relative to the best model using  $\Delta AIC_c$ , which was the difference between the lowest  $AIC_c$  value ( $AIC_{cmin}$ ) and  $AIC_c$  values from the other models. Primary inference was drawn from models within two units of  $AIC_{cmin}$ , although models within four units may have limited empirical support (Burnham and Anderson, 2002). Akaike weights ( $w_i$ ) also were calculated to determine the weight of evidence in favor of each model (Burnham and Anderson, 2002). Analyses were conducted using SPSS software (SPSS, 2005).

### 3. Results

A total of 1268 red-backed salamanders were captured under 195 of 260 coverboards (75.0%) in 2004 and 1481 salamanders under 203 of 260 boards (78.1%) in 2005. In 2004, woodland edge habitats contained the largest percentage of occupied coverboards (90%) followed by woodland reference sites (88.3%), ungrazed meadows (75%), silvopastures (71.7%), and grazed pastures (37.5%). In 2005, woodland reference sites contained the largest number of occupied coverboards (98.3%) followed by woodland edges (83.3%), silvopastures (80%), ungrazed meadows (72.5%), and grazed pastures (42.5%). In contrast, ungrazed meadows had the highest relative abundance of salamanders in 2004 and 2005, whereas grazed meadows had the lowest relative abundance of salamanders in both years (Fig. 1).

During daytime surveys of transects and night surface searches in both years, red-backed salamanders were only detected in woodland reference and woodland edge sites. Thirty-nine individual salamanders were detected during

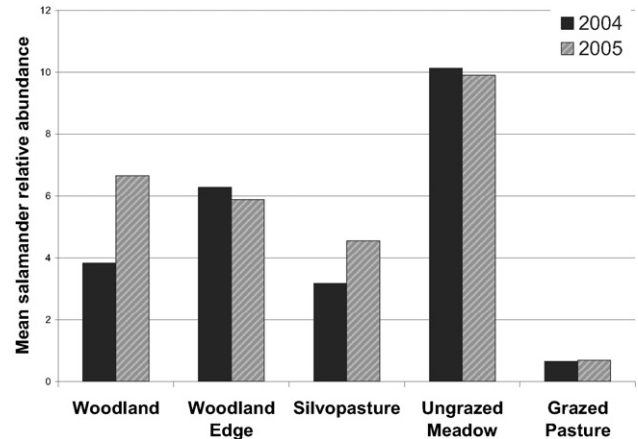


Fig. 1. Mean relative abundance of red-backed salamanders by habitat type on three Appalachian Farming Service Research Center experimental farms in Raleigh County, WV, USA, 2004–2005.

transect and night surveys in 2004, and 34 salamanders were detected in 2005. In both years, the majority of those observed were juveniles. Salamanders were found under a variety of natural cover objects, including emergent rock, and woody debris. Salamanders were captured most often under rocks in both 2004 (48% of captures) and 2005 (47% of captures), and less often under fine woody debris (33% in 2004 and 18% in 2005) and coarse woody debris (18% in 2004 and 35% in 2005). No salamanders were captured during daytime surveys while raking through leaf litter. Only one juvenile salamander was captured during night surface surveys in 2004 (on leaf litter) and no salamanders were captured during night searches in 2005.

In 2004, the best model of the 13 logistic regression models explaining salamander presence was “herbaceous disturbance” (Table 1). Salamander presence was positively associated with greater cover of herbaceous vegetation and negatively associated with the degree of habitat disturbance (Table 2). The mean percent cover of herbaceous vegetation was highest in ungrazed meadows ( $\bar{x} = 39.2 \pm 6.3\%$ ) and lowest in grazed meadows ( $\bar{x} = 0.0 \pm 0.0\%$ ). The second-best model, the single variable “disturbance type,” received limited empirical support ( $\Delta AIC_c < 4$ ; Table 1) and indicated that salamander presence decreased in increasingly disturbed habitats (Table 2). Weight of evidence ( $w_{best\ model}/w_{second\ best\ model}$ ) for the “herbaceous disturbance” model was 4.3 times greater than the “disturbance type” model, indicating relatively little uncertainty in selection of the best candidate model (Burnham and Anderson, 2002). Overall, evidence for a habitat disturbance effect on salamander presence was strong in that the sum of Akaike weights for the two supported models containing this variable was 0.85 (Table 1). The remaining 11 models explaining salamander presence in 2004 received no empirical support ( $\Delta AIC_c > 4$ ,  $w_i \leq 0.07$ ).

In 2005, the best-approximating model explaining salamander presence, and the only one to receive empirical support, was the “multi-level” model (Table 1). Salamander



Table 1

Best-approximating models ( $\Delta AIC_c \leq 4$ ) explaining influence of habitat attributes on presence (logistic regression) and abundance (linear regression) of red-backed salamanders on three Appalachian Farming Service Research Center farms in Raleigh County, WV, USA, 2004–2005

	$-2LL$	$K^b$	$AIC_c^c$	$\Delta AIC_c^d$	$w_i^e$
2004 logistic models <sup>a</sup>					
Herbaceous disturbance	246.672	6	259.004	0.000	0.692
Disturbance type	251.678	5	261.914	2.910	0.161
2005 logistic models <sup>a</sup>					
Multi-level	197.098	9	215.818	0.000	0.991
	RSS	$K^b$	$AIC_c^c$	$\Delta AIC_c^d$	$w_i^e$
2004 linear models <sup>a</sup>					
Herbaceous vegetation	165.164	3	-26.256	0.000	0.573
Multi-level	153.763	10	-25.134	1.122	0.327
Ground cover	161.409	7	-22.267	3.989	0.078
2005 linear models <sup>a</sup>					
Ground cover	230.596	7	40.449	0.000	0.379
Multi-level	223.540	10	40.712	0.263	0.333
Herbaceous vegetation	241.340	3	41.240	0.791	0.256

<sup>a</sup> See text for model variable description.

<sup>b</sup> Number of estimable parameters in approximating model.

<sup>c</sup> Akaike's Information Criterion corrected for small sample size.

<sup>d</sup> Difference between  $AIC_c$  of the current model and the best model ( $AIC_{cmin}$ ).

<sup>e</sup> Akaike weight. Probability that the current model ( $i$ ) is the best-approximating model among those considered.

presence was positively associated with increasing cover of herbaceous vegetation and overhead canopy (Table 2). This model also indicated that salamander presence was less likely in more disturbed habitat types, particularly within grazed meadows (Table 2). Weight of evidence for the “multi-level” model was 99 times greater than the next best model, “disturbance type,” indicating almost no uncertainty

Table 2

Parameter estimates ( $B$ ) and standard errors (S.E.) from the best-approximating models explaining influence of habitat attributes on presence of red-backed salamanders on three Appalachian Farming Services Research Center farms in Raleigh County, WV, USA, 2004–2005

Model	$B$	S.E.	$R^{2a}$
Herbaceous disturbance <sup>b</sup>			
Herbaceous vegetation	0.020	0.010	0.239
Woodland edges	-0.197	0.611	
Silvopastures	-0.940	0.499	
Ungrazed meadows	-1.377	0.576	
Grazed meadows	-2.356	0.525	
Multi-level <sup>c</sup>			
Herbaceous vegetation	0.033	0.012	0.391
Percent rock	-0.296	0.083	
Canopy cover	0.003	0.021	
Average soil moisture	-0.074	0.050	
Woodland edges	-5.448	1.987	
Silvopastures	-4.951	2.205	
Ungrazed meadows	-6.163	2.916	
Grazed meadows	-6.721	2.872	

Coefficients of the categorical variable disturbance type were calculated relative to the woodland reference habitat type.

<sup>a</sup> Nagelkerke  $R$  square.

<sup>b</sup> Logistic regression model explaining presence of red-backed salamanders in 2004.

<sup>c</sup> Logistic regression model explaining presence of red-backed salamanders in 2005.

in selection of the best candidate model. The remaining 12 models explaining salamander presence in 2005 received no empirical support ( $\Delta AIC_c > 9$ ,  $w_i \leq 0.01$ ).

In 2004, the best-approximating model explaining abundance of red-backed salamanders was the single variable “herbaceous vegetation” (Table 1). Salamander abundance increased with greater cover of herbaceous vegetation (Table 3). The second-best model, “multi-level,” also received strong empirical support ( $\Delta AIC_c = 1.12$ ; Table 1). A third model, “ground cover,” received only limited empirical support ( $\Delta AIC_c = 3.99$ ; Table 1). This model indicated that salamander abundance was positively associated with increased cover of herbaceous vegetation and leaf litter (Table 3). Percent cover of leaf litter was highest in woodland reference sites ( $\bar{x} = 60.4 \pm 3.4\%$ ) and absent in both grazed pastures ( $\bar{x} = 0.0 \pm 0.0\%$ ) and ungrazed meadows ( $\bar{x} = 0.0 \pm 0.0\%$ ). Weight of evidence for the herbaceous vegetation model was only about 1.7 times greater than the multi-level model, indicating some uncertainty in selection of the best candidate model. However, evidence for the effect of herbaceous vegetation on salamander abundance was strong in that the sum of Akaike weights for the three supported models containing this variable was 0.97 (Table 1). The remaining 10 models explaining salamander abundance in 2004 received no empirical support ( $\Delta AIC_c > 8$ ,  $w_i \leq 0.01$ ).

In 2005, the best-approximating model explaining salamander abundance was the “ground cover” model (Table 1). Salamander abundance was positively associated with increasing amounts of herbaceous vegetation and leaf litter (Table 3). The second-best model, “multi-level,” also received strong empirical support ( $\Delta AIC_c = 0.26$ ; Table 1). This model indicated that salamander abundance was

Table 3

Parameter estimates from the most highly supported models explaining the influence of biotic and abiotic habitat attributes on abundance of red-backed salamanders on three Appalachian Farming Service Research Center farms in Raleigh County, WV, USA, 2004–2005

Model	B	S.E.	R <sup>2a</sup>
Herbaceous vegetation <sup>b</sup>			0.299
Herbaceous vegetation	0.022	0.002	
Multi-level <sup>b</sup>			0.347
Herbaceous vegetation	0.020	0.003	
Percent rock	−0.035	0.020	
Canopy cover	−0.009	0.004	
Disturbance type	−0.289	0.133	
Ground cover <sup>c</sup>			0.191
Herbaceous vegetation	0.019	0.003	
Coarse woody debris	−0.001	0.015	
Percent rock	−0.056	0.030	
Fine woody debris	−0.006	0.010	
Percent leaf litter	0.007	0.003	
Herbaceous vegetation <sup>c</sup>			0.154
Herbaceous vegetation	0.017	0.003	
Multi-level <sup>c</sup>			0.216
Herbaceous vegetation	0.016	0.003	
Percent rock	−0.067	0.030	
Canopy cover	−0.011	0.005	
Average soil moisture	0.031	0.021	
Disturbance type	−0.499	0.155	

Coefficients of the categorical variable disturbance type were calculated relative to the woodland reference habitat type.

<sup>a</sup> Nagelkerke R square.

<sup>b</sup> Linear regression model explaining abundance of red-backed salamanders in 2004.

<sup>c</sup> Linear regression model explaining abundance of red-backed salamanders in 2005.

positively influenced by increased herbaceous cover and soil moisture, and negatively associated with increased rock cover, canopy cover, and degree of habitat disturbance (Table 3). The third-best model, “herbaceous vegetation,” also received strong empirical support ( $\Delta AIC_c = 0.79$ ; Table 1) and provided further evidence of a positive relationship between salamander abundance and density of herbaceous vegetation. Weight of evidence was similar for all three models, and the ground cover model was only about 1.2 times greater than the multi-level model, thereby indicating considerable uncertainty in selection of the best candidate model (Burnham and Anderson, 2002). Collectively, these models provide evidence for a positive effect of herbaceous vegetation and a negative effect of disturbance on salamander abundance, as the sum of Akaike weights was 0.97 (Table 1). The remaining 10 model sets explaining salamander abundance in 2005 received no empirical support ( $\Delta AIC_c > 5$ ,  $w_i \leq 0.02$ ).

#### 4. Discussion

According to the models that received empirical support for explaining both presence and abundance, red-backed

salamanders appeared to be negatively associated with agricultural habitats when compared to woodland reference sites with no ground disturbance and intact forest canopies. These results are consistent with numerous studies documenting declines in the occurrence and abundance of woodland salamanders in forest stands recently subjected to both clearcutting and selective harvest practices (deMaynadier and Hunter, 1995; Knapp et al., 2003; Russell et al., 2004a). In contrast, others have reported that woodland salamanders were not significantly affected by selective logging or firewood cutting (e.g., Ford et al., 2002; McKenny et al., 2006).

Although previous research has documented red-backed salamanders dispersing across relatively narrow bands of field (i.e.,  $\leq 55$  m; Marsh et al., 2004) or into residential areas (Gibbs, 1998), no studies have reported large numbers of woodland salamanders in permanently open, agricultural habitats. At least two factors may explain the unexpected use of meadow and silvopasture treatments by red-backed salamanders. First, all habitat models that received empirical support included the variable “herbaceous vegetation,” indicating that this microhabitat feature was a dominant influence on salamander presence and abundance. Red-backed salamanders increased within agricultural habitat types as percent cover of herbaceous vegetation increased. This was particularly apparent within ungrazed meadows, which supported the highest relative abundance of salamanders per coverboard. The presence of a dense vegetative layer (0.30–1.2 m tall) and lack of disturbance (i.e., grazing) in ungrazed meadows may have partially compensated for the loss of canopy cover, leaf litter, and woody debris after forest conversion. However, with increasing grazing intensity in the silvopasture and grazed meadow treatments, mean cover of herbaceous vegetation decreased dramatically, with consequent reductions in salamander presence and abundance. In the more arid western United States, intensive livestock grazing has been attributed to declines of California tiger salamanders (*Ambystoma californiense*) from loss of vegetative cover and soil compaction (Harvey et al., 2000), whereas light grazing does appear to be compatible with the persistence of this species (Marty, 2005). Retention of dense natural herbaceous vegetation, in combination with limited or no grazing pressure, may at least partially mitigate changes associated with conversion of forest stands to open, agricultural habitats.

Likewise, the relatively large numbers of salamanders captured along woodland edges also could be explained by the presence of dense herbaceous vegetation. Previous studies (deMaynadier and Hunter, 1998; Young and Yahner, 2003) have reported negative effects of forest edges on red-backed salamanders, with reduced numbers in comparison to more interior forest sites. Structural microhabitat variables potentially limiting to red-backed salamanders near forest edges include reduced overhead canopy and litter cover resulting in decreased soil moisture and higher temperatures (deMaynadier and Hunter, 1998). In this study,

woodland edges contained the second-highest percentage of herbaceous ground cover ( $\bar{x} = 31.8 \pm 3.2\%$ ), which may have at least partially negated these edge effects. Similarly, amphibian abundance in the upper Midwest (Nuzzo and Mierzwa, 2000) and nearby central Appalachian forests (Duguay and Wood, 2002) has been positively associated with increased cover of herbaceous vegetation in areas where forest floor habitats have been altered by grazing, clearcutting, fire exclusion, and excessive deer herbivory.

Secondly, the placement of artificial coverboards in silvopastures, meadows, and pastures undoubtedly facilitated persistence or re-colonization of red-backed salamanders on these disturbed sites. Within silvopasture, meadow, and pasture sites, essentially all natural cover objects (e.g., woody debris, surface rocks) were removed to promote forage production, leaving only the coverboards as potential refugia. Although salamanders were found under natural cover objects during transect and night-time surface searches of woodland reference and edge sites, no salamanders were detected in silvopastures, meadows, or pastures during these searches. Previous research has indicated that retention of woody debris on the forest floor may at least partially mitigate negative effects of timber harvest practices on salamanders (Grover, 1998; McKenny et al., 2006). The present study suggests that artificial cover objects may play the same role in agriculturally modified habitats (Riedel et al., 2006).

If persistence of red-backed salamanders in large pastures and silvopastures depends on the presence of dense herbaceous vegetation and coverboards, the combination of natural and artificial cover may not only partially mitigate effects of forest removal for resident salamanders but also provide temporary refugia for dispersers (Marsh et al., 2004). Red-backed salamanders tend to be highly territorial and larger individuals (i.e., older adults) have a territorial advantage (Mathis, 1990). Therefore, these artificial refugia may be particularly important for newly mature salamanders as they disperse to find new breeding territories (Marsh et al., 2004). However, coverboards may artificially attract salamanders to agricultural habitats that otherwise are unsuitable and incapable of supporting resident populations (i.e., sink habitats). Therefore, salamanders found under artificial cover may not accurately reflect typical demography (e.g., age structure, sex ratios) or physiological condition of populations under natural cover (Monti et al., 2000; Hyde and Simons, 2001; Ash et al., 2003).

The presence and often large numbers of red-backed salamanders observed in agriculturally modified habitats may indicate that this species is less sensitive to or recovers more quickly from habitat disturbance than previously thought. This ability may be associated with the unusually large range and habitat distribution of the species when compared to other woodland salamanders (Marsh et al., 2004). Red-backed salamanders often have been suggested as indicators of the status of other woodland salamanders as well as ecosystem function and integrity in general (e.g.,

Petranka, 1998; Welsh and Droege, 2001). However, if viable populations of red-backed salamanders occur in heavily disturbed habitats and are relatively insensitive to processes such as forest fragmentation (Marsh et al., 2004), the use of this species as an indicator of late-successional forest biodiversity or ecosystem integrity may need to be reevaluated.

Although the rugged topography of the central Appalachian region has restricted the development of large, widespread agricultural activity, land clearing and small farm ownership associated with second- or retirement homes has increased dramatically. Concurrently, opportunities to employ silvopastures and other agroforestry systems are increasing in the central Appalachians (Buegler, 2004). Use by small landowners of agroforestry systems that are potentially less harmful to woodland salamander populations than other forms of forest conversion could mitigate somewhat for the loss of forest cover. Moreover, results of this study suggest that retaining dense patches of herbaceous vegetation in both ungrazed meadows and pastures (i.e., protected from mowing or grazing), in combination with placement of artificial cover objects, may be useful for linking isolated patches of woodlands and accelerate the recovery of salamander populations in disturbed habitats (Mitchell et al., 2006).

## Acknowledgments

The USDA Agricultural Research Service Appalachian Farming Service Research Center (AFSRC), USDA Forest Service Northern Research Station, and University of Wisconsin–Stevens Point provided financial and logistical support of this research. We thank D. Belesky, J. Neel, and other AFSRC staff for their assistance with this work. B. Harter, M. McDougal, and M. Allen provided valuable field assistance. M. Hansen, J. Hardin, L. Werner, and two anonymous reviewers provided helpful comments and suggestions on an earlier draft of this manuscript. Animals were captured, handled, and marked in accordance with University of Wisconsin–Stevens Point IACUC standards.

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