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The Abundance of Salamanders in Forest Stands with Different Histories of Disturbance

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ABSTRACT

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Because of the importance of salamanders in forest food chains, the effects of forest management practices on populations of these animals warrant consideration. We compared the numbers and activity patterns of salamanders in areas of a deciduous forest in central New York State that had been cut selectively for firewood, or clearcut, or planted with conifers. Numbers of salamanders were lower in three recently disturbed habitats than in adjacent old-growth control stands. The frequency of above-ground activity by both species of salamanders was positively correlated with the density of understory vegetation and the depth of leaf litter. Small-scale habitat disruption associated with harvesting firewood increased the numbers of the terrestrial eft stage of the red-spotted newt (*Notophthalmus viridescens*) but had no effect on numbers of red-backed salamanders (*Plethodon cinereus*). A recently clearcut area had fewer red-backed salamanders than adjacent old-growth forest had, but the numbers of salamanders in a 60-year-old second-growth forest were indistinguishable from those in the adjacent old-growth forest. Populations of salamanders in a conifer plantation were low. Thus, salamanders seem to be resilient to limited disturbance of forests, but major changes are likely to affect populations of salamanders and, consequently, of birds and mammals that depend on salamanders for food.

INTRODUCTION

Salamanders are the most abundant vertebrate animals in many forest ecosystems, and the annual biomass production by salamanders can be a major factor in the forest food chain. In the deciduous forests of the eastern United States, population densities of the red-backed salamander (*Plethodon cinereus*) can reach 0.9–2.2 individuals/m^2 (Heatwole, 1962; Jaeger, 1980a). The

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biomass of salamanders in the Hubbard Brook Experimental Forest in New Hampshire is twice that of birds and equal to that of small mammals, and the annual production of biomass by the salamanders exceeds that of birds or mammals (Burton and Likens, 1975a,b). The importance of salamanders as food sources for both avian and mammalian predators is indicated by direct observations of predation and by the ubiquity among salamanders of defensive mechanisms directed against these predators (Brandon and Huheey, 1975; Brodie, 1977; Brodie et al., 1979; Brodie and Brodie, 1980; Jaeger, 1981; Tilley et al., 1982).

Furthermore, salamanders play a unique functional role in forest ecosystems because of their very small body sizes and their physiological characteristics. More than 80% of the species of salamanders have adult body masses smaller than 1 g, whereas most small birds and mammals weigh 20 g or more (Pough, 1980). Because they are so small, salamanders exploit prey that is too small to be utilized by birds or mammals, and they convert the biomass of the prey into packages that can be captured by larger animals (Pough, 1983). The conversion process is efficient, because salamanders are ectotherms and have the lowest metabolic rates of any terrestrial vertebrates (Feder, 1983). As a result of their high conversion efficiencies, 40–80% of the energy ingested by salamanders is used to produce new biomass (gross conversion efficiency calculated from Fitzpatrick, 1973, and from Burton and Likens, 1975a). As a consequence of these characteristics, salamanders are quantitatively and qualitatively important components of the energy flow of many forest ecosystems despite their inconspicuousness (Burton and Likens, 1975a,b; Bury, 1983), but they are rarely considered in evaluations of forest management practices (Bury et al., 1980).

Structural and vegetative characteristics of a forest that affect the temperature and moisture regimes of the forest floor are important in determining the microclimates and microhabitats that are available to salamanders (Heatwole, 1962; Heatwole and Lim, 1961). Forest management practices that open the canopy and reduce the density of understory vegetation or the depth of the leaf litter may affect the abundance and above-ground activity of salamanders. We investigated the consequences of several forest management practices by surveying the nocturnal activity of salamanders in forest stands with different histories of disturbance.

MATERIALS AND METHODS

Our study sites were in the Connecticut Hill Wildlife Management Area in Tompkins and Schuyler counties, New York (42°22′N, 76°40′W). This mosaic of abandoned farms and forest is located about 15 km SW of Ithaca, New York, and is administered by the New York State Department of Environmental Conservation. Four forest stands on Connecticut Hill were chosen to represent different kinds of disturbance: an area clearcut in 1977; a 25-year-old clearcut planted with conifers; a site from which firewood had been cut one year before our study; and a 60-year-old second-growth forest. All of these sites had been in cultivation at some time. Each stand was paired with an adjacent portion of old-growth forest that served as a control. The topography of the control plots indicated that they had never been cultivated. In each of the eight plots we established two transects, 50×2 m. The 'old growth' and 'disturbed' transects of each pair were located as close together as possible (10–50 m) to minimize differences in soil and exposure. The percentage of the 50-m transect covered by understory vegetation at a height of 1 m was measured in the center of the transect and 5 m to each side, a total of six 50-m surveys per stand. The depth of leaf litter was determined 1 m to each side of the midline of each transect at 5, 25, and 45 m from the start, giving a total of 12 measurements per stand. Soil samples were taken from the upper 5 cm of soil on 30 July and on 7 and 21 August. Equal volumes of soil from 1 m to the left and right of the midline of each transect were taken at distances of 5, 15, 25, 35, and 45 m. The subsamples at each distance were combined and returned to the laboratory in closed containers, weighed, and dried to constant weight at 60°C.

We counted the salamanders above ground on 10 nights between 27 July and 14 August, 1984. Each night one transect from each of the four disturbed stands and its old-growth control were censused. We alternated between the two transects in each stand on successive nights. Thus, each transect and its adjacent control were surveyed five times during the study.

The use of inferential statistics may constitute 'pseudoreplication' when the experimental units of interest (in this case forest stands) are not replicated (Hurlbert, 1984). In our experiment we replicated the old-growth vs. disturbed condition four times, but were unable to find replicates of the four types of disturbance. Instead, we paired each disturbed site with an adjacent old-growth site. We present three levels of analysis that provide progressively more information, possibly at the cost of increasing violations of statistical assumptions. The SAS statistical package was used for analyses (Ray, 1982) except as noted in the Results. First, we calculated descriptive statistics (mean and range of the numbers of salamanders observed in each stand), and used stepwise multiple regression to identify characteristics of the eight stands that were correlated with the abundance and activity of salamanders. Next, we compared each disturbed stand with its adjacent old growth control using a one-level nested analysis of variance (transects nested within stands). Finally, we used a two-level nested ANOVA (transects within stands within categories of disturbance) to make comparisons among different kinds of disturbance. We used Tukey's Honestly Significant Difference for these experimentwise comparisons among stands. Note that there are ecological differences among the four control stands and among the four disturbed stands. In particular, the 60-year-old second-growth forest (stand 7) has regenerated a closed canopy of deci-

TABLE 1

Numbers of salamanders and the frequency of above-ground activity

Stand		*Plethodon cinereus*				*Notophthalmus viridescens*			
Number	Description	Frequency	Mean		Range	Frequency	Mean		Range
1	Recent clearcut	3	0.3	b	0–1	7	1.7	b	0–6
2	Old growth	8	2.2	b	0–5	6	2.4	b	0–6
3	Conifer plantation	3	0.7	b	0–4	2	0.2	b	0–1
4	Old growth	5	1.5	b	0–4	10	5.3	a	1–9
5	Firewood cutting	10	1.6	b	1–3	9	1.2	b	0–2
6	Old growth	4	2.1	b	0–9	3	0.3	b	0–1
7	Second-growth forest	10	7.7	a	2–16	6	1.6	b	0–6
8	Old growth	8	4.0	a,b	0–13	7	1.6	b	0–4

Analysis of Variance

Source	df	SS	MS	F	*P*	SS	MS	F	*P*
Between categories	1	0.31	0.31	0.00	n.s.	30.01	30.01	1.21	n.s.
Among stands	6	393.98	65.66	7.26	<0.01	148.67	24.78	4.04	<0.037
Between transects	8	72.30	9.04	1.16	n.s.	49.10	6.14	1.99	n.s.
Within transects	64	499.20	7.80			197.60	3.09		
Total	79	965.99				425.39			

Frequency is the number of times one or more salamanders were observed in ten surveys of each stand. Means and ranges are presented by stands (200 m^2) because the transects within a stand did not differ significantly. Means bracketed by a line did not differ ($P > 0.05$) in pairwise comparisons of disturbed sites and controls. Means denoted by the same letter did not differ at $P = 0.05$ by Tukey's Honestly Significant Difference in an experimentwise comparison.

duous trees, and in this respect it differs from the other three disturbed habitats. This variability within categories would tend to obscure differences resulting from habitat modification.

RESULTS

Red-backed salamanders (*Plethodon cinereus*) and the terrestrial eft stage of the red-spotted newt (*Notophthalmus viridescens*) were the only species of salamanders we found in the transects; the population densities of the two species were similar (Table 1). No significant differences resulted from variation between the two transects within a stand, and the transects within stands are combined for all analyses. The characteristics of the vegetation and soil of the 16 transects are presented in Table 2.

Two measurements provide information about the effects of habitat modi-

TABLE 2

Vegetation and soil moisture of the stands surveyed

Stand	Most abundant species of trees	Ground cover (%)		Litter depth (cm)		Soil moisture (%)	
		mean	range	mean	range	mean	range
1	Recent clearcut *Populus tremuloides, Quercus borealis* *P. grandidentata, Acer rubrum*	69.1	35.5–84.8 a	1.9	0.5–3.0 b	22.5	19.3–26.4 cd
2	Old growth *A. rubrum, Q. borealis,* *Castanea dentata, Quercus alba*	54.0	28.2–80.5 ab	2.8	1.0–4.0 ab	27.2	19.2–33.8 abc
3	Conifer plantation *Picea mariana, Pinus resinosus*	9.8	0.3–35.3 b	2.7	0.5–6.0 ab	19.4	14.4–22.4 d
4	Old growth *Q. borealis, Tsuga canadensis,* *A. rubrum, C. dentata*	72.7	59.9–89.6 a	2.8	1.5–6.0 ab	31.3	21.0–44.2 a
5	Firewood harvesting *A. rubrum, Fraxinus americanus* *Pinus strobus, Fagus grandifolia*	57.2	42.1–77.9 ab	4.8	2.0–9.0 a	28.4	23.2–35.3 ab
6	Old growth *Amelanchier* sp., *P. strobus,* *A. rubrum, Acer pennsylvanicum*	43.0	19.4–64.5 ab	3.2	1.0–5.0 ab	26.1	22.9–29.1 bc
7	Second-growth forest *A. rubrum, Amelanchier* sp., *F. grandifolia, P. strobus*	24.6	17.0–33.3 ab	4.2	3.0–6.5 ab	20.6	14.2–28.5 d
8	Old growth *Q. borealis, A. pennsylvanicum,* *T. canadensis, C. dentata*	56.1	30.3–74.5 ab	3.0	0.5–5.0 ab	26.6	19.6–35.6 abc

Ground cover by understory vegetation was measured at a height of 1 m along the center of each transect and 5 m to each side. Leaf litter depth was measured at six sites within each transect, providing a total of 12 samples per stand. Soil was sampled three times during the study at 20 sites within each transect (40 sites per stand). The disturbed stands and their adjacent old-growth controls are listed sequentially. Means designated by the same letter do not differ at $P=0.05$ by Tukey's Honestly Significant Difference in an experimentwise comparison.

fications on salamander populations: the total numbers of salamanders recorded in different stands estimate the relative sizes of the populations, whereas the proportion of nights that salamanders engage in above-ground activity is related to the microclimatic characteristics of the stands. Total numbers and frequency of activity were not correlated among stands ($P > 0.05$ for both species, Kendall Rank Correlation; Sokal and Rohlf, 1969).

The frequency of above-ground activity by salamanders ranged from 20 to 100% of the surveys, and was positively correlated with the depth of the leaf litter and the percent cover of understory vegetation. Leaf litter depth explained 63% of the variance in night-to-night activity by red-backed salamanders in the eight stands ($P=0.019$); adding percent cover raised the total r^2 for the model to 0.67. For efts, percent cover entered the model first and explained 62% of the variation, and leaf litter depth entered at the second step, raising the total r^2 for the model to 0.79 ($P=0.022$). Soil moisture content was not significantly correlated with frequency of above-ground activity for either species of salamander ($P>0.76$ for both).

None of the microhabitat characteristics was significantly correlated with the abundance of red-backed salamanders or of efts. Night-to-night differences in the numbers of salamanders present were the largest source of variation in total numbers for both species, accounting for 61.0% of the variance for red-backed salamanders and 54.8% for efts. Differences among stands were the next largest sources of variation in numbers of salamanders, accounting for 37.0% of the variance for red-backed salamanders and 32.8% for efts. The second-growth forest and its adjacent old-growth control plot had the largest number of red-backed salamanders, and the recent clearcut had the fewest. Efts were most abundant in the old-growth plot adjacent to the conifer plantation and rarest in the plantation, and were more abundant in the firewood stand than in its old-growth control.

Numbers of salamanders did not differ significantly in the four old-growth stands compared to the four disturbed stands. However, the 60-year-old second-growth forest (stand 7) has reverted to a closed canopy of deciduous trees that is very like its old-growth control, and its inclusion blurs the distinction between the 'disturbed' and 'old-growth' categories. When the comparison is limited to the other three areas, both species of salamanders were more abundant in the old-growth habitats than in the disturbed sites (efts 2.7 versus 1.0, $P<0.05$; red-backed salamanders 1.9 versus 0.9, $P<0.05$).

DISCUSSION

Our survey suggests that small-scale modification of forest habitats has little detrimental effect on populations of salamanders. Indeed, the abundance of retreat sites for salamanders provided by the piles of slash in the stand cut for firewood is probably responsible for the large numbers of efts in this stand compared to the adjacent old-growth forest. In a deciduous forest in Vermont, efts, which are more tolerant of heat and dryness than are red-backed salamanders, were able to occupy areas where the canopy had been opened by logging, whereas red-backed salamanders were confined to adjacent uncut forest (Pough, 1974).

Complete removal of the forest canopy does appear to be deleterious, particularly for red-backed salamanders. We found few red-backed salamanders of either species in the 7-year-old clearcut, and clearcuts of the same age in Virginia and California also showed no evidence of repopulation (Blymer and McGinnis, 1977; Bury, 1983). Repopulation of clearcut areas by red-backed salamanders can occur, as shown by the high densities of this species in the second-growth forest in our study. (These appear to be the first data showing that salamander populations in a once-cultivated area can return to the levels seen in old-growth forest.) However, the return of red-backed salamanders appears to be slow, perhaps because the soil-litter interface is an important microhabitat for them, and its recovery is a prerequisite for repopulation of a site by salamanders. The depth of leaf litter was the best predictor of the frequency of above-ground activity by red-backed salamanders in our study, explaining 63% of the variation among stands, and studies in New Hampshire suggest that about 65 years is required to rebuild organic matter in the forest floor to precutting levels (Likens et al., 1978).

Conifer plantations of the sort represented by stand 3 in our study appear to be inimical to salamanders. Population densities of both species were low in those transects, and surface activity was observed on only two (efts) and three (red-backed salamanders) of the ten nights of the study. Only large adult red-backed salamanders were found in the conifer plantation, suggesting that the population of salamanders in this area may depend on immigration of individuals from the old-growth forest. Furthermore, significantly fewer efts were found in the conifer plantation than in the adjacent old-growth forest, despite the location of the conifers between the old-growth stand and the breeding pond that was the source of the efts. To reach the old-growth stand after they metamorphosed in the pond, efts would have to pass through the conifers or detour around them. Thus, the low population density of efts in the conifers reinforces our conclusion that this habitat is unsuitable for salamanders. The inhospitality of pure stands of conifers to salamanders may be a general phenomenon; amphibians were found to be more abundant in a natural oak-hickory stand in South Carolina than in managed pine habitats (Bennett et al., 1980).

Differences in the life histories of red-backed salamanders and efts probably lead to differences in their responses to the habitat disturbance we studied. The biology of red-backed salamanders makes this species particularly sensitive to the effects of changes in forest habitats and microhabitats: red-backed salamanders are completely terrestrial and lack an aquatic larval stage; instead, eggs are deposited in moist places in logs or beneath rocks and hatch into juveniles that are miniatures of the adults (Bishop, 1941). Thus, the forest must provide microhabitats suitable for all stages of the life history of the species. In contrast to the life-long terrestriality of red-backed salamanders, the eft stage is a terrestrial interval in the life of the red-spotted newt between an aquatic larva and an aquatic adult (Gill, 1978), and the spatial distribution of efts is determined partly by the distribution of the ponds where the adults live and reproduce.

Because plethodontids are the dominant kinds of forest salamanders (Burton and Likens, 1975b), alterations of the habitat that restrict the abundance or surface activity of plethodontids could reduce the resource base for birds and small mammals. Subtle interactions between forest management practices and salamander populations are likely to be important. Plethodontid salamanders have been described as opportunistic exploiters of moisture (Feder, 1983); when the forest is wet, plethodontids forage widely and climb understory plants and tree trunks to capture prey (Jager, 1978). At these times nearly all salamanders have full stomachs. As the forest becomes drier, the foraging activity of the salamanders is increasingly restricted and the proportion of individuals with empty stomachs rises. The salamanders are forced to remain in moist microhabitats beneath rocks and logs, and ultimately to retreat down holes into the soil where they do not feed (Jaeger, 1972, 1980a,b). Inability to forage limits the biomass conversion that is the basis for the importance of salamanders in the forest food chain. When understory vegetation and leaf litter depth are reduced, opportunities to forage above ground occur less frequently. As a result, the food intake and biomass production of salamanders can be expected to decline. Furthermore, salamanders sheltering beneath rocks or logs are probably less accessible to most predators than are salamanders in the leaf litter. Therefore, a reduction of above-ground activity by salamanders resulting from forest management practices could reduce both their numbers and availability as prey, and thereby limit their role in the food chain of a forest.

Our study indicates that woodland salamander populations are resilient to some forest management practices. They accommodate small-scale changes in the habitat with little change in population sizes and activity patterns. Aboveground activity is correlated with the density of understory vegetation and with the depth of leaf litter. Modifications of the forest that affect these characteristics of the microhabitats of the salamanders can be deleterious to salamanders, as they are to many other species of wildlife (Bury et al., 1980). At a minimum, sound management of forests requires protection of significant representative areas from all forms of manipulation to preserve habitats for species that flourish in the conditions provided by old-growth forests.

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