Effects of Edge Contrast on Redback Salamander Distribution in Even-Aged Northern Hardwoods

Richard M. DeGraaf and Mariko Yamasaki

ABSTRACT. Terrestrial salamanders are sensitive to forest disturbance associated with even-aged management. We studied the distribution of redback salamanders (*Plethodon cinereus*) for 4 yr at edges between even-aged northern hardwood stands along three replicate transects in each of three edge contrast types: regeneration/mature, sapling/mature, and poletimber/mature in northern New Hampshire. We used 2 m^2 coverboard clusters at the edge, and at 5, 10, 20, and 40 m into the younger and mature stands. Salamanders were surveyed 12 times per year from May to October, approximately once every 2 wk, usually within 24 hr of a rain event. Habitat variables included board station soil temperature, litter depth, organic layer depth, depth to soil mottling, herbaceous cover, down log cover, three classes of understory hardwood stem density [0.5–1m tall, 1–2 m tall and <10 cm dbh, and >2 m tall], softwood stem density, *Rubus*/other stem density, and overstory basal area (ba) and mean dbh. A total of 4,038 redback salamanders were detected during 432 transect counts. The mean salamander density was $0.41/m^2$ across regenerating stand transects, $0.47m^2$ across sapling transects, and 0.69 m^2 across poletimber transects. We analyzed salamander distribution by edge type, replicate, year, station (distance from edge), and their interactions. There were significant differences in salamander detections among edge types, replicates, station, and years for both counts across entire younger forest/mature forest transects and across the younger forest transect sections. There were significant interactions between edge type and distance from edge. Salamander detections were greater ($P < 0.001$) in pole/mature edges than in sapling/mature and regeneration/mature edges in all years. Counts in sapling and regeneration stands were not different. The pattern of salamander abundance was similar across all edge types: low abundance 40 m out in the younger stand, increased abundance near or at the edge, a decrease just inside the edge, peak abundance in the mature stand (20 m inside the edge), and decline at 40 m in the mature stand. Salamander counts differed among years across all transects, tracking yearly precipitation differences. Counts also varied seasonally; early spring and late summer counts were higher ($P < 0.001$) than counts in early to mid-summer and fall. Salamander counts were negatively related to total understory stem density, density of hardwood stems >2 cm tall and <10 cm dbh, and percent herb cover, and positively related to soil organic layer depth (P values <0.10). A stepwise regression model included percent herbaceous ground cover, number of hardwood stems >2 m tall and <10 cm dbh, and organic soil layer depth, and explained 29% of the variation in redback salamander counts. Our findings are consistent with reported recovery times for redback salamanders after clearcut harvesting; recovery rates even along edges may take about 30 yr. Seasonal and yearly variation must be taken into account if terrestrial salamanders are used in monitoring programs. FOR. SCI. 48(2):351–363.

Key Words: Redback salamanders, forest management, edge effects.

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Even-aged silviculture in extensively forested landscapes creates a shifting mosaic of habitats that are used by various wildlife species or groups of species over time as regenerating stands develop and mature after clearcutting. Habitat provision is a spatially and temporally dynamic process in managed forests. The sizes and juxtapositions of harvest units and mature stands are variable, and young stands that are avoided by mature forest species will provide primary habitat for such species in the future (Hagan et al. 1996). Likewise, early successional species will likely find preferred habitat when mature stands are cut. Most research on habitat use in relation to stand age in North America has focused on birds and mammals. In New England northern hardwood forests, for example, four distinct avifaunas successively breed in regenerating, sapling, poletimber, and sawtimber stands (DeGraaf 1987, 1991). Small mammals are less sensitive to forest structure than are birds (Healy and Brooks 1988, DeGraaf et al. 1991). Amphibians in northern forests are tolerant of a range of forest habitats, but are more abundant in hardwood than in coniferous stands (Pough et al. 1987, DeGraaf and Rudis 1990). Although forestry practices can have negative effects on some amphibians, maintaining sustainable populations can be compatible with timber harvesting (deMaynadier and Hunter 1995, Brooks 1999, Harpole and Haas 1999). Clearcut harvesting can result in a temporary decline in amphibian numbers (Pough et al. 1987, Petranka et al. 1993). In New England, this decline has been reported for the terrestrial-breeding redback salamander (DeGraaf and Yamasaki 1992), the wetland-breeding wood frog (*Rana sylvatica*), and mole salamanders (*Ambystoma* spp.; deMaynadier and Hunter 1998). The effects of intermediate levels of timber harvesting on amphibians are less well known (Harpole and Haas 1999) although crown thinning had no effect on numbers of redback salamanders in southern New England oak (*Quercus* spp.) forests (Brooks 1999).

Edge effects produced by the contrast between recent clearcuts and mature stands diminish during forest succession (Harris 1984, p. 131–134); such edges are ephemeral as far as breeding bird composition in New England northern hardwoods is concerned (DeGraaf 1992). The effects of edges on avian nesting success in extensively forested landscapes have been well documented (King et al. 1996, 1998), and have been recently found to be species-specific (Flaspohler et al. 2001). Furthermore, in a review of edge studies conducted in extensive northern hardwood/conifer forest landscapes, Manolis et al. (2000) concluded that all avian nest studies with sufficient power reported edge effects. The effects of forest fragmentation—habitat loss, isolation, and edge effects—in agricultural landscapes have been documented for passerine birds (Gates and Gysel 1978, Whitcomb et al. 1981, Brittingham and Temple 1983) and on vascular plants (Ranney et al. 1981, Palik and Murphy 1990, Fraver 1994). It does not appear, however, that significant fragmentation effects occur in extensively forested landscapes managed for timber (Small and Hunter 1988, Yahner and Scott 1988, DeGraaf 1992, McGarigal and McComb 1995, Hagan et al. 1996).

Terrestrial salamanders, despite their small sizes, nocturnal activities, and fossorial habits that render them inconspicuous, are the most abundant vertebrates in many temperate forest ecosystems (deMaynadier and Hunter 1995). For example, Heatwole (1962) and Jaeger (1980) reported redback salamander densities of 0.9 and 2.2 individuals/m^2, respectively, in the eastern U.S. deciduous forest. Salamander biomass in a northern hardwood forest in New Hampshire was estimated to be twice that of the bird community in the breeding season and nearly that of the small mammal community (Burton and Likens 1975a); in southern Appalachian forests, salamander biomass might exceed that of all other vertebrates combined (Hairston 1987). A study of streamside old growth forest in the southern Appalachians yielded conservative estimates of total salamander density of 18,486 individuals/ha and wet biomass of 16.53 Kg/ha (Petranka and Murray 2001). Terrestrial salamanders are important components of forest floor detritus-based food webs, where they are consumers of small invertebrate prey (Pough 1983). Salamanders likely play a unique role in forest nutrient cycling by regulating the populations of soil invertebrates that mechanically break down organic material (Burton and Likens 1975b, Hairston 1987, Wyman and Hawksley-Lescault 1987). Within the forest floor detritus food web, terrestrial salamanders are top predators that regulate populations of soil microfauna, e.g., hymenoptera, collembola, aroneida, and other insect larvae (Fraser 1976, Jaeger 1972; see deMaynadier and Hunter 1995 for review). Finally, plethodontid salamanders may serve as indicator taxa for monitoring forest ecosystems because of their high sensitivity to perturbations (Vitt et al. 1990), their relative ease of sampling, syntopic occurrence with many other species, and their midlevel positions in the food web (Welsh and Droege 2001).

Terrestrial salamanders have several characteristics that render them sensitive to abrupt transitions in microhabitat and microclimate that occur across forest edges (see reviews by deMaynadier and Hunter 1995, Saunders et al. 1991, and Murcia 1995). Close contact with forest floor substrates, moist permeable skins that must remain cool and moist for respiration (Feder 1983), and poor dispersal capabilities (Stebbins and Cohen 1995) may render forest salamanders especially sensitive to local changes in microhabitat (deMaynadier and Hunter 1998). Furthermore, abundances of forest salamanders have been positively correlated with the amount and quality of coarse woody debris (Bury and Corn 1988, Welsh and Lind 1991, Petranka et al. 1994), litter depth and moisture (Pough et al. 1987, Wyman 1988, DeGraaf and Rudis 1990, Dupuis et al. 1995), understory vegetation density (Pough et al. 1987, Aubry and Hall 1991), and overstory canopy closure (Corn and Bury 1991, Welsh and Lind 1995), suggesting that many of the structural habitat changes induced by forest management probably have important effects on local terrestrial salamander populations (deMaynadier and Hunter 1998). For example, the abundance of redback salamanders increased significantly with increasing distance from clearcut edges in five conifer-dominated mature mixed-wood stands in Maine (deMaynadier and Hunter 1998).

In this study, we examined the distribution of redback salamanders by stand type and distance from mature forest edge created by even-aged timber harvesting in northern hardwood forests in New Hampshire. Our objectives were to (1) delineate edge effects by determining to what extent the effects of clearcutting extend into younger and mature forest, (2) determine how edge effects change as clearcut stands mature, (3) examine the relationships between salamander abundance and habitat structure across a gradient of stand ages in New England northern hardwoods, and (4) evaluate seasonal and yearly differences in salamander detectability.

Study Area

The study was conducted on the Bartlett Experimental Forest (BEF), part of the White Mountain National Forest (WMNF) in north-central New Hampshire. Soils of the region are typically stony, sandy, and acidic (Hoyle 1973), but vary greatly due to glaciation and topography. In the area of this study, the soils were classified as fine sandy loams on both valley bottom and mountain side land-type associations (S. Fay, soil scientist, WMNF, pers. comm.). Total annual precipitation ranges from 1,016 to 1,778 mm per year, with 36 to 48% falling as snow (NOAA 2000). Mean frost-free period for BEF is roughly 90 to 120 days (NOAA 2000). The region's current mature forest resulted from logging during 1882–1892 (Belcher 1980) and from selective removals in old-growth stands (Blum 1961). Mature stands in this study were at least 95 yr old, regeneration stands were 2–9 yr old, sapling stands 25–27 yr old, and poletimber stands 38–60 yr old in 1993. All stands were at elevations from 250 to 550 m, on slopes <24°.

Mature stands contained American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), with paper birch (*B. papyrifera*), white ash (*Fraxinus americana*), red maple (*A. rubrum*), red spruce (*Picea rubens*), and hemlock (*Tsuga canadensis*) occurring in varying minor proportions. Younger stands were composed of the same species and also included pin cherry (*Prunus pensylvanica*), aspen (*Populus tremuloides* and *P. grandidentata*), striped maple (*A. pensylvanicum*), hobblebush (*Viburnum alnifolium*), Canada yew (*Taxus canadensis*), elderberry (*Sambucus pubens*), and raspberry (*Rubus* sp.).

Methods

Salamander Sampling

The relative abundance of redback salamanders was surveyed during 1993–1996 using cover boards (DeGraaf and Yamasaki 1992, Fellers and Drost 1994, Davis 1997). Numbers of redback salamanders under boards have been correlated with independent indices of abundance in New England (DeGraaf and Yamasaki 1992). Also, the surface catch of terrestrial salamanders has been strongly correlated with the estimation of absolute population size in the southern Appalachian (Smith and Petranka 2000). Surveys were conducted along three replicate transects across each of three edge conditions: mature/regeneration, mature/sapling, and mature/poletimber. The nine edges were each located across a different clearcut; 18 different stands, ≥0.2 km apart, were used in the study. Board clusters (stations) were systematically placed after randomly choosing stand edges and transect locations. Transects were perpendicular to the edge, 80 m long, and extended 40 m into each stand. At the midpoint on the edge, and at points 5, 10, 20, and 40 m in each stand, a cluster of 5 air-dried hemlock boards, 2 m long, 25 cm wide, and 2.5 cm thick (45 boards/transect) were placed side by side, about 0.5 m apart and in close contact with the litter for their entire length. Boards were placed on the litter in 1990 to simulate fallen woody debris (DeGraaf and Yamasaki 1992) and were left undisturbed for 3 yr before sampling began to allow the boards to weather. During salamander sampling, all boards were carefully lifted on one edge, the number of salamanders recorded by species, and the boards carefully replaced. Salamanders were not handled except in a few instances where closer inspection was needed for species identification.

Sampling was conducted 12 times per year from May through October at approximately 2 wk intervals and usually within 24 hr of a rain event. Because surface foraging activities of plethodontid salamanders are regulated by forest moisture levels (Jaeger 1978, Feder 1983), all boards were checked on a single day to avoid effects of time-since-rainfall in all sampling periods. Board station soil and air temperatures were recorded at one station on both treated and mature sides of each transect at the time of salamander sampling and averaged by transect.

Habitat Variables

Habitat was characterized in 1990–1991 using the stations as sampling foci. Trees >10 cm dbh were tallied by 2.54 cm class using a 10 factor variable-radius prism plot located at each 20 m board cluster (2/transect). Understory woody stems >0.05 m tall and <10 cm dbh were counted by species and 3 height classes (0.5–1.0, 1.1–2, >2m) on 3 permanent, circular 1.6 m^2 plots per board cluster. Understory plots were offset 90° to each side of the transect at a distance of 10 m from the center of the board clusters at the 5, 10, 20, and 40 m stations. There were 24 plots/transect (total = 216). In addition, species and percent cover of herbaceous ground cover and woody seedlings <0.5 m tall were recorded on circular 4.04 m^2 (milacre) plots centered on the offset plots at the 5, 10, 20, and 40 m stations. There were 16 plots/transect, 144 total.

We dug two small holes near each station with as little disturbance as possible to estimate undecomposed litter depth, soil organic layer depths (O_i, O_e, and O_a), and depth to mottling to the nearest 2 mm. Undecomposed litter depth was measured under the weight of a clipboard in order to standardize the observation. The partially decomposed O_i, the typically brownish humus O_e, and the blackish thoroughly decomposed O_a layer depths were then summed. Mottling in the soil indicated the depth to a seasonal water table. There were 16 samples/transect, 144 total.

The percent cover of down logs was estimated by tallying all logs >15 cm in diameter and >0.5 m long encountered along two 1 × 10 m belt transects perpendicular to each station (edge stations excluded). The length and midpoint width of logs within the dimensions of the belt transect were recorded; their areas calculated, summed and divided by the area of the transect to obtain the percent coverage.

Statistical Analyses

We used SAS in a multifactor analysis of variance to assess the influence of edge type (regeneration/mature, sapling/mature, poletimber/mature), year of observation, and station on the distribution of salamanders. In this analysis, replicates were treated as random, and station locations (distances from edge) were treated as fixed but recognized as being nested within edge types. The observations over time were repeated measures, and the highest order interaction of replicates with distance and time variables were assumed to be negligible. For an assessment of year, station, and edge types, averages across dates in a year were used. Seasonal effects were examined in separate analyses for each year, incorporating possible effects due to transect type and distance, because the 12 survey dates were not the same each year. Pairwise comparisons among the different levels of each factor were carried out using Tukey's method. We used a square root transformation on the salamander counts because they were from non-normal distributions. Similar conclusions were obtained using the transformed and untransformed data; therefore the reported results are based on the untransformed data (Conover 1980).

Correlation and regression analyses were used to assess the influence of habitat variables on total salamander counts over the course of the study. A simple correlation was formed for each habitat variable with the number of salamanders and a test for zero correlation, equivalently zero slope in a linear regression of salamander count on the habitat variable, was carried out. Residual analyses were run to ensure that the model was reasonable and that other factors not used in the model (e.g., stand type) were not needed. Stepwise regression analysis was used to build a model for predicting salamander counts from habitat variables. We used Mann-Whitney two-sample rank tests to examine the differences in microhabitat characteristics between treated and mature stands in each edge type.

We used SYSTAT to test the serial randomness of periodic observations of salamanders at the 81 board stations using a mean square successive difference procedure. We also used a two-sample *t*-test to assess the relationship of two roughly equal categories of total salamander observations (0–8 and ≥9 salamanders per transect) and average soil temperature under board stations along transects (Zar 1984).

Results

Salamander Populations

A total of 4,038 redback salamanders were detected during 432 transect counts (9 transects × 12 counts per year × 4 yr) conducted over the study period (Table 1). Other species detected were 1 dusky (*Desmognathus fuscus*), 7 two-lined *(Eurycea bislineata)*, and 4 spring salamanders *(Gyrinophilus porphyriticus)*, 3 garter snakes *(Thamnophis sirtalis)*, and 2 unknown snakes. The overall mean number of salamanders per station was 1.04 (SE = 0.02), with counts ranging from 0–7. All 81 board stations yielded salamanders over the 4 yr, although one regeneration and one sapling station had 0 counts in 2 of the 4 yr. Placement of cover boards alters habitat structure; nevertheless, periodic counts of 60 of 81 board stations (74%) were determined to be random observations. The mean density of redback salamanders detected under cover boards was $0.41/m^2$ across regenerating/mature transects, $0.47/m^2$ across sapling/mature transects, and $0.69/m^2$ across poletimber/mature transects.

A four-way ANOVA analyzed salamander distribution by treatment (edge type), replicate, station, year, and their interactions (Table 2). There were significant differences in salamander detections among edge types, replicates, station, and years, for both counts across entire mature forest–younger forest transects (Table 2a) and across the younger forest transect sections (Table 2b). There were significant interactions between edge type and station for counts both across the entire transects and across the younger forest transect (Figure 1). Salamanders were more abundant ($P > 0.001$, Tukey HSD pairwise comparisons) in the pole–mature edge type than in sapling–mature and regeneration–mature edge types in all years. Salamander counts in sapling and regeneration stands were not different (Tukey HSD).

Salamander counts differed among years across all transects (Figure 2). Salamander counts in 1994 and 1996 were similar ($P = 0.692$) as were those in 1993 and 1995 ($P = 0.201$). Counts in 1993 and 1995 each were different from those in both 1994 and 1996. In addition to significant yearly variation, redback salamander detections varied significantly within season. Early spring and late summer counts were higher ($P < 0.001$) than counts in early- and mid-summer and fall (Figure 3). Total transect salamander counts ranged from 0 to 29 per observation period. Higher salamander counts (≥9 per transect) occurred when soil temperatures along transects were cooler (early spring and late summer) than during the summer ($t = 3.81$, $df = 430$, $P < 0.001$) (Figure 4).

Habitat Structure

Overstory basal areas ranged from 0.6–8.4 m^2 on treated (young) sides of transects to 9.9–11.8 m^2 on mature sides of transects. Mean dbh of live trees >10 cm tall ranged from 8.9 –19.1 cm on treated (young) sides of transects to 22.6–31.5 cm on mature sides of transects. Total density of understory stems (hardwood, softwood, and other) >0.5 m tall and <10 cm dbh was highly variable between the treated and mature sides of transects and not different ($P = 0.56$), though the individual hardwood height categories were not quite significantly different ($P = 0.14$) (Table 3). The density of pin cherry and *Rubus* stems was greater on the treated (young) side of the regeneration transects ($P < 0.01$). Density of hardwood stems >2 m but <10 cm dbh was greater on the treated (young) side of the sapling transects ($P < 0.01$). Total density of understory stems (hardwood, softwood, and other) >0.5 m tall and <10 cm dbh was greater on the mature side of the pole transects ($P = 0.02$). Mean percent cover of down logs >15 cm in diameter was greater on the mature side of transects ($P = 0.03$) and on the mature side of pole transects

Table 1. Mean (SE) counts[a] and yearly totals of redback salamanders under 2.0 m^2 cover board stations during May–October across three types of stand edges in even-aged northern hardwoods, Bartlett, New Hampshire, 1993–1996 (0 m = edge; positive stations = mature side of transect; negative stations = younger side of transect).

	Station (distance from edge)									
Edge type	–40 m	–20 m	–10 m	–5 m	0 m	5 m	10 m	20 m	40 m	Total
Regeneration										
1993	0.33	0.47	0.25	0.42	0.97	0.53	0.83	1.25	1.56	0.74
	(0.10)	(0.13)	(0.08)	(0.11)	(0.21)	(0.12)	(0.15)	(0.17)	(0.25)	(0.06)
1994	0.56	0.56	0.56	0.72	1.39	0.61	1.19	1.72	1.78	1.01
	(0.14)	(0.12)	(0.12)	(0.16)	(0.26)	(0.16)	(0.20)	(0.29)	(0.31)	(0.07)
1995	0.03	0.36	0.36	0.33	0.56	0.22	0.78	1.22	0.94	0.53
	(0.03)	(0.14)	(0.12)	(0.08)	(0.13)	(0.11)	(0.17)	(0.23)	(0.19)	(0.05)
1996	0.44	0.72	0.64	0.64	1.06	0.94	1.36	1.56	1.33	0.97
	(0.12)	(0.20)	(0.14)	(0.14)	(0.21)	(0.21)	(0.20)	(0.22)	(0.24)	(0.07)
Total	0.34	0.53	0.45	0.53	0.99	0.58	1.04	1.44	1.40	0.81
	(0.05)	(0.08)	(0.06)	(0.06)	(0.10)	(0.08)	(0.09)	(0.12)	(0.13)	(0.03)
Sapling										
1993	0.50	0.36	0.78	0.86	1.06	0.81	0.61	1.22	0.92	0.79
	(0.11)	(0.12)	(0.15)	(0.18)	(0.21)	(0.16)	(0.13)	(0.19)	(0.17)	(0.06)
1994	0.44	0.78	0.69	1.33	1.44	1.00	1.06	1.42	1.25	1.05
	(0.09)	(0.23)	(0.13)	(0.24)	(0.21)	(0.20)	(0.17)	(0.25)	(0.19)	(0.07)
1995	0.58	0.39	0.67	0.67	0.53	0.53	0.78	1.06	0.72	0.66
	(0.13)	(0.15)	(0.14)	(0.18)	(0.12)	(0.13)	(0.16)	(0.21)	(0.19)	(0.05)
1996	0.78	0.81	1.17	1.11	1.72	0.97	1.39	1.78	1.39	1.24
	(0.17)	(0.15)	(0.21)	(0.23)	(0.26)	(0.13)	(0.22)	(0.22)	(0.21)	(0.07)
Total	0.58	0.58	0.83	0.99	1.19	0.83	0.96	1.37	1.07	0.93
	(0.06)	(0.08)	(0.08)	(0.10)	(0.11)	(0.08)	(0.09)	(0.11)	(0.10)	(0.03)
Pole										
1993	1.06	1.25	1.08	1.44	1.53	1.06	0.83	1.06	1.08	1.15
	(0.19)	(0.26)	(0.20)	(0.28)	(0.25)	(0.20)	(0.15)	(0.19)	(0.20)	(0.07)
1994	1.06	1.56	1.50	2.19	1.44	1.56	1.47	1.67	2.00	1.61
	(0.17)	(0.25)	(0.26)	(0.25)	(0.23)	(0.25)	(0.24)	(0.21)	(0.29)	(0.08)
1995	0.56	0.67	1.53	1.25	0.78	0.92	1.25	1.00	1.06	1.00
	(0.14)	(0.15)	(0.27)	(0.16)	(0.17)	(0.20)	(0.27)	(0.16)	(0.16)	(0.06)
1996	0.81	1.64	1.56	2.00	1.75	1.75	1.78	2.64	1.67	1.73
	(0.15)	(0.23)	(0.22)	(0.25)	(0.22)	(0.23)	(0.26)	(0.27)	(0.25)	(0.08)
Total	0.87	1.28	1.42	1.72	1.38	1.32	1.33	1.59	1.45	1.37
	(0.08)	(0.12)	(0.12)	(0.12)	(0.11)	(0.11)	(0.12)	(0.12)	(0.12)	(0.04)
Yearly total										
1993	68	75	76	98	128	86	82	127	128	868
x (SE)	0.63	0.69	0.70	0.91	1.19	0.80	0.76	1.18	1.18	0.89
	(0.08)	(0.11)	(0.09)	(0.12)	(0.13)	(0.09)	(0.08)	(0.11)	(0.12)	(0.04)
1994	74	104	99	153	154	114	134	173	181	1,186
x (SE)	0.68	0.96	0.92	1.42	1.43	1.06	1.24	1.60	1.68	1.22
	(0.08)	(0.12)	(0.11)	(0.14)	(0.13)	(0.12)	(0.12)	(0.14)	(0.16)	(0.04)
1995	42	51	92	81	67	60	101	118	98	710
x (SE)	0.39	0.47	0.85	0.75	0.62	0.56	0.94	1.09	0.91	0.73
	(0.07)	(0.09)	(0.12)	(0.09)	(0.08)	(0.09)	(0.12)	(0.12)	(0.10)	(0.03)
1996	73	114	121	135	163	132	163	215	158	1,274
x (SE)	0.68	1.06	1.12	1.25	1.51	1.22	1.51	1.99	1.46	1.31
	(0.09)	(0.12)	(0.12)	(0.13)	(0.13)	(0.12)	(0.13)	(0.14)	(0.13)	(0.04)
Grand total	257	344	388	467	512	392	480	633	565	4,038
x (SE)	0.59	0.80	0.90	1.08	1.19	0.91	1.11	1.47	1.31	1.04
	(0.06)	(0.06)	(0.06)	(0.04)	(0.06)	(0.06)	(0.06)	(0.07)	(0.07)	(0.02)

[a] n = 12 counts/yr, May–Oct.

(P = 0.05). Litter and organic layer depths and the soil depth to mottling were similar between treated (young) and mature sides of transects (P > 0.32). Mean herb cover percent was similar between treated (young) and mature sides of transects (P = 0.28) (Table 3).

Salamander counts were negatively related to total understory stem density, density of hardwood stems >2 cm tall and <10 cm dbh, and positively related to percent herb cover and soil organic layer depth (P values < 0.10) (Table 4). Because the habitat variables are themselves correlated, stepwise regression was run to develop a model of combined habitat variables for predicting redback salamander counts in even-aged northern hardwoods. The resulting model included percent herbaceous ground cover, number of hardwood stems >2 m and <10 cm dbh, and organic layer depth, and explained 29% of the variation in salamander abundance (Table 5).

Discussion

Redback Salamander Distribution in Relation to Edge

Forest regeneration harvests lower the abundance of plethodontid salamanders in both coniferous (Grialou et al. 2000) and deciduous forests (Herbeck and Larsen 1999).

Table 2. ANOVA of redback salamander counts (averaged across 12 survey dates/yr) by edge type, replicate, station (distance from edge), year, and possible interactions for mature-young forest transects, and younger forest transects, Bartlett, New Hampshire, 1993–1996.

	Mature-young forest transects			Younger forest transects		
Source	DF	*F* value	*P*	DF	*F* value	*P*
Edge type	2	80.23	0.0001	2	110.12	0.0001
Replicate	6	6.25	0.0001	6	18.27	0.0001
Station	8	22.02	0.0001	3	17.72	0.0001
Year	3	51.22	0.0001	3	17.24	0.0001
Edge*station	16	4.23	0.0001	6	3.66	0.0040
Edge*year	6	1.75	0.1125	6	0.83	0.5545
Station*year	24	1.76	0.0225	9	1.90	0.0712
Edge*station*year	48	0.85	0.7351	18	1.04	0.4380
Rep*station (edge)	48	9.29	0.0001	18	7.98	0.0001
Rep*year (edge)	18	2.95	0.0002	18	2.14	0.0165

In the present study, abundance of redback salamanders increased significantly as stands developed from regeneration to saplings and by the poletimber stage was not different from those in adjacent mature stands. Regeneration stands were <10 yr old at the beginning of the study; sapling stands were 25 to 27 yr old. Redback salamander counts differed between sapling-mature and poletimber-mature edge types, so recovery to preharvest levels may require about 30 yr even along silvicultural edges. Reductions of plethodontid salamander populations in response to clearcutting are fairly temporary in the northeastern United States, however, if site conversions are not involved. For example, in southern Quebec, redback salamander populations had recovered between 30 and 60 yr after clearcutting (Bonin 1991). In New York, no differences in abundance of redback salamanders were reported between a 60-yr-old second-growth forest and an adjacent old-growth stand (Pough et al. 1987). In northern New Hampshire, the number of redback salamanders detected under cover boards did not differ between poletimber stands 40–50 yr old and adjacent sawtimber stands 80–100 yr old (DeGraaf and Yamasaki 1992). The results of the present study are consistent with the recovery times reported from northeastern North America; redback salamander abundance was initially depressed after even-age management, but there were no differences in abundance between poletimber stands 35 to 60 yr old and mature stands >95 yr old.

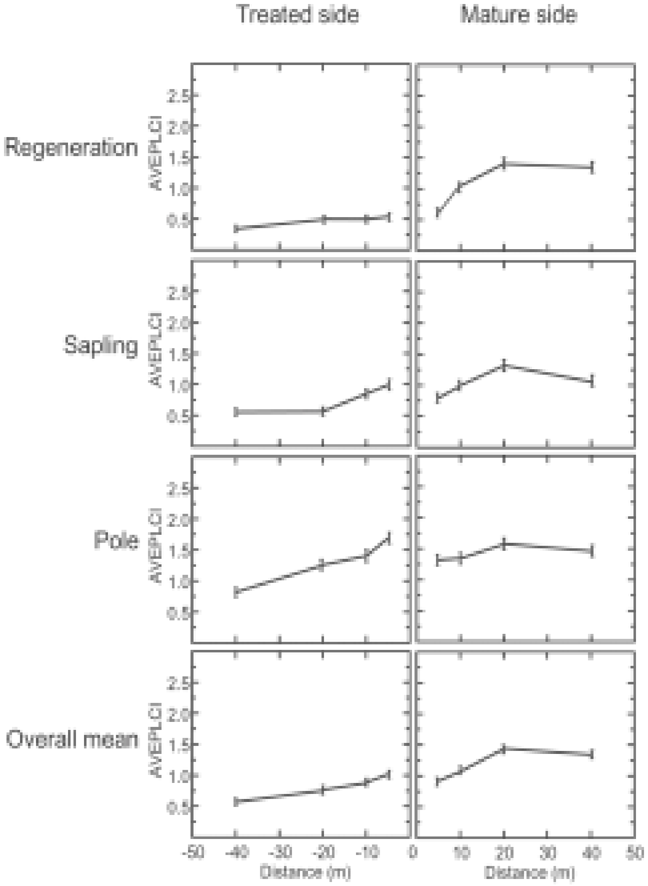

Figure 1. Mean redback salamander abundance per 2 m^2 cover board station across silvicultural edges produced by clearcutting in New England northern hardwoods, Bartlett, NH, 1993–1996.

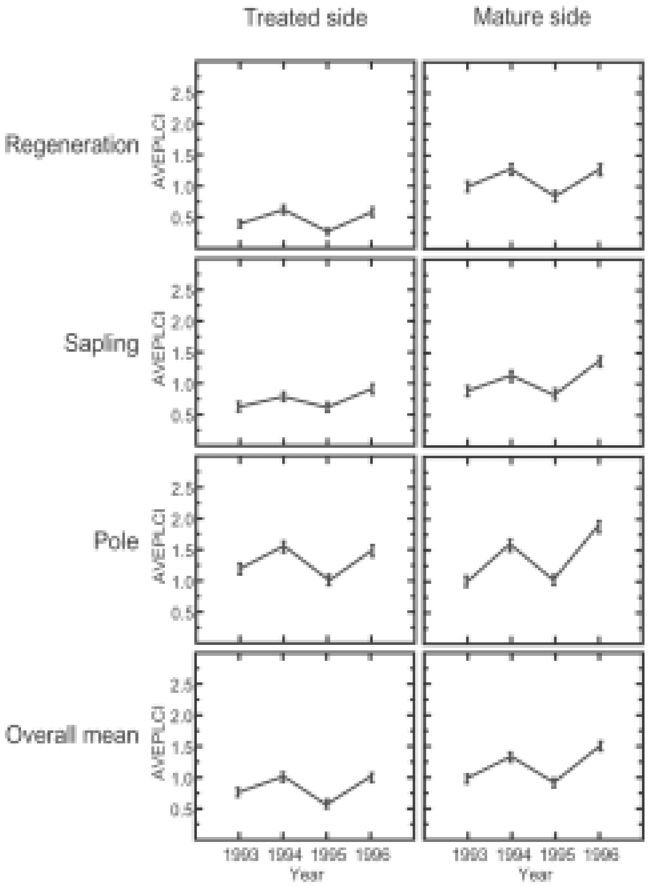

Figure 2. Mean yearly redback salamander abundance per 2 m^2 cover board station across silvicultural edges produced by clearcutting in New England northern hardwoods, Bartlett, NH.

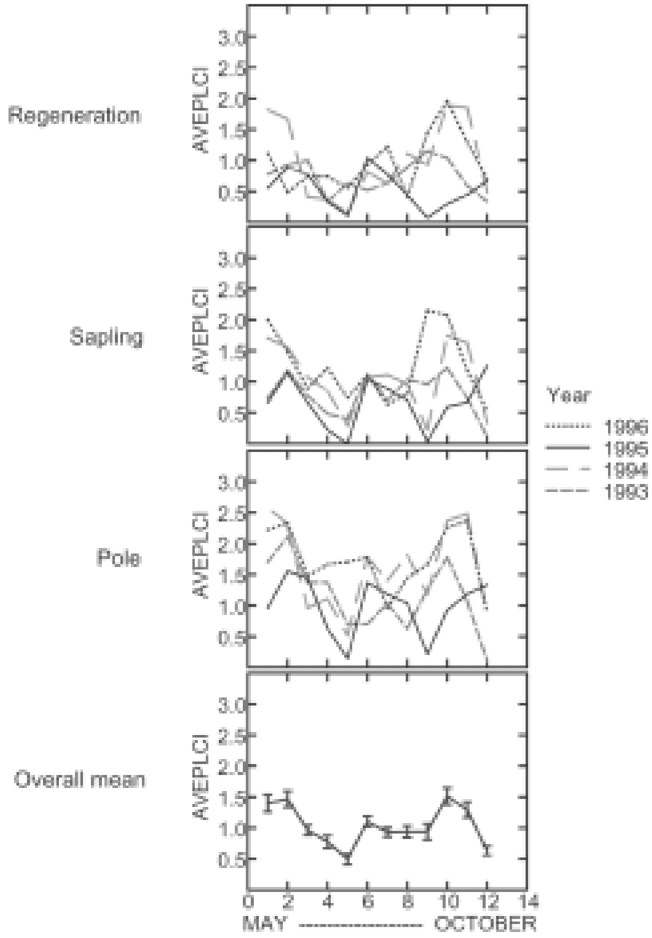

Figure 3. Seasonal (May–October) abundance of redback salamanders per 2 m^2 cover board station in New England northern hardwoods, Bartlett, NH, 1993–1996.

In the Southeast, recovery of salamander populations in intensively managed pine forests occurs more quickly than that reported for the Northeast. Recovery of four salamander species to preharvest levels was lowest on 0- to 12-yr-old plots but equal on 13–39 and ≥40-yr-old plots (Harper and Guynn 1999). In the Pacific Northwest, the western redback salamander (*Plethodon vehiculum*) did not differ in abundance in 45 Douglas-fir stands 55 to 730 yr old; all stands originated after fire, and the youngest age-category (55–80 yr) was about the rotation age of many stands in eastern North America (Aubry et al. 1988). Western redback salamanders were 3–6 times more abundant in old-growth stands 380–500+ yr old than in younger stands of logging origin (Dupuis et al. 1995). However, abundance of redback salamanders, and of amphibians in general, is lower in coniferous than in deciduous forest in eastern North America (DeGraaf and Rudis 1990, Wyman and Jancola 1992).

DeGraaf and Yamasaki (1992) reported that average redback salamander density under cover boards in northern New Hampshire was 0.7/m^2, less than half the average density (1.55/m^2) in the present study. Likely reasons for the differences are the 2 m^2 area of cover board stations in the present study compared to 0.3 m^2 area, and the 4 yr data set in the present study compared to 1 yr in DeGraaf and Yamasaki (1992). The seven-fold increase in cover board area yielded a two-fold increase in estimated density; we believe that 1.55 redback salamanders/m^2 is probably closer to the actual density than the 0.7/m^2 reported earlier because of the larger cover board stations, longer survey period, and more intensive sampling with respect to edge distance and season. The calculated redback salamander density of 15,500/ha in the present study is very close to the conservatively calculated density of 18,486 individuals/ha (all species) in the southern Appalachians. This density is seven times that reported for the Hubbard Brook Experimental Forest (Burton and Likens 1975a).

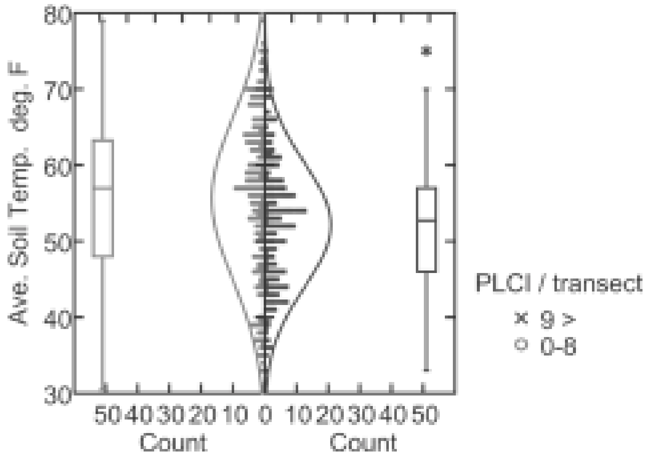

Figure 4. Redback salamander counts in two categories, 0–8 and ≥9 individuals per transect, in relation to surface soil temperature beneath cover boards in New England northern hardwoods, Bartlett, NH, 1993–1996.

Within-stand treatments have been shown to have slight effects on redback salamander populations compared to clearcuts. For example, in southern New England, reduction of hemlock (*Tsuga canadensis*) stocking to 60% of preharvest levels in green tree salvage in hemlock-hardwood stands resulted in ephemeral reductions in salamander abundances, which increased within a few years of logging (Brooks 2001). In southwestern Virginia, the relative abundance of terrestrial salamanders was significantly lower after group-cut, shelterwood, leave-tree harvests, and clearcut, but not after understory removal (Harpole and Haas 1999). Neither crown thinning nor understory removals by high densities of white-tailed deer (*Odocoileus virginianus*) affected redback salamander populations in Massachusetts oak forests (Brooks 1999).

Patterns of redback salamander distribution across silvicultural edges have not been as intensively studied as the general effects of timber harvesting methods or responses to seral stages. Our results show a fairly consistent pattern across three degrees of edge contrast produced by clearcutting in New England northern hardwoods. Relative abundances of redback salamanders increased on the younger sides of edges as stands progressed from regeneration to sapling to poletimber stages. Also, the pattern of salamander abundance was similar across all three degrees of edge contrast: low abundance 40 m out in the younger stand, increased abundance near or at the edge, a decrease just inside the edge, peak abundance in the mature stand 20 m inside the edge, and decline at 40 m in the mature stand (Figure 1). Two untested

Table 3. Summary statistics for microhabitat characteristics at salamander board stations by transect type, measured in 1990; Bartlett, NH (*n* = 72 stations, edge stations excluded).

Transect type	Microhabitat characteristics	Treated mean	Mature mean	Transect mean	Overall mean
Regeneration	Stand age in 1993				
	Rep 1	9	100+		
	Rep 2	8	100+		
	Rep 3	2	100		
	Ground layer				
	Litter depth (cm)	2.24 (0.41)	2.34 (0.29)	2.29 (0.25)	
	Organic layer depth (cm)	6.84 (1.14)	9.25 (1.19)	8.04 (0.85)	
	Depth to mottling (cm)	37.89 (0.66)	37.31 (1.29)	37.60 (0.71)	
	Herb cover (%)	16.56 (2.90)	22.74 (5.01)	19.65 (2.92)	
	Down log cover (%)	1.28 (0.44)	1.44 (0.47)	1.36 (0.32)	
	Understory layer				
	Hardwood stems 0.5–1 m	12,286.55 (3,204.40)	6,263.39 (1,579.76)	9,274.975 (1,856.49)	
	Hardwood stems 1–2 m <10 cm dbh	1,4036.89 (3,900.04)	3,603.59 (994.84)	8,820.229 (2,248.77)	
	Hardwood stems > 2 m	18,961.80 (4,721.42)	3,723.71 (1,298.51)	11,342.77 (2,873.57)	
	Hardwood stems/ha	45,285.3 (11,181.7)	13,590.72 (3,662.1)	29,438 (6,635)	
	Softwood stems/ha	1,166.8 (459.4)	1,544.4 (744.8)	1,355.6 (429.7)	
	Rubus/other stems/ha	16,610.8 (3,958.6)	789.2 (417.1)	8,700 (2,552.1)	
	All understory stems/ha	63,062.9 (14,633)	15,924.4 (4,722.1)	39,501 (8,982.7)	
	Overstory layer				
	BA m^2	0.6 (0.06)	11.8 (1.6)		
	Mean dbh (cm)	8.9	29.2		
Sapling	Stand age in 1993				
	Rep 1	25	100+		
	Rep 2	26	100+		
	Rep 3	27	111		
	Ground layer				
	Litter depth (cm)	3.16 (0.24)	3.06 (0.33)	3.11 (0.20)	
	Organic layer depth (cm)	6.92 (0.89)	6.59 (0.79)	6.76 (0.58)	
	Depth to mottling (cm)	38.74 (0.53)	37.43 (1.57)	38.08 (0.82)	
	Herb cover (%)	14.37 (3.54)	17.18 (3.39)	15.77 (2.41)	
	Down log cover (%)	0.65 (0.39)	1.00 (0.37)	0.83 (0.26)	
	Understory layer				
	Hardwood stems 0.5–1 m	1,647.37 (355.75)	2,350.92 (621.61)	1,999.14 (357.81)	
	Hardwood stems 1–2 m	823.67 (131.71)	1,132.55 (239.78)	978.11 (137.61)	
	Hardwood stems >2 m <10 cm dbh	5,371.05 (684.58)	3,397.68 (896.32)	4,384.39 (588.65)	
	Hardwood stems/ha	7,842.1 (744.8)	6,881.1 (969.4)	7,361.7 (606.1)	
	Softwood stems/ha	51.4 (36.8)	51.4 (36.8)	128.7 (52.4)	
	Rubus/other stems/ha	0	0	0	
	All understory stems/ha	7,893.5 (735.6)	7,087.2 (993.1)	7,490.5 (610.1)	
	BA m^2	6.2 (2.2)	9.9 (1.5)		
	Mean dbh (cm)	17.5	31.5		

(continued)

hypotheses offer plausible explanations for the patterns we observed. Although we did not mark individuals and our transects extended only 40 m to either side of the edge, such a pattern of abundance is not inconsistent with movement from (at least the edges of) the disturbed site toward the mature stand after clearcutting. Perhaps two shorter movements by different groups of individuals are involved: movement from the disturbed site to the forest edge and movement from the forest edge into the mature stand, and eventual dispersal from the mature stand into the younger stand by the poletimber stage. The total distance involved is 60 m. Alternatively, individuals moving from the mature stands may "pile up" (J. Petranka, pers. comm.) at the edges because conditions there (e.g., higher temperatures, increased light, or reduced humidity) discourage movement into regenerating or sapling stands. Consistent with studies of forest bird communities in the Northeast (e.g., DeGraaf 1992, Thompson and Capen 1988), no forest amphibians were shown to have edge affinities in northern New England (deMaynadier and Hunter 1998). In that study, the relationship between total salamander abundance and station was greater for recent clearcuts than that for older ones, suggesting a stronger negative response by salamanders to newly harvested edges.

Terrestrial salamander populations have been shown to decline in dry environments produced by logging (Petranka et al. 1993, 1994). The question of whether the animals perish on site, disperse to more hospitable conditions, or persist on site in a subterranean, lowered state of activity, has been posed but not tested (de Maynadier and Hunter 1995), largely because most studies do not employ marked

Table 3. (continued)

Transect type	Microhabitat characteristics	Treated mean	Mature mean	Transect mean	Overall mean
Pole	Stand age				
	Rep 1	59	100+		
	Rep 2	58	100+		
	Rep 3	38	96		
	Ground layer				
	Litter depth (cm)	3.29 (0.31)	3.48 (0.39)	3.39 (0.24)	
	Organic layer depth (cm)	12.11 (2.77)	10.61 (1.80)	11.36 (1.62)	
	Depth to mottling (cm)	39.85 (1.63)	40.06 (1.06)	39.95 (0.95)	
	Herb cover (%)	16.21 (2.50)	20.38 (3.89)	18.29 (2.32)	
	Down log cover (%)	0.12 (0.08)	2.08 (0.81)	1.10 (0.45)	
	Understory layer				
	Hardwood stems 0.5–1 m	1,681.69 (230.70)	5,113.67 (1,438.49)	3,397.68 (797.16)	
	Hardwood stems 1–2 m	669.23 (224.02)	1,664.52 (5,25.27)	1,166.87 (297.91)	
	Hardwood stems >2 m <10 cm dbh	1,098.23 (240.90)	1,235.52 (284.51)	1,166.87 (182.86)	
	Hardwood stems/ha	3,448.3 (498.2)	8,013.8 (2,004.3)	5,731.3 (1,116.4)	
	Softwood stems/ha	686.4 (320)	995.3 (333.1)	840.9 (228.1)	
	Rubus/other stems/ha	0	51.4 (51.4)	25.7 (25.7)	
	All understory stems/ha	4,135.5 (445.8)	9,060.6 (2,113.7)	6,597.9 (1,174.7)	
	BA m^2	8.4 (1.4)	11.8 (0.3)		
	Mean dbh (cm)	19.1	22.6		
Overall mean	Ground layer				
	Litter depth (cm)	2.9 (0.2)	3.0 (0.2)		2.93 (0.14)
	Organic layer depth (cm)	3.4 (0.4)	3.5 (0.3)		8.72 (0.67)
	Depth to mottling (cm)	38.8 (0.6)	38.3 (0.7)		38.54 (0.49)
	Herb cover (%)	15.7 (1.7)	20.1 (2.4)		17.91 (1.47)
	Down log cover (%)	0.69 (0.21)	1.51 (0.33)		1.10 (0.20)
	Understory layer				
	Hardwood stems 0.5–1 m	5,205.20 (1,345.73)	4,575.99 (771.83)		
	Hardwood stems 1–2 m	5,176.58 (1,649.86)	2,133.57 (413.33)		
	Hardwood stems >2 m <10 cm dbh	8,477.05 (2,011.92)	2,785.63 (551.46)		
	Hardwood stems/ha	18,858.7 (4,822)	9,495.2 (1473)		14,177.1 (2,562.5)
	Softwood stems/ha	634.8 (197.2)	915.3 (281.7)		774.9 (171.5)
	Rubus/other stems/ha	5,536.8 (1,842.4)	280.2 (149)		2,908.7 (969.4)
	All understory stems/ha	25,030.6 (6,575.7)	10,690.7 (1,821.4)		17,860.7 (3,492.8)

individuals. Terrestrial salamanders are notoriously difficult to mark reliably.

Some salamander species can remain inactive in underground retreats as deep as 90 cm (Grizzell 1949) for long periods of time as "sit and wait" exploiters of suitable surface feeding conditions (Feder 1983). Such individuals are not likely to be detected in studies of habitat change because sampling is conducted at the surface—under cover boards, in pitfall traps, litter searches, etc. (deMaynadier and Hunter 1995). The issue of resident animal fate is important to our understanding of the effects of habitat change due to clearcutting. If a population of subterranean individuals remains on site, it will likely affect the rate and extent to which the overall population in the developing stand recovers to preharvest level, because population growth will be a combination of both vertical movement and horizontal recolonization from adjacent suitable habitats.

Table 4. Pearson correlation coefficients between microhabitat and understory characteristics and total redback salamander counts per station and *P*-value for testing Ho: Rho = 0; *N* = 72.

	Total PLCI	*P* value
Microhabitat characteristics		
Litter depth (cm)	0.133	0.265
Organic layer depth (cm)	0.381	0.001
Depth to mottling (cm)	–0.052	0.663
Herb cover %	0.211	0.076
Down log cover %	0.171	0.151
Understory characteristics		
Hardwood understory stems 0.5–1.0 m	–0.090	0.454
Hardwood understory stems 1–2 m	–0.188	0.114
Hardwood understory stems >2 m <10 cm dbh	–0.289	0.013
Softwood understory stems	0.251	0.873
All understory stems	–0.234	0.048

Dramatic movements by plethodontid salamanders have been observed. Madison and Shoop (1970) report an experimentally displaced Jordan's salamander (*Plethodon jordani*) moving 60 m in a 12 hr period—evidence of long-distance dispersal despite small home range. Also, large numbers of Peaks of Otter salamanders (*Plethodon hubrichti*) dispersed from clearcut sites in Virginia (see de Maynadier and Hunter 1995 for review). Such disturbances, however, likely result in the deaths of plethodontid salamanders on site based on several natural history traits (Petranka 1994). Such traits include aggressive territoriality and philopatry, and vertical (not horizontal) movement

Table 5. Result of stepwise regression of habitat variables on total redback salamander counts, Bartlett, New Hampshire [R^2 = 0.2899, *df* = 3 (regression) 68 (error), *F* = 9.26, Prob > *F* = 0.0001).

Variable	Parameter estimate	SE	*F*	Prob. >*F*
Intercept	28.678	6.567	19.07	0.001
Herbaceous cover	0.285	0.115	6.19	0.015
Hardwood stems >2m <10 cm dbh	–0.002	0.001	10.00	0.002
Organic litter depth	4.545	1.258	13.05	0.001

under cover objects in response to dehydration produced by clearcutting (Jaeger 1980). Once underground for prolonged periods, individuals probably slowly perish (Petranka 1994) due to limited feeding and reproductive opportunities (Fraser 1976, Jaeger 1972) and the environment becoming increasingly toxic to osmoregulation (Frisbie and Wyman 1992). In sum, the idea that salamanders can remain sequestered underground for years until favorable conditions return is untenable (J. Petranka, pers. comm.). The present study encompasses time frames in which redback salamanders would have to surface to feed. See deMaynadier and Hunter (1995) for an exhaustive review of the "perish" hypothesis.

Because of its negative response to clearcutting, the redback salamander has been considered a "management sensitive species" (deMaynadier and Hunter 1998). deMaynadier and Hunter's (1998) study used pitfall and drift fence arrays, not cover boards, to assess amphibian populations, and their transects extended 75 m to either side of silvicultural edges compared to our 40 m lengths. Their results confirm the general pattern of lower abundance in younger stands, and increasing abundance with stand development compared to that in adjacent uncut stands. The sampling distances used (0, 25, 50,7 5 m), however, did not yield analysis of complex patterns of abundance within short distances of the forest edge as did our analysis at 0, 5, 10, 20, and 40 m. Silvicultural edges produce temporary effects compared to those resulting from maintained edges in agricultural landscapes (e.g., Angelstam 1986, DeGraaf 1992). Our results, based on a finer grain sampling design, suggest that redback salamanders are negatively affected at silvicultural edges for only short distances in the remaining stand. deMaynadier and Hunter (1998) considered redback salamanders to be negatively affected to distances of 25–35 m along silvicultural edges; our results show that the distance may be even less. The detection of such effects is a function of sampling transect length; the limited data available for redback salamanders near forest edges does not support the existence of edge effects beyond 70 m into the adjoining forest. For example, redback salamanders sampled across forest edges using cover boards increased in abundance up to 65 m in mature stands, after which abundances declined (DeGraaf and Yamasaki 1992).

Seasonal and Yearly Variation

Within the sampling period, redback salamander detections followed a strong seasonal pattern across all edge types, with peaks of abundance in spring and late summer, and lowest abundance in early summer and early fall (Figure 3). This seasonal pattern closely tracks soil temperature and is typical for the species throughout the East (Petranka 1998, p. 342). Being lungless, redback salamanders respire primarily through their moist skins. Surface activity (and detectability) is therefore reduced in the hottest months (Fraser 1976, Maglia 1996, Taub 1961). Likewise, yearly abundances track overall precipitation, with lowest abundances in drier years and highest abundances in wetter years across all edge contrast types (Figure 2). These patterns bear on the design of monitoring efforts, which are most efficient when detections are likely to be high.

Statewide averages for New Hampshire indicate that 1993 and 1995 were the 17th and 5th driest summers, respectively, in the preceding 100 yr; 1994 and 1996 were average for summer precipitation. Statewide averages for New Hampshire indicate 1994 and 1995 were two of the hottest summers in the preceding 100 yr; 1993 ranked among the 10 hottest summers and 1996 ranked 72nd (NOAA ftp site ftp.ncdc.noaa.gov/pub/data/cirs/0103.pctst and 0103.tmpst). Although numbers of salamanders are higher with advancing stand development, yearly patterns of abundance are related to overall precipitation and are not mitigated by stand development.

Habitat Relationships

Despite detailed measurement of microhabitat conditions, few variables were related to redback salamander abundance. The depth of the decomposing soil organic layer was the variable most strongly correlated with total salamander counts. Microsites with deeper soil organic layers on enriched and fine till hardwood sites (Leak 1982) probably moderate the drying of sites between rain events over time. Microsites with shallow organic layers may experience more frequent and extensive drying over time resulting in fewer salamander observations. The relationship to litter depth is consistent with results reported for redback salamanders (DeGraaf and Yamasaki 1992) and for amphibian assemblages (DeGraaf and Rudis 1990, deMaynadier and Hunter 1998) elsewhere in northern New England. In the regression model, the percent of herbaceous ground cover, number of hardwood stems >2 m tall and <10 cm dbh and organic layer depth were the only significant variables. Understory conditions were highly variable in our stands, but random locations of transects across edges yielded consistently similar litter and soil conditions—depth to mottling, litter, and organic layer depths (Table 3). Litter and soil conditions are important determinants of terrestrial salamander distribution (Heatwole 1962, Pough et al. 1987, DeGraaf and Rudis 1990); their similarity across treatments in this study allows a clear examination of treatment, edge, and temporal effects.

Downed logs were not related to redback salamander distributions. Percent cover by downed woody debris was either unimportant to amphibians or negatively related to abundance of same species in Maine (deMaynadier and

Hunter 1998). These results stand in marked contrast to those reported from other regions, including the Pacific Northwest (Bury and Corn 1988, Raphael 1988) the southern Appalachians (Petranka et al. 1994), and the Missouri Ozarks (Herbeck and Larsen 1999). Summer conditions are likely cooler in northern New England than in the Ozarks and southern Appalachians, where soil surface temperatures on sunny days may greatly exceed lethal temperatures for salamanders (J.W. Petranka, pers. comm.). Moisture regimes and decay rates of woody debris vary regionally and likely yield salamander responses to habitat conditions that vary regionally. Until animals are sampled in similar ways and variables are measured consistently across regions, habitat relationships will be difficult to generalize, even for widespread species such as the redback salamander.

New England northern hardwoods regenerate rapidly after clearcutting, and the reported negative relationships between salamander capture rates and high levels of ambient light (deMaynadier and Hunter 1998) is rapidly moderated by stand regeneration postcutting. Besides rapid regeneration of hardwood tree species, initial high densities of *Rubus* and pin cherry (Marquis 1967) quickly moderate high levels of ambient light that dry the forest floor after clearcutting.

Conclusions

Even-aged management with clearcut regeneration lowers the abundance of redback salamanders in New England northern hardwoods. At silvicultural edges, redback salamander abundance increased on the younger sides of edges as stands developed from regeneration to sapling to poletimber stages. The pattern of salamander abundance was similar across all three degrees of edge contrast: low abundance 40 m out in the younger stand, increased abundance near or at the edge, or decrease just inside the edge, peak abundance in the mature stand 20 m inside the edge and a decline at 40 m in the mature stand. Recovery of redback salamander populations to pre-harvest each may take >30 yr even at stand edges.

Seasonal and year variation in redback salamander detections were dramatic. Across all edge contrast types, detections were highest in spring and late summer, and lowest in early summer and early fall. Yearly abundances trailed over precipitation, with lowest abundances in drier years and highest abundances in wetter years across all edge contrast types. Redback salamander abundances are higher with advancing stand development; yearly patterns of abundance are related to overall precipitation and are not mitigated by stand development. Monitoring efforts should focus on periods of peak abundance and span the range of yearly precipitation to index treatment effects adequately.

Regarding habitat relationships, the depth of the decomposing soil organic layer was the only positive and the most strongly correlated variable with redback salamander counts. In the regression model, the percent herbaceous ground cover, number of hardwood stems >2 m tall and <10 cm dbh, and organic layer depth were the significant variables. Down logs and percent cover by downed woody debris were not related to redback salamander distribution in our New Hampshire study.

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