Effects of Silvicultural Edges on the Distribution and Abundance of Amphibians in Maine

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Abstract: *Amphibians share several biological characteristics that may cause them to be sensitive to abrupt transitions in microhabitat and microclimate that occur across forest edges. To better understand the importance of edge effects on amphibians in a forested landscape, we sampled the distribution of populations along drift fences placed perpendicular to silvicultural edges of varying contrast in central Maine. Within the community of amphibians sampled (14 species), salamanders generally were more sensitive to even-aged harvesting and associated edge effects than were anurans, but forest habitat generalists and specialists were identified within both groups. We conservatively estimated the depth of edge effects at 25–35 m for a subset of management-sensitive species (Plethodon cinereus, Ambystoma maculatum, A. laterale, and Rana sylvatica). An index of edge contrast, calculated using ambient light penetration levels, was valuable in predicting the magnitude of edge effects among sites that included silvicultural edges of different age and origin (old field plantations versus recent clearcuts). Some structural microhabitat variables relevant to forest management were identified as potentially limiting to amphibians near forest edges, including canopy cover, litter cover, and a measure of stumps, snags, and their root channels. Our observations are consistent with the results of other work on biotic edge effects in the eastern United States and suggest that impacts from intensive forest management practices extend beyond the boundaries of harvested stands.*

Efectos de Bordes Silviculturales en la Distribución y Abundancia de Anfibios en Maine

Resumen: *Los anfibios comparten diversas características biológicas que pueden ser la causa de que sean sensitivos a transiciones abruptas en microhábitats y microclimas que ocurren a lo largo de los bordes de bosques. Para entender mejor la importancia de los efectos de bordes en anfibios en un paisaje boscoso, muestreamos la distribución de poblaciones a lo largo de vallas de desvío colocadas perpendicularmente a bordes silviculturales de contrastes variantes en la parte central de Maine, USA. Dentro de la comunidad de anfibios muestreados (14 spp), las salamandras generalmente fueron más sensitivas a la tala de edad constante y efectos asociados al borde que los anuros, pero tanto especies generalistas y especialistas de hábitat boscoso fueron identificadas dentro de ambos grupos. Conservativamente estimamos la profundidad del efecto de borde a 25–35m para un subset de especies sensitivas al manejo (Plethodon cinereus, Ambystoma maculatum, A. Laterale y Rana sylvatica). Un índice de contraste de borde, calculado usando niveles de penetración de luz ambiental fue valioso para predecir la magnitud de los efectos de borde entre sitios que incluyeron bordes silviculturales a diferentes edades y orígenes (plantaciones viejas contra clareados recientes). Algunas variables estructurales de microhábitat relevantes para el manejo forestal fueron identificadas como potencialmente limitantes para anfibios cercanos a los bordes de bosques, incluyendo la cobertura del dosel, cobertura de bojarasca y una medición de varas, tocones y sus canales de raíces. Nuestras observaciones son consistentes con los resultados de otro trabajo en efectos bióticos de borde en el este de los Estados Unidos y sugieren que los impactos de prácticas de manejo forestal intensivo se extienden mas allá de los límites de los sitios cosechados.*

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Introduction

Forest fragmentation can threaten native wildlife populations by eliminating blocks of continuous habitat or by degrading the quality of remaining habitat for those species sensitive to an increase in the amount of forest edge (Yahner 1988; Murcia 1995). The effects of forest fragmentation have received a great deal of attention in agricultural or densely populated regions, where important impacts on passerine birds (Gates & Gysel 1978; Whitcomb et al. 1981; Brittingham & Temple 1983; Wilcove 1985; Terborgh 1989) and vascular plants (Ranney et al. 1981; Ambrose & Bratton 1990; Palik & Murphy 1990; Brothers & Spingarn 1992; Fraver 1994) have been documented. In these regions impacts on native biota from habitat loss, isolation, and edge effects become a persistent phenomenon following the incremental conversion of forested matrix to agricultural and urban land uses. But, the effects of silvicultural fragmentation in areas that are mostly forested remains poorly understood and actively investigated (Rosenberg & Raphael 1986; Small & Hunter 1988; Yahner & Scott 1988; DeGraaf 1992; Rudnicky & Hunter 1993*a*, 1993*b*; McGarigal & McComb 1995; Mills 1995; Hagan et al. 1996).

Habitat fragmentation is a spatially and temporally dynamic process in forested landscapes subject to extensive even-aged timber management. For example, the size and juxtaposition of harvested and mature stands vary, and young stands that are avoided by species associated with mature forest may later provide primary habitat (Hagan et al. 1996). Furthermore, edge effects produced by the contrast between recent clearcuts and mature stands are diminished during forest succession (Harris 1984; DeGraaf 1992). Although the process of fragmentation in forested landscapes may generate only temporary effects at the stand scale, cumulative impacts to sensitive wildlife populations may be significant at the landscape scale. For example, the intensity of industrial timber management often limits the presence of mature forest source-habitats from which colonists (propagules) can reinvade nearby disturbed patches. This may be especially important to less mobile members of the forest ecosystem, such as salamanders (Kramer et al. 1993), vernal herbs (Meier et al. 1995), and flightless invertebrates (Mader 1984; Baur & Baur 1990).

The ecology of forest edges is characterized by changes in biotic elements (parasites, predators, and herbivores) and abiotic elements, (microclimate, disturbance regime) both of which have been implicated in the negative edge effects documented in bird and plant communities (reviews by Yahner 1988; Paton 1994; Murcia 1995). Amphibians are the most abundant vertebrates in many temperate forest ecosystems (Burton & Likens 1975*a*), and their populations may play a critical role in structuring communities of forest floor decomposers, thereby affecting nutrient cycling rates (Burton & Likens 1975*b*; Hairston 1987; Wyman, in press). But despite increasing attention to relationships between amphibians and forest management practices (deMaynadier & Hunter 1995), the effects of forest fragmentation, and of edge effects in particular, remain largely unstudied for this taxon (DeGraaf & Yamasaki 1992; deMaynadier 1996).

Amphibians share several biological characteristics that may cause them to be especially sensitive to the abrupt transitions in microhabitat and microclimate that occur across forest edges (reviews by Saunders et al. 1991 and Murcia 1995; see also Brothers & Spingarn 1992; Chen et al. 1990, 1993*a*, 1993*b*). Many species maintain close contact with forest floor substrates and, unlike other forest vertebrates, have a highly permeable skin that needs to remain relatively cool and moist for efficient respiration (Feder 1983). Physiological constraints, coupled with relatively poor dispersal capabilities (Sinsch 1990) and small home ranges (Stebbins & Cohen 1995), may cause many amphibian species to be especially sensitive to local changes in climate and microhabitat. Furthermore, the populations of several forest amphibian species are positively correlated with the quantity and quality of coarse woody debris, litter depth and moisture, understory vegetation density, and overstory canopy closure (deMaynadier & Hunter 1995), suggesting that many of the structural habitat changes characteristic of management-induced forest edges are likely to have important effects on local amphibian populations.

We examined the response of a forest amphibian community to edge habitats created by even-aged timber harvesting in central Maine. Our objectives were to (1) identify species-specific differences in sensitivity to forest edges, (2) compare the relative influence of low- and high-contrast edge boundaries, and (3) identify microhabitat elements relevant to forest management that may be limiting to amphibian populations near forest edges.

Methods

Study Sites

We conducted our study on five privately managed woodlots located within a heavily forested region of Penobscot County, Maine (latitude: 45°06′N, 45°16′N; longitude: 68°45′W, 68°53′W). At each site a relatively mature control stand abutted a treatment stand—a conifer plantation or naturally regenerating clearcut—creating a well-defined forest edge for study. Sites were chosen to represent different levels of edge contrast based on the age and management intensity of treatments (Table 1). Control stands at the plantation study areas (sites 4 and 5) were composed primarily of northern hardwoods (*Fagus grandifolia, Acer saccharum, Betula alleghaniensis,* and *Fraxinus americana*), and both treatment stands

Table 1.   Description of forest stand treatments, controls, and edge characteristics of five study sites in central Maine.

Site	Treatment disturbance	Control type	Aspect	Edge contrast gradient index*
1	2-year-old clearcut	mixed woods, 70–90 years old	west	0.927
2	9- to 11-year-old clearcut	mixed woods, 70–90 years old	south-southwest	0.854
3	9- to 11-year-old clearcut	mixed woods, 70–90 years old	south-southwest	0.558
4	5-year-old conifer plantation (*Pinus resinosa*)	northern hardwoods, 60–80 years old	west	0.883
5	25-year-old conifer plantation (*P. resinosa* and *Picea abies*)	northern hardwoods, 70–90 years old	west	0.063

The correlation coefficient (Pearson) describing the relationship between ambient light penetration levels and position along a 140-m edge transect.

showed evidence of past agricultural activity. In contrast, the clearcut study areas (sites 1–3) showed no evidence of agricultural activity on treatments or controls and were composed of conifer-dominated mixed woods (*Tsuga canadensis, Fagus grandifolia, Picea rubens,* and *Betula alleghaniensis*).

Amphibian Sampling

At each site we established one 140-m transect perpendicular to the forest edge with five drift fences, each 20 m long and separated by 10-m gaps (Fig. 1). Each fence included four pairs of pitfall traps spaced at 5-m intervals. In this manner the transect was sampled at 0–10 m, 20–40 m, and 50–70 m from the forest edge in both control and treatment stands. Drift fences were constructed of partially opaque polyethylene supported by mason string, 40–50 cm high, attached to hardwood stakes. Pitfall traps buried along the fence's edge consisted of two number 10 cans taped end to end (36 cm depth) and a funnel made from a plastic bowl to prevent escape by climbing animals anuran metamorphs and red-backed salamanders (*Plethodon cinereus*). Local stand disturbances such as abandoned skidder trails, rock walls, large canopy openings, and beaver flowages, coupled with installation constraints inherent to drift fence construction in rocky forest soils, prevented random placement of sample transects. Instead, we intentionally avoided previously disturbed areas of the forest and attempted to locate transects as close to the middle of each stand edge as possible. This design also helped to avoid confounding edge effects caused by management practices at the periphery of the stand.

We monitored all five drift fence transects continuously from 1 June to 21 September 1993, for a total of 113 days. In addition, as part of a pilot season, we sampled study sites 2 and 3 (9- to 11-year-old clearcuts) from 6 June to 4 October 1992. Trapped specimens were identified, measured snout to vent (anterior angle), and toe-clipped. Data from recaptured individuals were not used in any analyses. Capture data for spring peepers (*Pseudacris crucifer*) and gray treefrogs (*Hyla versicolor*) were omitted from all analyses except those measuring stand species richness because of the potential
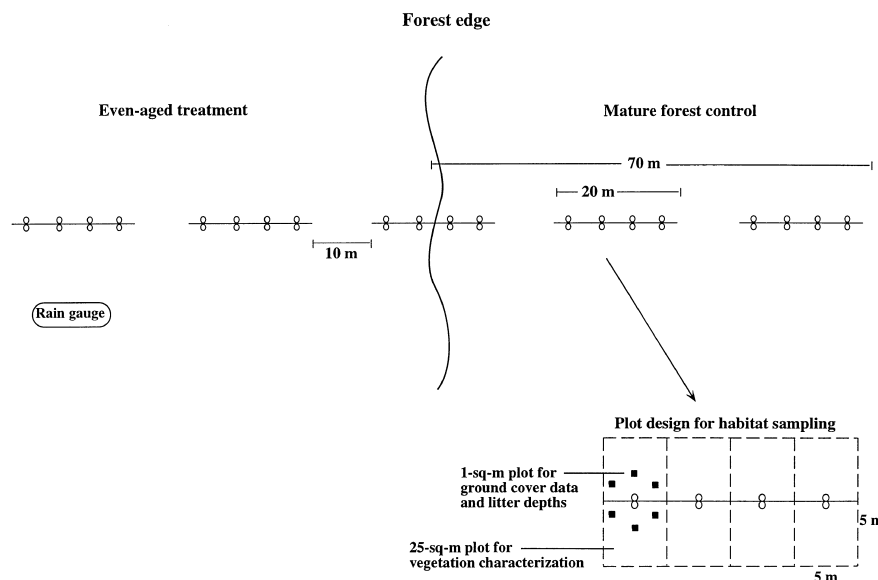

Figure 1. *Drift fence transect design along which samples of amphibians were taken to determine their distribution and abundance across silvicultural edges at five sites (Table 1) in Penobscot County, Maine, 1992–1993.*

bias inherent during pitfall trapping of treefrogs (i.e., trap and fence climbing; Dodd 1991; Gibbons & Semlitsch 1981). Traps were generally visited soon after rainfall events or after 7 days, whichever came first (average length 4.8 days). When traps were checked, rainfall was measured to the nearest 0.5 mm with a rain gauge located in each treatment stand. Live animals were released approximately 5 m from the point of capture on the opposite side of the drift fence to help minimize the probability of immediate recapture.

Habitat Sampling

Habitat variables were chosen based on their relevance both to forest management practices and to the natural history of forest amphibians (Table 2). Visual estimates of percent cover by seven categories of ground cover were made in six 1-m^2 plots located in a 2-m radius circle centered around each paired-pitfall station (total of 24 plots per fence, 120 per transect). Litter depth measurements (mm) were made with a ruler in the center of each ground cover plot (Fig. 1). Seven physiognomic vegetation categories (e.g., herbaceous plants versus woody shrubs) were measured through visual estimates of percent cover within three height classes (0–0.5, 0.5–3, and >3 m) from 25-m^2 plots associated with each pitfall trap (total of 8 plots per fence, 40 per transect). A visual estimate of percent cover by woody slash was also recorded for each vegetation plot. Finally, a sunfleck ceptometer (Decagon Devices, Inc.) was used to measure sunlight penetration to the forest floor, thus serving as an index of total forest canopy density and a surrogate measure of microclimate (Chen et al. 1993*a*, 1993*b*; Matlack 1993). Sunfleck measurements were recorded from 1100 to 1400 hours on cloudless days from each of four cardinal directions centered 1 m above every paired-pitfall station (total of 16 per fence, 80 per transect). Field measurements of all habitat variables were conducted from early August to early September of 1993.

Statistical Analyses

We eliminated trap data influenced by raccoon (*Procyon lotor*) or skunk (*Mephitis mephitis*) predation, flooding, and temporary trap closures while damaged fences were repaired. This resulted in variable levels of trapping effort within and among study sites, so all statistical comparisons of amphibian species abundance and richness were made based on a standardized catch-per-unit effort measurement (animals/100 trap nights). Data collected during the 1992 pilot season (study sites 2 and 3) were included only in analyses of species richness and recapture rates after we tested for year-specific differences. Exact probability values are reported for all univariate and multivariate statistical tests that yielded significance levels less than 0.10. Statistical analyses

Table 2. Microhabitat variables measured along clearcut-mature forest edge transects in central Maine.

Habitat variables	Transformations
Ground cover[a]	
Woody cover	log
Bare soil	log
Rock	dummy (0–1)
Conifer litter	square-root
Deciduous litter	none
Snag, stump, and/or roots ("bole-root")	square-root
Moss	square-root
Vegetative and structural characteristics[b]	
Grass	dummy (0–1)
Forbs and ferns	square-root
Nonvascular plants	square-root
Conifer canopy (>3 m)	square-root
Hardwood canopy (>3 m)	none
Midstory cover (0.5–3.0 m)	square-root
Ground-level cover (0–0.5 m)	none
Slash	none
Other measurements[c]	
Ambient light level	log
Litter depth	none
Distance to coarse woody debris	log

[a] *Based on visual estimates of percent cover for 1-m^2 plots.*
[b] *Based on visual estimates of percent cover for 25-m^2 plots. Data for vegetation categories derived from height-stratified (0–0.5, 0.5–3, and >3 m) measurements of seven physiognomic classes, including conifer trees, deciduous trees, woody shrubs, ferns, forbs, grasses, and nonvascular plants.*
[c] *Ambient light penetration measured with a sunfleck ceptometer at a height of 1 m; litter depth (mm) measured the organic layer with a ruler; distance to coarse woody debris (cm) measured from individual pitfall stations to nearest suitable woody cover object (stump or slash).*

were conducted with the SYSTAT package (Wilkinson et al. 1992).

We took advantage of major differences in management history among our study sites by asking separate questions and conducting separate analyses for the pooled study sites ($n = 5$) and for the clearcut sites alone ($n = 3$). Among clearcut treatments, simple linear regression models were used to analyze the effects of harvest-induced edges on amphibian distribution. Statistical comparisons of specific regression models were made using *t* tests of slope coefficients (Zar 1984). To identify preferred breeding habitat for the only entirely terrestrial species in our study, we compared the relative proportion of immature red-backed salamanders (<32 mm snout-vent length, Sayler 1966; Kleeberger & Werner 1982) sampled from clearcuts and adjacent mature stands using data collected over 20 m from the forest edge. The effects of rainfall and seasonality on amphibian capture rates were analyzed by regression analysis in forest control and harvest treatment locations, separately, in an effort to test the hypothesis that climatic conditions exert a stronger influence on surface activity in recently managed stands than in closed-canopy controls. Multiple regression analysis was also used

to explore the relationship between microhabitat availability and the abundance of species or groups (e.g., salamanders) with over 200 captures at clearcut study sites. Models were constructed using forward, interactive, stepwise regression methods, and only those variables with both *t* values greater than 2.0 and tolerance values greater than 0.1 were included in model construction (Wilkinson et al. 1992). All microhabitat regressions were performed using a subset of variables that were not highly intercorrelated ($r < 0.80$).

Data from both clearcut and old field plantation study sites were used to make general inferences about the effects of even-aged management practices on amphibians. Differences in species richness and overall abundance for regenerating versus mature forest stands were analyzed using paired *t* tests after we corrected for differences in trapping effort (trap nights). Through calculation of a simple "management-sensitivity index," a subset of species within the larger amphibian community sampled (14 species) was identified as those potentially most sensitive to even-aged forestry practices. The index was constructed by calculation of the proportion of all captures that were taken from drift fences located entirely within closed-canopy control forest (20–70 m from the edge). One-sample *t* tests were used to identify species or groups (i.e., ambystomids, aquatic ranids) caught disproportionately often in this relatively undisturbed portion of the transect. Using graphical analysis, we also identified the depth of clearcut-induced edge effects on "management-sensitive species." A locally weighted regression smoothing procedure (LOWESS, tension = 0.5; Cleveland 1979; Wilkinson et al. 1992) helped to identify asymptotes in forest-interior capture abundance, signaling the end of detectable edge effects.

Regression analysis and comparisons of slope coefficients were used to evaluate the effects of low- and high-contrast edges (i.e., young versus old plantations and clearcuts, respectively) on the distribution of salamanders and anurans. Finally, it was possible for us to do a synthetic analysis of the effects of edge contrast among all study sites by examining the relationship between closed-canopy forest captures (over 20 m from the edge) of management-sensitive species and a quantitative index of site contrast gradient. The site contrast index measured the intensity of association (using Pearson's correlation coefficient) between ambient light penetration levels near the forest floor and position along the 140-m forest edge transect.

Results

Effects of Harvesting, Rainfall, and Seasonality

A total of 2394 amphibians of 14 species (6 salamanders and 8 anurans) was captured in 1993 (Table 3), with 9 species common to every study site. Two ranid species, the leopard frog (*Rana pipiens*) and bullfrog (*R. catesbeiana*), were limited in their distribution to a single site that included a beaver flowage oriented parallel to the edge transect and equidistant ($\approx$200 m) from clearcut and control drift fences. The 4 most common species, eastern newts (red efts; *Notophthalmus viridescens*), wood frogs (*Rana sylvatica*), and spotted (*Ambystoma maculatum*) and red-backed salamanders, collectively accounted for 73.1% of all captures.

Trap success in mature forest controls averaged 14.2 animals per 100 trap nights, slightly higher than the average capture rate for three upland forest types in New Hampshire (11.8 animals per 100 trap nights; DeGraaf & Rudis 1990). The capture rate was significantly lower ($t = 4.06$, $p = 0.015$) in treated stands (clearcuts and

Table 3.   List of amphibian species captured and their capture abundance from drift–fence transects bisecting forest edges in central Maine, 1993.

Species	Common name	Total captured	Number of sites where captured
Salamanders		1280	
Notophthalmus viridescens	eastern newt (red eft)	646	5
Ambystoma maculatum	spotted salamander	358	5
Plethodon cinereus	red-backed salamander	230	5
Ambystoma laterale	blue-spotted salamander	28	5
Eurycea bislineata	two-lined salamander	15	4
Hemidactylium scutatum	four-toed salamander	3	2
Anurans		1114	
Rana sylvatica	wood frog	515	5
Rana palustris	pickerel frog	150	5
Rana pipiens	leopard frog	147	1
Bufo americanus	American toad	135	5
Rana clamitans	green frog	135	5
Pseudacris crucifer	spring peeper	26	5
Rana catesbeiana	bull frog	3	1
Rana septentrionalis	mink frog	3	2

plantations), where 6.6 animals were captured per 100 trap nights, a value for which comparative results are unavailable in New England. Significantly fewer salamander species (means: 5.4 versus 4.4 species; $t = 3.88$, $p = 0.018$) were found in treatment stands than in paired controls, but no significant differences were detected for anurans (5.8 versus 5.2 species; $t = 0.46$, $p = 0.669$) or for amphibians as a group (11.2 vs. 9.6 species; $t = 2.05$, $p = 0.109$). The only species absent from nearly all treatment stands (four of five) was the two-lined salamander (*Eurycea bislineata*), a forest stream-breeding plethodontid that actively forages and migrates through upland habitats adjacent to riparian zones (MacCulloch & Bider 1975; Conant & Collins 1991).

Rainfall and seasonality (early summer and fall versus midsummer) helped to explain a significant proportion of the variance in salamander capture abundance among trapping periods ($r^2 = 0.26$, $p < 0.001$). Salamanders appeared to be most active on the forest floor, and thus more vulnerable to pitfall capture, during rainy periods in the early summer or fall. In contrast rainfall did not enter the model for anuran captures, and season alone accounted for a modest amount of variation ($r^2 = 0.11$, $p < 0.001$). We tested the hypothesis that forest floor moisture conditions are relatively more limiting to salamanders on regenerating sites by comparing regression models for the effect of rainfall on salamander activity in treatment versus control stands separately. The model for treatment stands had slightly better explanatory power than the model for control stands ($r^2 = 0.16$, $b = 0.37$ animals/mm versus $r^2 = 0.13$, $b = 0.25$ animals/mm; both $p < 0.001$), but the difference in slope coefficients was not statistically significant ($t = 1.13$, df = 210, $p < 0.25$).

Effects of Proximity to Edge

The location of clearcut edges had significant effects on the relative abundance and distribution of several amphibian species and groups. For example, the abundance of six species of salamanders and seven species of anurans increased significantly with increasing proximity to forest interior locations ($r^2 = 0.79$, $b = 0.09$ animals/m and $r^2 = 0.63$, $b = 0.07$ animals/m, respectively; $p < 0.001$). Furthermore, differences in life history between six species that make extensive use of upland activity areas (e.g., wood frogs: $r^2 = 0.80$, $b = 0.10$ animals/m, $p < 0.001$; see Fig. 2 for all species included) and seven semiaquatic species that use upland habitats mainly during dispersal or migration (e.g., bullfrogs: $r^2 = 0.26$, $b = 0.05$ animals/m, $p = 0.004$) served as a valuable distinction for predicting group response to forest clearcut edges ("residents" versus "dispersers"; test of slopes: $t = 3.37$, df = 56, $p < 0.001$).

Using transect data from all five study sites, we made an effort to rank abundant species (>100 captures) according to an index of management sensitivity (Fig. 3; see description of index in methods). Within each transect, only two of five drift fences were located entirely within mature, closed-canopy forest, yielding expected index capture rates of 40%. The subset of species identified as sensitive to recent forest management practices included red-backed salamanders, wood frogs, and mole salamanders (*Ambystoma maculatum* and *A. laterale*). The proportion of closed-canopy transect captures for all three species or groups (averaging 71.4%, 66.2%, and 58.7% for red-backed salamanders, wood frogs, and mole salamanders, respectively) was significantly higher than expected on the basis of trapping ef-
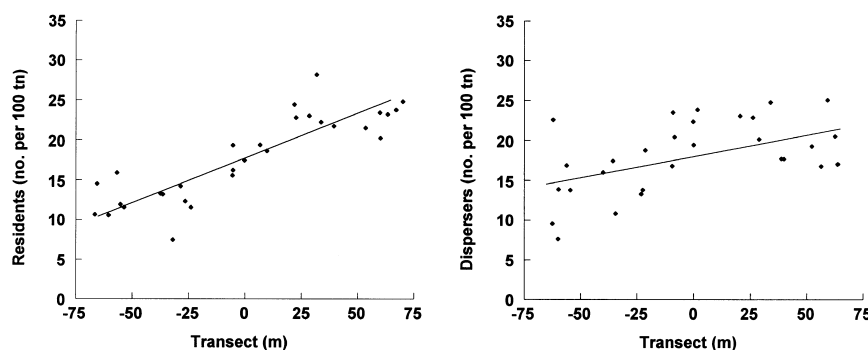

Figure 2. Relative abundance of six species that make extensive use of upland activity areas ("residents"; includes data from wood frogs, American toads, and red-backed, mole, and four-toed salamanders; $r^2 = 0.80$, $b = 0.11$ animals/m, $p < 0.001$) versus seven species that are semi-aquatic as adults and use upland habitats mainly during dispersal or migration ("dispersers"; includes eastern newts, two-lined salamanders, and green, pickerel, leopard, bull, and mink frogs; $r^2 = 0.28$, $b = 0.05$ animals/m, $p = 0.003$). Slope coefficients for the two groups are significantly different ($t = 3.37$, df = 56, $p < 0.001$). Values on the x-axis indicate transect distance (m) into mature forest (positive values) or clearcuts (negative values). Abundance data (captures per 100 trap nights) were arcsine transformed.
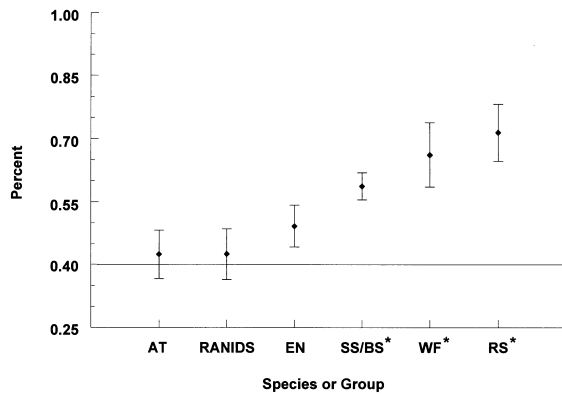
Figure 3. Species ranked according to a "manage-
ment-sensitivity index." Plotted points represent the
mean proportion of captures (n = 5) made in closed-
canopy drift-fence locations (>20 m into control
stands), and error bars indicate 1 SE around the
mean. Species with higher index values (right side of
graph) were captured more often than expected (40%)
in relative forest interior transect locations. Asterisks
indicate statistical significance (p < 0.03). Common
name abbreviations are used for the following species:
AT, American toad; RANID, aquatic ranid frogs (5 spe-
cies); EN, eastern newt; SS/BS, spotted and blue-spotted
salamanders; WF, wood frogs; and RS, red-backed sala-
manders.

fort across the forest edge gradient. In addition, a signifi-
cantly greater proportion of immature red-backed
salamanders (<32 mm snout-vent length) were found in
clearcuts (23.08%, $n = 39$) than in adjacent mature
stands (10.43%, $n = 230$; $Z = 1.963$, $p < 0.05$). To sum-

marize, several species appeared to prefer conditions
under closed-canopy mature stands, whereas others
showed weak or random associations with respect to
the location of forest edges. In contrast to the seral habi-
tat associations characteristic of northeastern forest bird
communities (e.g., Titterington et al. 1979; DeGraaf
1987; Thompson & Capen 1988), no members of the
amphibian community analyzed in this study appeared
specialized for early successional forest habitat.

For the subset of "management-sensitive species"
identified above, we used graphical analysis to approxi-
mate the depth of forest edge effects for control stands
abutting recent clearcuts (sites 1–3, <12 years old). A lo-
cally weighted regression smoothing technique (LOW-
ESS) fitted sigmoid curves to each of the species exam-
ined and revealed a consistent asymptote in the abundance
of forest interior captures at approximately 25–35 m
(Fig. 4).

Trends Related to Edge Contrast

Recently cut stands that contrast strongly with adjacent
mature forest create "hard edges" that are potentially
less permeable to species movements (Stamps et al.
1987; Yahner 1988) and more likely to generate strong
edge effects (Gates & Gysel 1978; Thomas et al. 1979;
Harris 1984; Angelstam 1986). We tested the hypothesis
that degree of edge contrast has an important effect on
the local distribution of salamander and anuran popula-
tions. First we examined sites with conifer plantations as
treatments (sites 4 and 5). A significant amount of the
variation in salamander captures ($r^2 = 0.59$) and anuran
captures ($r^2 = 0.67$) was explained by distance from for-
est edge at the young plantation site, in contrast to the
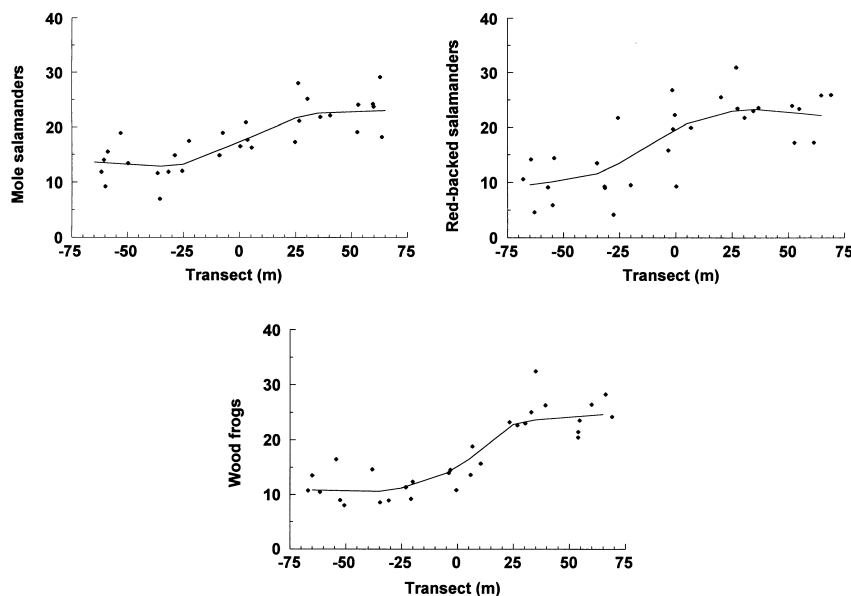older, closed-canopy plantation site (salamanders: $r^2 =$

Figure 4. Distribution of "manage-
ment-sensitive species" across forest-
clearcut edge transects. A locally
weighted regression smoothing tech-
nique (LOWESS, tension = 0.5) fits sig-
moid curves for each species exam-
ined and indicates a consistent
asymptote in the abundance of forest
interior captures at approximately
25–35 m from the forest edge. Values
along x-axis indicate transect dis-
tance (m) into mature forest (positive
values) or clearcuts (negative values).
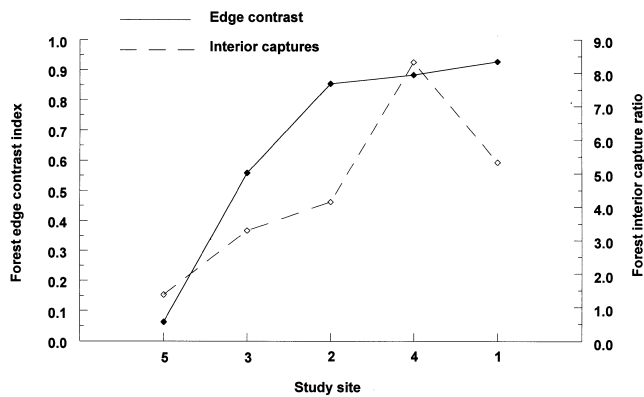Abundance data (captures per 100
trap nights) were arcsine transformed.

*Figure 5. Relationship (*r = 0.90, *p = 0.05) between "forest interior" captures of management-sensitive species (calculated as the ratio of control stand captures—>20 m from edge—to treatment area captures) and an index of site contrast gradient (calculated as the correlation coefficient of ambient light levels and location along forest edge transect). Management-sensitive species include wood frogs, mole salamanders, and red-backed salamanders, as determined from previous analysis (Fig. 3). See Table 1 for a description of study sites.*

0.06; anurans: $r^2 = 0.09$) where edge effects were undetectable. Furthermore, slope coefficients for the young plantation edge were significantly greater than for the older plantation edge for both both salamanders ($t = 2.64, p < 0.01$) and anurans ($t = 2.42, p < 0.025$).

For clearcut-induced forest edges, results varied depending upon the taxon analyzed. For example, the regression slope for salamander abundance versus distance from edge at the 2-year-old clearcut site ($r^2 = 0.73, b = 0.11$ animals/m) was significantly greater than the slope observed at older clearcuts ($r^2 = 0.52, b = 0.06$ animal/m; $t = 1.53$, df $= 26, p < 0.10$), suggesting a stronger response by salamanders to newly harvested edges. Anurans, however, did not show the same pattern of response to age of clearcut edges (young clearcut: $r^2 = 0.55, b = 0.04$ animals/m, $p = 0.016$; older clearcuts: $r^2 = 0.68, b = 0.08$ animal/m, $p < 0.001$). In summary, although anuran response varied by treatment (plantation versus clearcut), there appeared to be a positive relationship between edge contrast and the magnitude of edge effects detected for salamanders.

In an effort to make landscape-scale inferences about effects of forest management, we ranked each of the five study sites with a quantitative index of contrast gradient (index values describe the relationship between levels of ambient light penetration and position along the 140-m forest-edge transect; Table 1). An index of site contrast gradient was significantly and positively correlated ($r = 0.90, p = 0.05$) with the proportion of management-sen-

sitive species (i.e., red-backed salamanders, mole salamanders, and wood frogs) captured in relative forest interior locations (>20 m from edge; Fig. 5).

Microhabitat Relationships

Relationships between amphibian abundance and microhabitat characteristics of forest edges were analyzed by means of correlation and regression analyses on a subset of 18 uncorrelated ($r < 0.80$) habitat variables (Table 2). In the investigation of microhabitat relationships we were interested primarily in identifying habitat elements limiting to amphibians in stands that had been clearcut and left to regenerate naturally because intensive site preparation for plantation establishment is relatively uncommon in New England. Analyses were thus confined to the three study sites with clearcut-induced edges. The five best univariate associations and the single best multivariate model (based on maximum adjusted r^2) are presented in Table 4 for the most commonly captured species (>200 individuals) and for larger groups—all salamanders (6 species) and aquatic ranids (5 species).

Consistently significant relationships were found between species abundance and local canopy cover levels, measured as either percent cover by conifers, deciduous trees, and/or decreasing ambient light levels. For nearly all species and groups examined we found a positive association between capture rate and percent cover by snags, stumps, and their associated root channels ("bole-root" in Tables 2 and 4), a variable that may serve as an index to the amount of available surface and fossorial refuge sites. Variables describing litter characteristics consistently ranked among the five best univariate models for several groups. Hardwood litter coverage and litter depth were both important habitat variables for red-backed salamanders, mole salamanders, and salamanders as a group, and conifer litter had significant predictive value for aquatic ranids. Variables characteristic of logging disturbances—bare soil, grass, and high ambient light levels—generally had negative associations with capture rates.

Finally, in contrast to the microhabitat results of others (Bury & Corn 1988; Raphael 1988; Welsh & Lind 1991; Petranka et al. 1994; Dupuis et al. 1995), we found that percent cover by downed woody material was either unimportant or had negative relationships with the abundance of some species. Woody ground cover and slash accumulation was high on our treated stands because of previous on-site delimbing practices. Although harvest disturbances often generate a large amount of coarse woody debris in close proximity to forest edges (Williams-Linera 1990; Chen et al. 1992; Mills 1995), the habitat value of the material may be limited if it is of recent decay class or small in diameter (often tops and branches only) and isolated from the syner-

Table 4. Summary of regression analyses for amphibian-microhabitat relationships along transects bisecting recent forest-clearcut edges in central Maine.[a]

Species/group	Model variables	b[b]	r² (adjusted)	p
Red-backed salamander	Ambient light	−	0.433	<0.001
	Hardwood litter	+	0.397	<0.001
	Hardwood canopy	+	0.305	0.001
	Conifer canopy	+	0.236	0.004
	Bare soil	−	0.158	0.017
	Hardwood litter, ambient light	+,−	0.555	<0.001
Ambystoma spp.[c]	Ambient light	−	0.606	<0.001
	Conifer canopy	+	0.505	<0.001
	Bole-root	+	0.288	0.001
	Woody cover	−	0.244	0.003
	Nonvascular plants	+	0.192	0.009
	Litter depth, conifer canopy, mid-story cover, hardwood canopy, forb-fern, bole-root	+,+,−,+,+,+	0.709	<0.001
Eastern newt	Conifer canopy	+	0.432	<0.001
	Ground-level cover	−	0.320	0.001
	Ambient light	−	0.250	0.003
	Slash	−	0.194	0.01
	Bole-root	+	0.168	0.016
	Moss, conifer canopy	−,+	0.536	<0.001
All salamanders	Conifer canopy	+	0.565	<0.001
	Ambient light	−	0.559	<0.001
	Woody cover	−	0.349	<0.001
	Bole-root	+	0.248	0.003
	Hardwood litter	+	0.231	0.005
	Hardwood canopy, bare soil, conifer canopy	+,−,+	0.682	<0.001
Wood frog	Conifer canopy	+	0.647	<0.001
	Ambient light	−	0.637	<0.001
	Woody cover	−	0.362	<0.001
	Bole-root	+	0.225	0.005
	Nonvascular plants	+	0.216	0.006
	Ambient light, conifer canopy, grass	−,+,−	0.743	<0.001
Aquatic ranids[d]	Conifer litter	+	0.220	0.005
	Conifer canopy	+	0.116	0.037
	Bole-root	+	0.081	0.07
	Ambient light	−	0.068	0.089
	Hardwood canopy, conifer litter	+,+	0.322	0.002

[a] *Up to five best single variables and the best multivariate model is given.*
[b] *Indicates whether regression correlation was positive or negative.*
[c] *Includes pooled data from* Ambystoma maculatum *and* A. laterale.
[d] *Includes pooled data from all members of the genus* Rana *except wood frogs.*

gistic effects of other important variables, such as canopy cover.

Discussion

Species-Specific Trends

We documented a significantly lower abundance of amphibians and richness of salamanders in forest stands recently disturbed by even-aged management practices than in paired controls. This result is consistent with those of other studies from the eastern United States (Blymyer & McGinnes 1977; Enge & Marion 1986; Pough et al. 1987; Ash 1988; Petranka et al. 1993, 1994; Means et al. 1996; Mitchell et al. 1996). But, unlike previous studies that intentionally avoided sampling near forest edges,

we focused our trapping efforts there in order to observe species-specific responses to spatial and temporal habitat gradients that occur along stand boundaries of different age and management intensity.

Studying the distributional responses of species to well-defined disturbance boundaries allowed us to distinguish forest habitat generalists from specialists within the community of amphibians sampled. Most salamanders appeared to avoid clearcuts and their edges more than did most anurans, but clear exceptions existed within both groups. For example, red-backed salamanders and mole salamanders were most abundant along forest interior portions of the edge gradient. The terrestrial form of the eastern newt, the red eft, can tolerate warmer and drier conditions than can red-backed salamanders (Pough 1974), and our results suggest that they are also less closely associated with forest interior habitats. Among

anurans, wood frogs were more abundant in mature, closed-canopy locations than were either American toads (*Bufo americanus*), a species typically found in a diversity of habitat types (Conant & Collins 1991; Hunter et al. 1992), or any other ranid species. Comparing the responses of individual species to abrupt forest edges allowed us to identify a subset of the region's amphibian community that appeared to be relatively sensitive to the effects of intensive forest management practices: this subset consisted of red-backed salamanders, spotted and blue-spotted salamanders, and wood frogs. Although it may be tempting to generalize about the effects of forest fragmentation on amphibians as a group, particularly because their response is poorly understood (Rosenfield et al. 1992), our results suggest that species-specific distinctions are important.

In this study, red-backed salamanders, a member of the Plethodontidae, appeared to be most sensitive to clearcutting and forest edge effects, with quantitative (Fig. 3) and qualitative differences between populations in clearcut and mature forest stands. Qualitative differences may be related to the fact that adult red-backed salamanders aggressively defend small patches of the forest floor against intruding conspecifics (Jaeger 1981; Jaeger et al. 1982; Mathis 1990). The higher proportion of immature animals observed in recently harvested areas adjacent to mature stands suggests that open-canopy sites may serve as sink habitat for nonbreeding "floaters" (Mathis 1990) that are excluded from mature forest territories. Experimental evidence from natural habitats reveals significant correlations between snout-vent length in red-backed salamanders and both the size of cover objects (Mathis 1990) and the quality and quantity of prey (Gabor 1995) within a defended territory. Our results suggest that relative canopy closure also needs to be considered as a potentially important habitat attribute selected by territorial salamanders. Another plethodontid, the two-lined salamander, was strikingly absent from recently managed stands (1 of 15 captures, 6.7%) in this study. Clawson et al. (1997) similarly report that a related species, *Eurycea longicauda*, disappeared from floodplain hardwood sites in Alabama that were recently harvested by helicopter.

As a group, plethodontids may be especially affected by forest canopy loss because of their almost complete reliance upon cutaneous respiration. Because this form of respiration is "diffusion limited," it is most efficient when the skin is moist and when ambient temperature is cool (Feder 1983). Thus, opening the forest canopy may be especially deleterious for these lungless salamanders. A recent review of forestry-amphibian relationships identified plethodontids as a group particularly vulnerable to population decline following clearcutting, with 15 studies from across North America reporting a five-fold median difference in abundance between mature and recently harvested stands (deMaynadier &

Hunter 1995). Therefore, the significance of forest edge effects for amphibians may be particularly important in regions, such as southern Appalachia, where plethodontids make up a large proportion of the forest amphibian fauna.

The Spatial Extent of Edge Effects

Estimates in the literature that quantify depth of biotic edge effects are variable, probably due to differences in the sensitivity and vagility of taxa examined (e.g., plants versus birds), differences in methods of measurement (e.g., abundance, richness, or proportion of exotic species), and differences in study locations (e.g., latitude and edge orientation). Despite these confounding influences, however, most authors have found that forest edge effects disappear within the first 50 m for birds and plants (see reviews by Paton 1994; Murcia 1995). Many studies examining abiotic variables (e.g., air or soil moisture and temperature and incident light levels) have documented effects within the range of 8–25 m (Kapos 1989; Williams-Linera 1990; Laurance & Yensen 1991; Brothers & Spingarn 1992; Matlack 1993; reviewed by Murcia 1995; but see Chen et al. 1990 for microclimate effects up to 240 m). Because of the unique life history characteristics that may make amphibians valuable as an indicator taxon (Vitt et al. 1990; Dunson et al. 1992; Blaustein et al. 1994), more work is needed to identify the depth of forest edge effects for this group in different landscapes.

Our results suggest that the abundance of some management-sensitive species are negatively affected to distances of 25–35 m (Fig. 4) along silvicultural edges as old as 11 years, a penetration depth consistent with the findings of most previous edge-response work. This estimate may be conservative because (1) our control stands, although relatively mature compared to the treatment stands, were not as old as many of those used in previous studies, and (2) we lacked information beyond 70 m into the control forest, where further changes in amphibian abundance might conceivably have occurred. With regard to transect length, the limited data available for amphibians near forest edges does not support the notion that edge effects extend beyond 70 m. For example, DeGraaf and Yamasaki (1992) sampled red-backed salamanders across forest edges using cover boards, and although they did not explicitly test for edge-effect distance, they observed an increase in salamander abundance up to 65 m, after which captures declined. In a study of a forest-meadow ecotone in northern Florida, White (1983) reported no significant difference in capture abundance between pitfall traps placed directly at the forest edge and traps located 100 or 200 m into the forest interior. Regardless of the taxon being examined—salamanders, birds, or herbs—determining the inward limit of edge effects is partly a subjective process

because of the largely continuous and gradual nature of changes that occur from the edge to the interior of a forest stand (Chen et al. 1992; Fraver 1994). Nevertheless, empirical information for several forest taxa suggests that the proportion of functional interior habitat declines as the size of continuous forest stands decrease.

Edge Contrast in Forested Landscapes

Edge effects generated by logging practices are often temporary and probably have less impact than effects caused by maintained edges in agricultural landscapes (Whitney & Runkle 1981; Angelstam 1986; Small & Hunter 1988; DeGraaf 1992; Rudnicky & Hunter 1993a, 1993b; McGarigal & McComb 1995). In the short term, however, modern harvest practices often create stand boundaries that contrast greatly in vegetation structure and composition. With a large proportion of eastern forests under management, the cumulative effects of creating extensive amounts of edge habitat over large areas and over long periods of time may be significant for some forest interior species.

It has been speculated that forest edges of high contrast generate more intensive edge effects (Gates & Gysel 1978; Thomas et al. 1979; Harris 1984; Angelstam 1986), but empirical data supporting this notion are limited and conflicting (Ratti & Reese 1988; Yahner et al. 1989; Noss 1991; DeGraaf 1992). Furthermore, edge contrast evaluations are often subjective or based on arbitrary stand-age difference criteria (Helle & Muona 1985; Laurance & Yensen 1991) rather than on objective indices that describe structural habitat differences (McGarigal & McComb 1995). We used a quantitative index of edge contrast based on changes in levels of ambient light penetration across forest edge gradients, a variable that not only provides information on overstory canopy structure but also serves as a potentially valuable index of forest floor microclimate for amphibians (Welsh & Lind 1995, 1996). In this study, ranking sites according to an ambient light penetration index yielded results consistent with the hypothesis that edge effects are strongest along high-contrast stand boundaries (Fig. 5).

Edge contrast is likely to be maximized when target stands are harvested half-way through the rotation age of adjacent maturing stands (Harris 1984), a practice that can lead to reduced amounts of functionally available forest interior habitat. In contrast, natural disturbances seldom create abrupt forest edges characteristic of intensively managed landscapes (Noss & Cooperrider 1994). Disease, windstorms, and even stand-replacing forest fires tend to leave biological legacies of live and dead material that help to lessen the structural contrast between disturbed and intact stands (Hansen et al. 1991). Indeed, many microhabitat features correlated with species abundance in this and previous studies of amphibian habitat relationships—litter depth and type, canopy cover, understory vegetation density, and cover refugia abundance—are directly affected by intensity of forest harvesting. Forest managers who are careful to maintain some portion of these structural elements will probably help minimize edge effects and hasten the rate at which recently harvested stands are colonized by forest interior species.

Acknowledgments

Literature Cited

Ambrose, J. P. and S. P. Bratton. 1990. Trends in landscape heterogeneity along the borders of Great Smokey Mountains National Park. Conservation Biology **4:**135–143.

Angelstam, P. 1986. Predation on ground-nesting bird's nests in relation to predator densities and habitat edge. Oikos **47:**365–373.

Ash, A. N. 1988. Disappearance of salamanders from clearcut plots. Journal of the Elisha Mitchell Scientific Society **104:**116–122.

Baur, A., and B. Baur. 1990. Are roads barriers to dispersal in the land snail *Arianta arbustorum*? Canadian Journal of Zoology **68:**613–617.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence and susceptibility of populations to local and global extinctions. Conservation Biology **8:**60–71.

Blymer, M. J., and B. S. McGinnes. 1977. Observations on possible detrimental effects of clearcutting on terrestrial amphibians. Bulletin of the Maryland Herpetological Society **13:**79–83.

Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest song-birds to decline? Bioscience **33:**31–35.

Brothers, T. S. and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6:**91–100.

Burton, T. M., and G. E. Likens. 1975a. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia **1975:**541–546.

Burton, T. M., and G. E. Likens. 1975b. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology **56:**1068–1080.

Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: abundance of terrestrial herpetofauna related to stand age and moisture. Pages 11–22 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. General technical report RM-166. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Chen, J., J. F. Franklin, and T. A. Spies. 1990. Microclimatic pattern and basic biological responses at the clear-cut edges of old-growth Douglas-fir stands. Northwest Environmental Journal **6:**424–425.

Chen, J., J. F. Franklin and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. Ecological Applications **2:**387–396.

Chen, J., J. F. Franklin, and T. A. Spies. 1993*a*. Contrasting microclimates among clearcut, edge and interior of old-growth Douglas-fir forest. Agricultural and Forest Meterology **63:**219–237.

Chen, J., J. F. Franklin, and T. A. Spies. 1993*b*. An empirical model for predicting diurnal air-temperature gradients from edge into old-growth Douglas-fir forest. Ecological Modelling **67:**179–198.

Clawson, R. G., B. G. Lockaby, and R. H. Jones. 1997. Amphibian responses to helicopter harvesting in forested floodplains of low order, blackwater streams. Forest Ecology and Management **90:**225–235.

Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. Journal of the American Statistical Association **74:**829–836.

Conant, R., and J. T. Collins. 1991. Reptiles and amphibians, eastern/central North America. Houghton Mifflin, Boston.

DeGraaf, R. M. 1987. Managing northern hardwoods for breeding birds. Pages 348–362 in R. D. Nyland, editor. Managing northern hardwoods. Miscellaneous publication no. 13. College of Environmental Science and Forestry, State University of New York, Syracuse, New York.

DeGraaf, R. M. 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. Forest Ecology and Management **46:**95–110.

DeGraaf, R. M., and D. D. Rudis. 1990. Herpetofaunal species composition and relative abundance among three New England forest types. Forest Ecology and Management **32:**155–165.

DeGraaf, R. M., and M. Yamasaki. 1992. A nondestructive technique to monitor the relative abundance of terrestrial salamanders. Wildlife Society Bulletin **20:**260–264.

deMaynadier, P. G. 1996. Patterns of movement and habitat use by amphibians in Maine's managed forests. Ph.D. dissertation. University of Maine, Orono, Maine.

deMaynadier, P. G., and M. L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews **3(3&4):**230–261.

Dodd, K. C., Jr. 1991. Drift fence-associated sampling bias of amphibians at a Florida sandhills temporary pond. Journal of Herpetology **25:**296–301.

Dunson, W. A., R. L. Wyman and E. S. Corbett. 1992. A symposium on amphibian declines and habitat acidification. Journal of Herpetology **26:**349–352.

Dupuis, L. A., J. N. M. Smith, and F. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conservation Biology **9:**645–653.

Enge, K. M., and W. R. Marion. 1986. Effects of clearcutting and site preparations on herpetofauna of a north Florida flatwoods. Forest Ecology and Management **14:**177–192.

Feder, M. E. 1983. Integrating the ecology and physiology of plethondontid salamanders. Herpetologica **39:**291–310.

Fraver, S. 1994. Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. Conservation Biology **8:**822–832.

Gabor, C. R. 1995. Correlational test of Mathis hypothesis that bigger salamanders have better territories. Copeia **1995:**729–735.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology **59:**871–883.

Gibbons, J. W., and R. D. Semlitsch. 1981. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana **7:**1–16.

Hagan, J. M., W. M. Vanderhaegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology **10:**188–202.

Hairston, N. G., Sr. 1987. Community ecology and salamander guilds. Cambridge University Press, Cambridge, United Kingdom.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests: lessons from natural forests. BioScience **41:**382–392.

Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago.

Helle, P., and J. Muona. 1985. Invertebrate numbers in edges between clear-fellings and mature forests in Northern Finland. Silva Fennica **19:**281–294.

Hunter, M. L., J. Albright, and J. Arbuckle. 1992. The amphibians and reptiles of Maine. Bulletin 838. Maine Agricultural Experiment Station, University of Maine, Orono.

Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. American Naturalist **117:**962–974.

Jaeger, R. G., D. Kalvarsky, and N. Shimizu. 1982. Territorial behaviour of the red-backed salamander: expulsion of intruders. Animal Behavior **30:**490–496.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology **5:**173–185.

Kleeberger, S. R., and J. K. Werner. 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. Copeia **1982:**409–415.

Kramer, P., N. Reichenbach, M. Hayslett, and P. Sattler. 1993. Population dynamics and conservation of the Peaks of Otter salamander, *Plethodon hubrichti*. Journal of Herpetology **27:**431–435.

Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation **55:**77–92.

MacCulloch, D., and J. R. Bider. 1975. Phenology, migration, circadian rhythm, and the effect of precipitation on the activity of *Eurycea bislineata* in Quebec. Herpetologica **31:**433–439.

Mader, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation **29:**81–96.

Mathis, A. 1990. Territoriality in a terrestrial salamander: the influence of resource quality and body size. Behaviour **112:**162–175.

Matlack, G. R. 1993. Microenvironment variation within and among deciduous forest edge sites in the eastern United States. Biological Conservation **66:**185–194.

Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology **10:**426–437.

Meier, A. J., S. P. Bratton, and D. C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecological Applications **5:**935–946.

McGarigal, K., and W. C. McComb. 1995. Relationship between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs **65:**235–260.

Mills, S. L. 1995. Edge effects and isolation: redback voles on forest remnants. Conservation Biology **9:**395–403.

Mitchell, J. C., J. A. Wicknick, and C. D. Anthony. 1996. Effects of timber harvesting practices on Peaks of Otter Salamander (*Plethodon hubrichti*) populations. Amphibian & Reptile Conservation **1:**15–19.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10:**58–62.

Noss, R. F. 1991. Effects of edge and internal patchiness on avian habitat use in an old-growth Florida hammock. Natural Areas Journal **11:**34–47.

Noss, R. F., and A. Y. Cooperrider. 1994. Saving nature's legacy. Island Press, Washington, D.C.

Palik, B. J., and P. G. Murphy. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. Forest Ecology and Management **32:**187–202.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology **8:**17–26.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology **7:**363–370.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. Forest Ecology and Management **67:**135–147.

Pough, F. H. 1974. Natural daily temperature acclimation of eastern red efts, *Notophthalmus v. viridescens*. Comparative Biochemistry and Physiology **47A:**71–78.

Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management **20:**1–9.

Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–95 in R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. Pages 23–31 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and mammals in North America. General technical report RM-166. Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service, Fort Collins, Colorado.

Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management **52:**484–491.

Rosenberg, K. V., and M. G. Raphael. 1986. Effect of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263–272 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000. University of Wisconsin Press, Madison.

Rosenfield, R. N., C. M. Morasky, J. Bielefeldt, and W. L. Loope. 1992. Forest fragmentation and island biogeography: a summary and bibliography. Technical report. U.S. National Park Service, Washington, D.C.

Rudnicky, T. C., and M. L. Hunter. 1993*a*. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. Journal of Wildlife Management **57:**358–364.

Rudnicky, T. C., and M. L. Hunter. 1993*b*. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. Ecological Applications **3:**357–366.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology **5:**18–32.

Sayler, A. 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus*, in Maryland. Copeia **1966:**183–193.

Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology Ecology & Evolution **2:**65–79.

Small, M. F., and M. L. Hunter. 1988. Forest fragmentation and avian nest predation in forested landscapes. Oecologia **76:**62–64.

Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. American Naturalist **129:**533–552.

Stebbins, R. C., and N. W. Cohen. 1995. A natural history of amphibians. Princeton University Press, Princeton, New Jersey.

Terborgh, J. W. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey.

Thomas, J. W., C. Maser, and J. E. Rodiek. 1979. Edges. Pages 48–59 in J. W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture handbook no. 553. U.S. Forest Service, Washington, D.C.

Thompson, F. R. and D. E. Capen. 1988. Avian assemblages in seral stages of a Vermont forest. Journal of Wildlife Management **52:**771–777.

Titterington, R. W., H. S. Crawford, and B. N. Burgason. 1979. Songbird responses to commercial clearcutting in Maine spruce-fir forests. Journal of Wildlife Management **43:**602–609.

Vitt, L. J., J. P. Caldwell, H. M. Wilbur, and D. C. Smith. 1990. Amphibians as harbingers of decay. BioScience **40:**418.

Welsh, H. H., Jr., and A. J. Lind. 1991. The structure of the herpetofaunal assemblage in the Douglas-fir hardwood forests of northern California and southwestern Oregon. Pages 394–413 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. Wildlife and vegetation of unmanaged Douglas-fir forests. General technical report PNW-285. Pacific Northwest Research Station, U.S. Forest Service, Portland.

Welsh, H. H., Jr., and A. J. Lind. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus*, in northwestern California. Journal of Herpetology **29:**198–210.

Welsh, H. H., Jr., and A. J. Lind. 1996. Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus*, in northwestern California. Journal of Herpetology **30:**385–398.

Whitcomb, R. F., et al. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–205 in R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

White, D. J. 1983. The herpetofaunal community of an abrupt forest edge in North Florida. M.S. thesis. University of Florida, Gainesville.

Whitney, G. G., and J. R. Runkle. 1981. Edge versus age effects in the development of a beech-maple forest. Oikos **37:**377–381.

Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **66:**1211–1214.

Wilkinson, L., M. Hill, and E. Vang. 1992. Systat for windows. Version 5. Systat Inc., Evanston, Illinois.

Williams-Linera, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. Journal of Ecology **78:**356–373.

Wyman, R. L. In Press. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition, and the carbon cycle. Biodiversity and Conservation.

Yahner, R. H. 1988. Changes in wildlife communities near edges. Conservation Biology **2:**333–339.

Yahner, R. H., and D. P. Scott. 1988. Effects of forest fragmentation on depredation of artificial nests. Journal of Wildlife Management **52:**158–161.

Yahner, R. H., T. E. Morrell, and J. S. Rachael. 1989. Effects of edge contrast on depredation of artificial avian nests. Journal of Wildlife Management **53:**1135–1138.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.