Effects of Timber Harvesting on Southern Appalachian Salamanders

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Abstract: *We compared the species richness and abundance of salamanders on six recent clearcuts (<10 years old) with that of salamanders on 34 mature forest stands (>50 years old) in southern Appalachian forests in western North Carolina, U.S.A. Catches of salamanders from plots in mature forest stands were about five times higher than those on recent clearcuts. Almost all species and major taxonomic groups of salamanders were adversely affected by timber removal. Mean number of species collected per plot was about twice as great in mature forest stands as in clearcuts. Analyses of stand age versus salamander catch for 47 plots indicate that 50–70 years are required for populations to return to predisturbance levels following cutting. We conservatively estimate that clearcutting in U.S. national forests in western North Carolina results in a loss of nearly 14 million salamanders annually. It also is chronically reducing regional populations by more than a quarter of a billion salamanders (9%) below that which could be sustained if mature forests were not cut.*

Efectos de la tala del bosque sobre las salamandras en el sur de los Apalaches

Resumen: *Nosotros comparamos la riqueza de especies y abundancia de las salamandras en seis recientes cortas totales de bosque (<10 años) con la de rodales maduros (>50 años) en los bosques del sur de los Apalaches, en el oeste de Carolina del Norte, Estados Unidos. La captura de salamandras por plot en bosques de rodales maduros fue aproximádamente cinco veces mayor que en aquellos cortados reciéntemente. Casi todas las especies y los mayores grupos taxonómicos de salamandras fueron adversamente afectados por la tala. La media del número de especies capturada por plot fue aproximádamente dos veces mayor en los rodales de bosques maduros que en los cortados reciéntemente. Los análisis de edad del rodal versus captura de salamandras para 47 plots indican que entre 50-70 años son necesarios para que las poblaciones retornen a los niveles previos a la perturbación ocasionada por la tala del bosque.*

Nosotros estimamos en una forma conservadora que la tala de los Bosques Nacionales en el oeste de Carolina del Norte trae como consecuencia una pérdida de alrededor de 14 millones de salamandras anualmente. La tala también está reduciendo crónicamente las poblaciones a nivel regional en más de un cuarto de billones de salamandras (9%) por debajo del nivel que podría ser sostenido por los bosques maduros si no hubieran sido cortados.

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Introduction

Salamanders are important ecological components of many forest ecosystems in North America. In mesic forests in the eastern U.S., salamanders are often the most abundant group of vertebrates in both numbers and biomass (Burton & Likens 1975*a*, 1975*b*; Hairston 1987). Salamanders also play important roles in food webs, where they prey upon small invertebrates and serve as a food source for an array of larger predators (Pough et al. 1987; Corn & Bury 1989).

Despite their importance in many forest systems, salamanders have often been neglected in forest management studies (Bury et al. 1980; Pough et al. 1987). Studies in the Pacific Northwest indicate that many salamander species are adversely affected by timber harvesting (see Bury & Corn 1988; Raphael 1988; Welsch & Lind 1988; Corn & Bury 1989; Welsh 1990). Relatively few studies have been conducted in the eastern United States (Bennett et al. 1980; Enge & Marion 1986; Blymer & McGinnes 1977; Pough et al. 1987; Ash 1988; Buhlmann et al. 1988), and most are difficult to interpret because of lack of replication or pseudoreplication (Hurlbert 1984). Nonetheless, these studies collectively suggest that timber harvesting is detrimental to salamanders in eastern forests.

The southern Appalachians have an extraordinarily rich and and abundant salamander fauna that in many respects is unparalleled worldwide. As many as 35 species belonging to five families occur in the Appalachian region of North Carolina alone (Conant & Collins 1991). In addition, the local biomass of salamanders in southern Appalachian forest communities often exceeds that of all other vertebrate predators combined (Hairston 1987). Prior to the 1960s, timber harvesting often involved intense selective cutting in which all but a few large trees were removed from timbered tracts. Since the 1960s, clearcutting has almost completely replaced selective cutting as the preferred method of timber harvesting by the U.S. Forest Service in the southern Appalachians. Although most clearcuts are relatively small (typically <10–12 ha), they are often cut in larger blocks that are separated by narrow belts of uncut forest.

Almost no published data are available on the impact of clearcutting on southern Appalachian salamanders other than that of Ash (1988), who found that cutting completely eliminated a local population of *Plethodon jordani*. Here, we report on the effects of clearcutting on salamanders in western North Carolina. We also provide data on the recovery times of local populations following timber removal, and on the regional impact of timber removal on salamander abundance.

Methods

Salamanders were sampled between May 16 and August 8, 1991, from 47 sample plots in and adjoining the Craggy Mountains, Pisgah National Forest, Buncombe County, North Carolina (Fig. 1). The work was part of a collaborative effort to document and monitor long-term changes in biodiversity in the southern Appalachians. The study area is located about 25 km northeast of Asheville and encompasses about 6000 ha of mostly mixed mesophytic deciduous forests (Fig. 1). Forty-one sample sites were selected from equidistant points established by randomly placing a grid on a topographic map of the study area. These stands were selected to provide an unbiased estimate of the relative abundance and diversity of salamanders in different communities within the Craggy Mountains. The stands varied in age from 19 to 120 years and ranged in elevation from 817 to 1667 m. Six clearcuts between 2 and 10 years old were also sampled to determine the effects of timber harvesting on species abundance and diversity (Fig. 1). These ranged in elevation from 969 to 1280 m.

At all sites, a 50 × 50 m plot was established parallel and perpendicular to prevailing contours. Plots were centered on permanent plot markers, and each was sampled once by walking roughly parallel transects and turning all movable rocks, logs, bark, and other surface objects that could provide cover for salamanders. Cracks and crevices in rock outcrops were inspected for crevice-dwelling salamanders, and unsubmerged stones and logs in streams or seepages were turned and searched. Search time varied from 1.33 to 4 people-

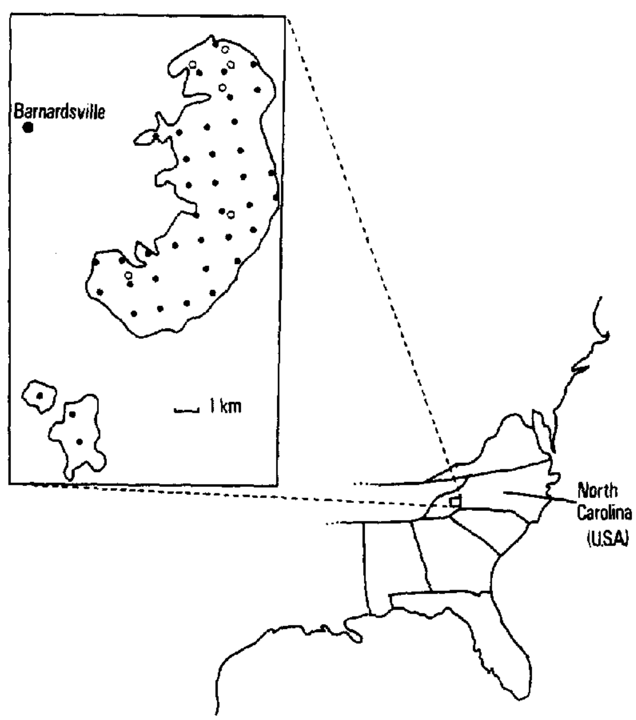

Figure 1. Location of the general study area in western North Carolina. Closed circles indicate the location of plots along grid coordinates. Open circles indicate the location of clearcuts.

hours/plot (mean = 2.38 people hours/plot). Conditions for collecting salamanders were ideal throughout the entire sampling period because of normal to above normal monthly precipitation during the summer of 1991. Specimens were identified to species except in a few instances where large *Desmognathus* specimens could not be captured. Plots in clearcuts were selected haphazardly and were located a minimum of 20 m from adjoining uncut forests. Sampling of clearcuts was staggered throughout the summer to prevent potential bias associated with seasonal changes in the surface activity of certain species.

Ages of forest stands were estimated from U.S. Forest Service CISC (Continuous Inventory of Stand Condition) data, which estimate stand age based on the age of canopy dominants. At four sites CISC data were lacking, and increment borings of the 2–6 largest trees in each stand were used to estimate stand age as a factor.

The effects of clearcutting on salamander populations were analyzed by comparing six clearcut sites less than 10 years old with 34 forest stands more than 50 years old. Stands more than 50 years old were selected for comparison because populations of most species appear to require a minimum of 50 years after mature stands are cut to return to predisturbance levels (see results). Analyses were restricted to the five most abundant species and to major taxonomic groupings. The remaining species were encountered so infrequently that meaningful statistical analyses were not possible.

An analysis of salamander catch as a function of plot age was conducted to provide a first-order approximation of the time required for populations to return to predisturbance levels following the harvesting of mature stands. Plots were grouped into six age categories (<10 years, 11–30 years, 31–50 years, 51–70 years, 71–90 years, >90 years) to allow sufficient sample sizes for detecting overall trends. Regression analysis using data from all 47 plots was used to determine whether salamander catch was dependent on stand age.

Because of the absence or rarity of certain species on clearcut plots, the assumptions of normality and homogeneity of variances were violated in some cases and could not be corrected by data transformations. The assumption of identical distributions for nonparametric rank tests such as the Mann-Whitney test was also clearly violated (see Petranka 1988). Since neither the assumptions of parametric nor of nonparametric tests were met in some instances, we elected to compare group means with the t-test for unequal variances whenever variances among groups differed significantly. All other comparisons were with standard t-tests.

Results

Effects of Stream Presence and Clearcutting on Salamander Abundance and Diversity

A total of 12 species of salamanders (n = 828 animals) was collected on the 47 sample plots (Table 1). Total number of salamanders collected per plot varied from 3 to 49 and averaged 17.6 ± 1.8 (±1 *SE*). Total number of species per plot varied from 1 to 7 and averaged 3.6 ± 0.2.

In mature forests, plots with streams or large seepages (hereafter referred to as "wet sites") averaged 5.0 ± 0.5 species per plot, compared to 3.7 ± 0.2 species per plot on "dry sites" that lacked streams or seepages ($t = -2.59$, $p = 0.01$). The mean number of salamanders collected from wet sites was also significantly higher than that collected from dry sites (31.1 ± 3.48 versus 16.9 ± 1.89; $t = -3.18$, $p = 0.003$). The significantly higher number of species and individuals collected on wet sites is primarily due to the greater abundance of *Desmognathus* species on these plots. *Desmognathus ochrophaeus* averaged 19.7 ± 3.6 individuals/plot on wet sites, compared to 5.3 ± 1.0 individuals/plot on dry sites ($t = -5.17$, $p < 0.0001$). In contrast, *Plethodon jordani* was significantly more abundant on dry sites compared to wet sites (mean = 6.9 ± 1.3 versus 2.9 ± 0.9 animals/plot, $p = 0.01$). The other large *Plethodon*

Table 1. Number and frequency of occurrence of amphibians found on plots.

Taxon	*Common name*	*Number (% of total) collected*	*Frequency of occurrence in plots*
Plethodon jordani	Jordan's salamander	263 (32)	72%
Plethodon glutinosus	slimy salamander	61 (7)	57%
Plethodon yonahlossee	yonahlossee salamander	58 (7)	45%
Plethodon cinereus	red-backed salamander	14 (2)	17%
Desmognathus ochrophaeus	mountain dusky salamander	338 (41)	70%
Desmognathus quadramaculatus	black-bellied salamander	13 (2)	11%
Desmognathus monticola	Seal salamander	2 (<1)	2%
Demognathus wrighti	pigmy salamander	26 (3)	30%
Desmognathus spp.	dusky salamanders	13 (2)	4%
Eurycea wilderae	Blue Ridge two-lined salamander	29 (3)	34%
Gyrinophilus porphyriticus	Spring salamander	3 (<1)	4%
Notophthalmus viridescens	red-spotted newt	8 (1)	13%

species showed similar tendencies, although none of the comparisons was significant. Overall, number of *Plethodon* (*P. jordani, yonahlossee, glutinosus, cinereus*) collected from dry sites was nearly twice than of wet sites (mean = 10.3 versus 4.6 *Plethodon* per plot; $t = -5.16$, $p = 0.0002$). Because the proportion of sites that were wet differed substantially among clearcut and mature forest stands (33% for clearcuts versus 15% for mature stands), wet and dry sites were analyzed separately to prevent confounding of the effects of cutting with those of stream presence.

Overall, clearcuts contained significantly fewer salamanders than mature forest stands did (Fig. 2). Trends for wet sites were generally similar to those of dry sites, although small sample sizes ($n = 2$ clearcuts and 5 mature forest sites) reduced the power of many tests to the point where differences were not significant.

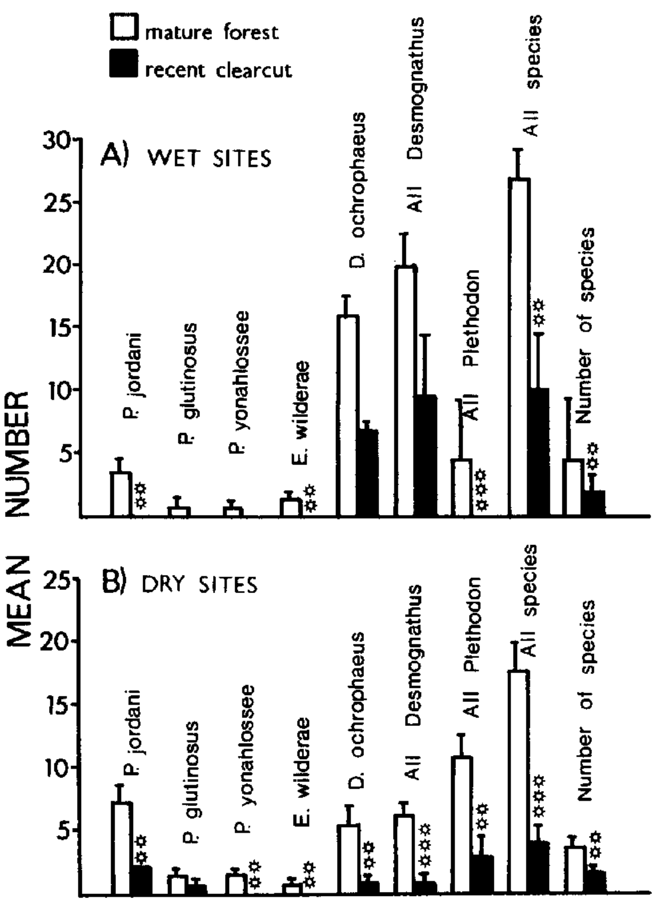

Figure 2. Numeric abundance and species richness of salamanders on recent clearcuts versus mature forest sites. Data on abundance are shown for the five most abundant species, all Desmognathus, *all* Plethodon, *and all species of salamanders combined. The bars on the far right are mean number of species collected per plot. Upper bars are* ±1 SE, *and asterisks indicate means that differ:* * = p < *0.05;* ** = p < *0.01;* *** = p < *0.001.*

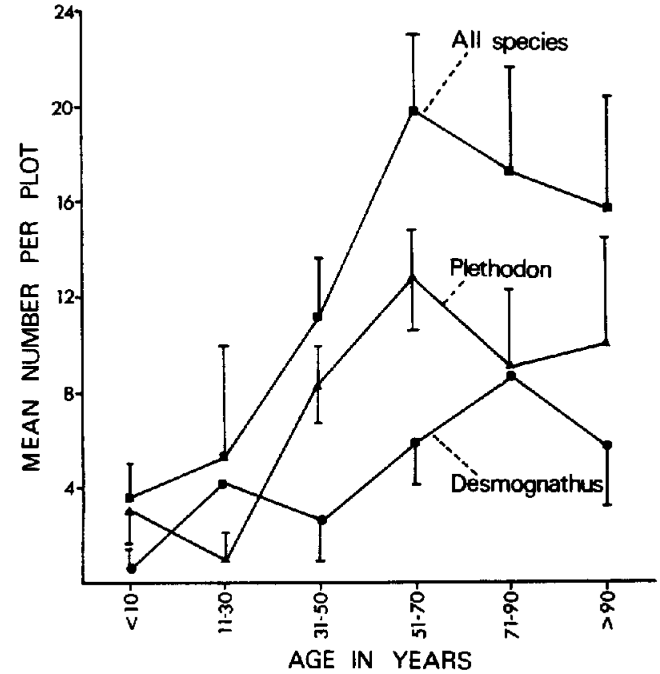

Figure 3. Relationship between stand age and salamander catch on dry sites. Trends are illustrated for total catch of all Desmognathus, *all* Plethodon, *and all species combined. Bars are* ±*1* SE.

Groups that did differ significantly were *P. jordani* ($p = 0.03$), *Eurycea wilderae* ($p = 0.005$), total number of *Plethodon* ($p > 0.001$), and total number of salamanders ($p = 0.01$). Clearcuts on wet sites also had significantly fewer species of amphibians than did mature forest sites on wet sites (respective means = 2.0 versus 4.6 species, $p = 0.007$).

For dry sites, clearcuts contained significantly fewer *P. jordani* ($p = 0.02$), *P. yonahlossee* ($p = 0.006$), *Eurycea wilderae* ($p = 0.01$), and *D. ochrophaeus* ($p = 0.002$) than did mature stands (Fig. 2). These sites also differed significantly in the total number of *Plethodon* ($p = 0.003$), total number of *Desmognathus* ($p = 0.001$), and total number of all salamanders ($p < 0.0001$) found on plots. *Plethodon glutinosus* was the only species tested that did not differ significantly ($p = 0.58$). Overall, densities of salamanders in mature stands were about five times higher than those on recent clearcuts. Total number of species found on clearcuts was also significantly lower ($p = 0.01$), with clearcuts averaging about half as many species of amphibians as mature forest sites (Fig. 2).

Estimates of Recovery Times for Disturbed Communities

General trends among age classes suggest that most salamander species require several decades to return to predisturbance levels (Fig. 3). Overall, total catch per plot increased with stand age for the first 70 years of regrowth ($p = 0.001$), with stand age explaining about 37% of the among-plot variation in total catch. For stands more than 70 years old, total catch of salamanders was independent of stand age ($p = 0.63$). Total number of *Desmognathus* ($p = 0.05$; $r^2 = 0.15$) and total number of *Plethodon* ($p = 0.0004$; $r^2 = 0.35$) captures also correlated significantly with age for stands less than 70 years old, but not for stands more than 70 years old ($p = 0.93$ for *Plethodon*; $p = 0.25$ for *Desmognathus*). Maximum catch per plot occurred in stands 51–70 years old, and was slightly less in older plots. General trends for total *Plethodon* caught and total *Desmognathus* caught were similar (Fig. 3) and suggest that salamander communities require about 50–70 years to recover to preharvest levels. This estimate may be conservative for clearcut sites because it is based on combined data for clearcut and selectively cut sites. Complete estimates of recovery rates on clearcut stands are not available because most clearcut sites are currently less than 30 years old.

Discussion

Impact of Clearcutting on Local Populations and Communities

We found that clearcutting strongly depletes local populations of salamanders and reduces local species richness. We estimate that about 75–80% of salamanders in mature stands are lost following timber harvesting by clearcutting. This estimate is conservative because it includes plots as old as 10 years that may have undergone partial recovery. Although the fate of salamanders on recent clearcuts is unclear, we assume that most died following timber removal and that few salamanders dispersed to surrounding forests.

Most southern Appalachian salamanders are sensitive to environmental disturbances that modify prevailing temperature, humidity, or soil moisture regimes because adults lack lungs and exchange gases almost entirely by cutaneous respiration. Because their skin must be kept moist to facilitate gas exchange, adults generally restrict their activity to moist forest-floor microhabitats and are active on the ground surface only at night when relative humidities are high. Adult plethodontid salamanders may rapidly dehydrate if microhabitats become too dry (see Duellman & Trueb 1986). Clearcutting degrades forest-floor microhabitats for salamanders by eliminating shading, reducing leaf litter, increasing soil-surface temperature, and reducing soil-surface moisture (Bury 1983; Ash 1988; Raphael 1988; Welsch 1990). Consequently, it is likely that most animals died from physiological stress following the removal of trees from sites. Increased sedimentation and general deterioration of stream quality may also have contributed to the decline of species with aquatic larval stages (Corn & Bury 1989).

Dispersal of plethodontid salamanders from plots following cutting is unlikely because adults have small home ranges and are strongly philopatric. Experimentally displaced *Plethodon* and *Desmognathus* species readily home back to their place of capture, and show no tendency to disperse away from home ranges when disturbed or handled (Duellman & Trueb 1986; Hairston 1987). Although certain plethodontids, such as *Desmognathus* and *Eurycea*, move seasonally to and from breeding sites, they are highly sedentary during most of the year.

Because we relied on surface counts to estimate relative population size, it is possible that the reduction in numbers that we observed on clearcuts does not reflect true population declines. One alternative explanation for the apparent decline in salamanders on clearcuts is that decreases in surface moisture following timber removal forced salamanders to move into subsurface retreats during the day. If this were the case, relatively few animals would be expected to be taken in daytime searches. However, studies by Ash (1988) based on nighttime searches of clearcut sites indicate that this is not the case. Ash (1988) intensively studied the effects of clearcutting on *P. jordani* on Rich Mountain South near Highlands, North Carolina, and noted a near complete elimination of this species the second summer after cutting. After the fourth summer, no salamanders were found on cut plots during nighttime searches. Changes associated with the decline of *P. jordani* included elimination of most shading during the first summer and a significant increase in the amount of bare soil. Our findings are consistent with those of Ash (1988) and others (Blymer & McGinnes 1977; Bury 1983; Enge & Marion 1986; Pough et al. 1987; Bury & Corn 1988; Corn & Bury 1989), which indicate that logging significantly reduces amphibian species abundance and diversity.

Impact of Clearcutting on Regional Populations

Because most individuals of forest-floor species such as *Plethodon jordani* and *Desmognathus ochrophaeus* are underground at any given time, daytime surface searches usually uncover only a small percentage of the existing population. Direct counts and mark-recapture studies show that many species in Appalachian forests occur at very high densities. Large *Plethodon* species like *P. jordani* and *P. glutinosus* typically have densities of 0.2–0.9 animals/m^2 of forest floor, while densities of *Desmognathus* species can be much higher on rock faces and near streams and seepages (Table 2). These estimates are conservative because they exclude larval stages of *Desmognathus* as well as young *Plethodon* that spend their first year or so after hatching underground (Hairston 1983).

Based on data provided in Table 2, we conservatively

Table 2. Estimated densities of salamander species based on mark-recapture or direct counts of populations in the Appalachian Mountains.

Species	*Location*	*Number/m²*	*Source*
P. jordani	southern Blue Ridge	0.18	Ash 1988
P. jordani	Great Smoky Mountains	0.26	Ash 1988
P. jordani	Balsam Mountains	0.33	Ash 1988
P. jordani	Great Smoky Mountains	0.86	Merchant 1972
P. jordani	Howards' Knob (Boone, N.C.)	0.50	Howard 1987
P. jordani	(average of all sites)	0.43	
P. glutinosus	Great Smoky Mountains	0.23	Merchant 1972
P. cinereus	Blackrock Mountain, Virginia	2.2	Jaeger 1980
D. ochrophaeus	Howards' Knob (Boone, N.C.)	2.05	Howard 1987
D. ochrophaeus	southern Blue Ridge	18–41*	Huheey & Brandon 1973
D. ochrophaeus	southern Blue Ridge	6–7*	Tilley 1980
D. ochrophaeus	Nantahala Mountains	0.70**	Hairston 1986

* *Rock-face populations whose densities are generally much higher than populations found on the forest floor.*
** *Estimate of forest-floor density based on repeated removals during a single night. Removal of 0.7 animals/m² did not significantly reduce the number of animals emerging from underground retreats, so the actually density was presumably far greater.*
All sites are in North Carolina except where noted.

estimate that *Plethodon* species collectively average 0.5 animals/m² of forest floor in southern Appalachian forests. In the Craggy Mountains, *Plethodon* species constituted only 48% of all salamanders collected (Table 1). Thus, a conservative estimate is that there is at least one salamander/m² of forest floor or about 10,000 salamanders/ha in mature forest stands in the Craggy Mountains. This value seems a reasonable first-order approximation of average densities of salamanders in the southern Appalachians as a whole, although in optimal habitats such as mesic cove forests or stream banks, local densities may be much higher. Howard (1987) estimated 22,608 salamanders/ha in mesic forests near Boone, North Carolina. However, densities of salamanders on dry ridgetops and low-elevation forests with sandy soils are presumably much lower.

Timber harvesting by clearcutting of national forests in western North Carolina has averaged 1,709 ha per year between 1981 and 1990 (personal communication from Ed Brown of the U.S. Forest Service). Assuming an 80% loss of resident animals following cutting and an average density of 10,000 salamanders/ha, we estimate that clearcutting on U.S. Forest Service lands in western North Carolina has eliminated an average of 13.7 million salamanders annually in recent years. Although the absolute number of animals being lost annually is substantial, it constitutes only about 0.34% of the estimated total number of salamanders found in national forests in western North Carolina. (This estimate is based on the percent of national forest holdings cut annually, after correcting for 20% survival in clearcuts).

Despite the fact that the annual loss of animals is less than 0.5%, significant reductions in regional populations could occur because of the long recovery period required for populations to return to predisturbance levels following timber harvesting. An estimate of the long-term effects of cutting on southern Appalachian populations can be obtained by using data on current stand age together with age-specific recovery rates derived from the regression of total salamander catch versus stand age. Using the regression model for stands less than 70 years old, we estimate that if forests continue to be cut at 1981–1990 rates, regional populations will be chronically reduced by about 8.5%, or 267 million animals below the numbers which could be sustained in mature forests. This estimate assumes that 80% of the salamanders are lost after removing timber, that 0.34% of the total salamanders on national forests are eliminated annually by cutting, and that populations fully recover in 50 years. This reduction percentage is similar to that which has occurred historically during the last 50 years, based on a current estimate that 16% of U.S. Forest Service lands in western North Carolina are less than 50 years old (data provided by E. Brown, U.S. Forest Service). Although these estimates are intended only as rough approximations, they provide a feel for the magnitude of losses related to timber harvesting.

Stiven and Bruce (1988) provided evidence that timber harvesting may influence the genetic diversity of local populations of black-bellied salamanders in the southern Appalachians. Our data suggest that the depletion of local populations of terrestrial species by clearcutting may be of sufficient magnitude to produce bottlenecks that would significantly alter genetic diversity. There are now conflicting theoretical views as to how population bottlenecks affect genetic diversity. Some have argued that bottlenecks should lower genetic diversity (Nei et al. 1975), while others have taken the opposite stance (Bryant et al. 1986; Goodnight 1987). Any resolution of the problem will require a more complete understanding of how patch dynamics, the scale of disturbance, and local population dynamics interact to influence regional genetic diversity.

We consider the chronic depletion of populations in national forests in western North Carolina by more than a quarter of a billion animals (9%) to be significant from a regional perspective, particularly when one considers that a significant portion of the eastern U.S. has been deforested since its colonization by Europeans. These losses seem to be sustainable in the sense that none of the species studied is in eminent danger of extinction. However, the chronic depletion of salamanders is clearly contributing to a decline in the general health of south Appalachian forest communities, particularly at the local level were salamander communities are severely perturbed during timber removal.

The estimated average reduction of 9% in numbers does not reflect the fact that the intensity of logging varies regionally. Timber removal tends to be concentrated in areas with moderate slopes that are outside of designated wilderness or recreation areas. Consequently, chronic reductions of salamander numbers in many regions far exceeds 9%. Whether alternative harvesting methods would reduce those losses is uncertain. Selective cutting would presumably have less impact on local salamander populations because the loss of shade and leaf litter following cutting would be reduced. In order to harvest a specific volume of timber, however, selective cutting requires that more acreage be cut than when clearcutting. Exactly how this tradeoff would ultimately affect salamander abundance remains to be determined.

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Literature Cited

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

Bennett, S. H., J. W. Gibbons, and J. Glanville. 1980. Terrestrial activity, abundance, and diversity of amphibians in differently managed forest types. American Midland Naturalist 103:412–616.

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

Bryant, E. H., S. A. McCommas, and L. C. Combs. 1986. The effect of an experimental bottleneck upon quantitative genetic variation in the housefly. Genetics 114:1191–1211.

Buhlmann, K. A., C. A. Pague, J. C. Mitchell, and R. B. Glasgow. 1988. Forestry operations and terrestrial salamanders: techniques in a study of the Cow Knob salamander, *Plethodon punctatus*. Pages 38–44 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and mammals in North America. Technical Report RM-166. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

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

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

Bury, R. B. 1983. Differences in amphibian populations in logged and old-growth redwood forest. Northwest Science 57:167–178.

Bury, R. B., and P. Corn. 1988. Responses of aquatic and streamside amphibians to timber harvest: a review. Pages 165–181 in K. J. Raedeke, editor. Streamside management: riparian wildlife and forestry interactions. Contribution No. 59. Institute of Forest Resources, University of Washington, Seattle, Washington.

Bury, R. B., H. W. Campbell, and N. J. Scott. 1980. Role and importance of nongame wildlife. Pages 197–207 in D. L. Flath and J. R. Torres, editors. Transactions of the 45th North American Wildlife and Natural Resources Conference, 1980. Wildlife Management Institute, Washington, D.C.

Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin, Boston, Massachusetts.

Corn, P. S., and R. B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. Forest Ecology and Management 29:39–57.

Duellman, W. E., and L. Trueb. 1986. Biology of amphibians. McGraw-Hill, New York, New York.

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

Goodnight, C. J. 1987. On the effect of founder events on epistatic genetic variance. Evolution 41:80–91.

Hairston, N. G., Sr. 1983. Growth, survival, and reproduction of *Plethodon jordani*: tradeoffs between selection pressures. Copeia 1983:1024–1035.

Hairston, N. G., Sr. 1986. Species packing in *Desmognathus* salamanders: Experimental demonstration of predation and competition. American Naturalist 127:266–291.

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

Howard, T. A. 1987. Population and biomass estimates in four species of terrestrial plethodontid salamanders. M.S. thesis. Appalachian State University, Boone, North Carolina.

Huheey, J. E., and R. A. Brandon. 1973. Rock-face populations of the mountain salamander, *Desmognathus ochrophaeus*, in North Carolina. Ecological Monographs 43:59–77.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

Jaeger, R. G. 1980. Microhabitats of a terrestrial salamander. Copeia 1980:265–268.

Merchant, H. 1972. Estimated population size and home range of the salamanders *Plethodon jordani* and *Plethodon glutinosus*. Journal of the Washington Academy of Science 62:248–257.

Nei, M., T. Maruyama, and R. Chakroborty. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

Petranka, J. W. 1988. Caught between a rock and a hard place. Herpetologica 46:346–350.

Pough, H. F., 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.

Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in douglas-fir forests of northwestern California. Pages 11–22 in R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and mammals in North America. Technical Report RM-166. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Stiven, A. E., and R. C. Bruce. 1988. Ecological genetics of the salamander *Desmognathus quadramaculatus* from disturbed watersheds in the southern Appalachian Biosphere Reserve Cluster. Conservation Biology 2:194–205.

Tilley, S. G. 1980. Life histories and comparative demography of two salamander populations. Copeia 1980:806–821.

Welsh, H. H., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology 4:309–319.

Welsh, H. H., Jr., and A. J. Lind. 1988. Old growth forests and the distribution of the terrestrial herpetofauna. Pages 439–455 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. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.