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Effects of Timbering on *Plethodon hubrichti* over Twelve Years

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ABSTRACT.—Clearcuts have been shown to adversely affect salamander populations, whereas impacts from milder forms of timbering are more variable. We determined the effects of clearcuts and shelterwood cuts on populations of the Peaks of Otter Salamander (*Plethodon hubrichti*) using counts of surface active salamanders found during multiple night collections. Sampling was done prior to and then periodically after timbering for 12 yr. Overall, the long-term trends in mean number of *P. hubrichti* at reference and shelterwood cut sites were not significantly different. In contrast, means at clearcut sites declined 41% during the first year posttimbering and then declined over the next three years to a low of 75% below pretimbering means. The means stabilized at 45% below pre-timbering means for the remainder of the study. Immediately after timbering 41% of the salamanders moved from transects established at the edge of clearcuts to reference transects that were 3–9 m away. Clearcuts had less canopy closure and dead leaf cover than reference and shelterwood cuts which likely degraded habitat for salamanders. Therefore, clearcutting forests is not advisable because of adverse impacts on salamanders, but forms of timbering that retain a portion of the forest canopy may be acceptable if it can be shown that the timbering method does not reduce salamander populations.

Clearcut harvesting of timber adversely affects salamander populations. Various study designs have been used to assess impacts, with the most common one being a comparison of counts of salamanders found in plots or transects in mature forests with similar plots or transects found in nearby tracts of forests that were clearcut various years prior to the study being conducted (reviewed extensively in deMaynadier and Hunter, 1995; Dupuis and Bunnell, 1999; Grialou et al., 2000; DeGraaf and Yamasaki, 2002). A critical assumption of this approach is that pretimbering population levels in the reference and treatment sites are similar. Because salamander dispersion patterns may be clumped (Kramer et al., 1993), this assumption may not be justified. A more appropriate study design includes pretimbering salamander counts, which has rarely been applied to timbering impacts on salamanders (Ash, 1997; Sattler and Reichenbach, 1998; Knapp et al., 2003). Because the adverse effects of clearcuts are generally great enough, both types of study designs noted above have determined that clearcuts significantly reduce salamander populations.

Two major lingering questions regarding impacts of clearcuts on salamanders are (1) how long does recovery to pretimbering levels take; and (2) what happens to the salamanders on the clearcut sites: do they emigrate or die on

site? The time it takes to return to pretimbering levels has been debated (Ash and Bruce, 1994; Ash and Pollock, 1999; Petranka, 1999), and estimates include 20–24 yr (Ash, 1997) and 50–75 yr (Petranka et al., 1993). The rate of return will vary depending upon the size of the clearcut, forest regrowth rates/litter regeneration rates and physiological and natural history characteristics of the salamander species impacted (Ash, 1997). The fate of salamanders on clearcut sites has not been investigated (Petranka et al., 1994).

Timbering treatments other than clearcuts are less frequently examined with regard to their impacts on salamander abundance. Alternative timbering practices involve some type of thinning such as shelterwood cuts where a portion of the basal area is retained; hence, the canopy is left intact to varying degrees. Both study designs noted above have been used to assess impacts from alternative timbering practices. The results have been more variable with some studies showing no impacts (Mitchell, et al., 1996; Messere and Ducey, 1998; Brooks, 1999; Grialou, et al., 2000), whereas others have shown minimal or short-term impacts (Sattler and Reichenbach, 1998; Harpole and Haas, 1999; Brooks, 2001) to long-term impacts (Herbeck and Larsen, 1999). Only Harpole and Haas (1999) and Sattler and Reichenbach (1998) used the study design that includes pretimbering salamander abundance data. Because the effects of timbering practices such as shelterwood cuts are likely to be less dramatic than clearcuts, study designs with the least number of assump-

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tions should be selected, such as those including pretimbering data.

We examined the impact of clearcuts and shelterwood cuts on the Peaks of Otter Salamander (*Plethodon hubrichti*), an endemic species found in a small portion of the Blue Ridge Mountains, Virginia. Much of its range is located on lands managed by the National Forest Service where timbering is permitted. Earlier we reported on the short-term effects of timbering on the Peaks of Otter Salamander (Sattler and Reichenbach, 1998), and here we examine (1) the effects of timbering on counts of surface-active salamanders over a 12-yr post-timbering period, (2) salamander movement in response to timbering, (3) vegetation parameters among the timbering treatments, and (4) the validity of counts of surface active salamanders as an index of population size.

MATERIALS AND METHODS

Sattler and Reichenbach (1998) detailed the methods used in this study. Here, we briefly summarize our methods used previously, plus describe additional methods used to analyze our data. Twelve sites were randomly assigned to three treatments (four sites per treatment): reference (no timbering), shelterwood cut (partial removal of canopy), and clearcut (total removal of canopy). We surveyed *P. hubrichti* one year prior to (1993) and multiple years after timbering (1994, 1995, 1997, 1999, 2001, and 2005). At each site, surface-active salamanders were counted on rainy nights in one 5×5 m plot. Two groups of four people surveyed plots at all 12 sites during a single night in order to (1) complete the survey during the two- to three-hour window of time when *P. hubrichti* have the highest level of surface activity, and (2) avoid temporal variation in salamander counts that can be high (Kramer et al., 1993). We also randomized the order in which sites were surveyed.

In 1993, baseline data were established for all 12 sites during 10 night surveys. We then used cumulative means to determine the number of surveys needed per year. If the mean following our 10th survey in 1993 was considered the most accurate statistic characterizing the surface-active salamanders, then our question was how many surveys do we need in order to be within 10% of that mean?

The four shelterwood cut and clearcut sites were timbered in May 1994. Following timbering, seven to eight surveys were conducted during each year noted above. Mean numbers of *P. hubrichti* were calculated per site for each year. Repeated-measures ANOVA with Huynh-Feldt adjustments to the probability levels

(SYSTAT, vers. 6.0 for Windows, SPSS, Inc., Chicago, 1996) was used to assess impacts since the means were repeated, nonindependent, measurements taken over time at each site (Sattler and Reichenbach, 1998). The reference site was compared pairwise with shelterwood cut and clearcut sites. The interaction between treatment and time was the key model parameter since this would indicate whether the populations at reference sites were changing differently from those at the timbered sites. If the treatment and time interaction or the time effect alone was significant ($P < 0.05$), the sums of squares were decomposed into linear through higher order polynomials. Adjustments were made to the polynomials to account for the uneven spacing for the years we collected data. A final check between pretimbering counts and counts obtained during the last year of the study was done with *t*-tests on the difference between counts using a one-tailed test since previous studies indicate that populations never increase relative to controls following timbering. For clearcut sites, a repeated-measures ANOVA with Huynh-Feldt adjustments to the probability levels was used to assess a time effect from the posttimbering year where the counts of salamanders were the lowest (1997) to the last year of the study to determine whether recovery was occurring. If there was a significant time effect, this would be evidence of sustained recovery.

Sattler and Reichenbach (1998) estimated population size at three of the 12 study sites (one site per treatment for the pretimbering year and two posttimbering years using the Jolly-Seber method for open populations). We examined correlations between our surface-active salamander counts (mean, median, minimum, and maximum counts) and these population estimates. The summary statistic that correlated to the highest degree with the population estimates was then used in a regression for estimating population size using counts of surface-active salamanders. Densities for characterizing nontimbered sites were calculated from population size estimates using the regression equation just noted and the mean surface active salamanders/25 m² for reference sites and pretimbering mean surface active salamanders/25 m² from shelterwood cut and clearcut sites. Densities were also calculated based strictly upon counts of surface active salamanders.

Sattler and Reichenbach (1998) noted high temporal and spatial variability in the surface-active salamander counts. To examine temporal variability in 2005, we placed a weather station (Vantage Pro2 weather station, Davis Instruments, Hayward, California) in our study area

that hourly measured parameters such as air temperature and rainfall. In addition, four moisture probes were placed under rocks and logs and under and within leaf litter. These measurements were also recorded hourly. We assessed several environmental parameters to determine whether they correlated with counts of surface-active salamanders. These included the maximum and minimum air temperature, mean leaf litter moisture (within the leaf litter and below the leaf litter), log and soil (under a rock) moisture and the rainfall amount on the day of the survey. Variables calculated from information prior to the survey day included rainfall on the previous day, rainfall summed over the survey day and the previous day, difference between rainfall on the collection and previous day, days since the last rainfall, and number of dry days 2, 4, 6, 8, 10, and 12 days before the survey day. Pearson correlation coefficients were calculated per site for counts of salamanders against these environmental variables. In addition, in order to consider data across sites with different mean abundances of salamanders, the abundance data for each collection period were taken as deviations from the mean number of salamanders per site.

Midway through our study (on 3 August 1999) we measured a variety of environmental variables on each plot. Percent canopy closure was recorded based on measurements along two transects across each plot at 1-m intervals. A GRS densitometer (Geographic Resource Solutions, Arcata, California) was used at 12 points per plot to determine the degree to which the canopy was open. Data were collected at the ground level and at 3 m while standing on a 2-m ladder. Soil moisture was measured by compositing soil collected from four quadrants of each plot. The sample was weighed and then dried to a constant mass. Percent moisture was then calculated using the difference in weight. A portion of the remaining soil had distilled water filtered through it and then the filtrate was evaluated with a pH meter as an estimate of soil pH. Percent ground cover was evaluated with a 0.5-m quadrant with 36 hazard points that was laid on the ground (i.e., the herbaceous vegetation was moved aside). At each point, the cover was categorized as leaves, rock, bare soil, branches, or stumps, and a percent was calculated for each category. Soil temperature in each quadrant of the plot was measured using a soil thermometer, and air temperature was recorded in the shade approximately 1 m above the forest floor in each quadrant of the plot. Finally, diameter at breast height (dbh) was recorded from the five largest trees in or nearest to the plot. Means per plot were calculated for soil and air temperatures and dbh. Principal component

analysis (PCA) was used to reduce the environmental variables into a smaller set of factors used in bivariate plots to see which factors distinguished the treatments.

In order to assess the potential for emigration at clearcut sites, an additional study was conducted in our study area. Four transects, each 6×100 m were established: two transects were reference transects and were not timbered and the other two were designated to be clearcut in June 1997. The sites were paired so that one reference and one clearcut transect ran parallel to each other, separated by a 6-m wide buffer area. When timbering occurred, the timbered area included half the buffer area (3 m wide portion of the buffer), the clearcut transect, and an area about 20 m beyond the transect. Prior to timbering, during fall (1996) and spring (1997), *P. hubrichti* were collected in the transects and uniquely marked by toe clipping. Salamanders in the 6-m buffer area between the pairs of transects were not marked. After timbering was initiated, salamanders were no longer marked. For two nights immediately following timbering, and five subsequent rainy nights, at least one pair of transects (one reference and one clearcut) was searched for salamanders. Recaptured salamanders allowed us to construct a 2×2 contingency table comparing for each treatment the number of salamanders remaining in the transect where they were originally captured to those that moved to the adjacent transect. Prior to this analysis, we constructed a similar contingency table for comparison of the two reference and two clearcut transects to see whether salamander movement patterns were homogeneous.

RESULTS

From 1993 to 2005, 3,441 salamanders were sighted on the plots. Of these, 94.8% were *P. hubrichti*, 4.04% *Plethodon cylindraceus*, 0.9% *Eurycea cirrigera*, 0.17% *Gyrinophilus porphyriticus*, 0.06% *Notophthalmus viridescens*, and 0.03% *Desmognathus* sp.

Cumulative means for the 10 surveys conducted per site in 1993 showed that the number of surveys needed to estimate a mean for surface active salamanders that would be within $\pm 10\%$ of the mean for all 10 surveys ranged from two to 10 (one site required two surveys; three sites, three surveys; one site, four surveys; five sites, seven surveys; one site, eight surveys; one site, 10 surveys). The modal value was seven, and this was selected as the minimum number of surveys to be conducted per site during each of the subsequent years of the study.

The pattern of change over time for the number of *P. hubrichti* at the reference sites was significantly different from the clearcut sites (repeated-measures ANOVA for treatment \times time interaction: $F_{6, 36} = 4.6$, Huynh-Feldt $P = 0.002$). Polynomials for this interaction indicated that the cubic polynomial accounted for 77.6% (cubic polynomial SS/interaction SS) of the change across time. Relative to 1993 (the year before timbering occurred), counts of salamanders at reference sites increased 23% (percentages based upon means across sites per treatment) in 1994 and then decreased 33% from 1994 to 2001 and then increased again 26% in 2005 (Fig. 1). In contrast, counts of salamanders at clearcut sites relative to pretimbering levels declined 41% during the first year when timbering occurred (spring of 1994) and then dropped to a low of 75% in 1997. In 1999, the counts rose and were 39% below pretimbering counts. Counts were stable beyond 1999 and finished in 2005 at 45% below pretimbering counts (Fig. 1). Differences in counts between 1993 and 2005 were significantly lower for clearcut sites relative to reference sites ($t_6 = 2.3$, $P = 0.03$; mean differences = 1.8 and -2.0 for reference and clearcut sites, respectively). For clearcut sites, 1997 to 2005, the time effect was not significant ($F_{3,9} = 4.6$, $P = 0.1$); hence, we cannot project beyond the time limit of our study to determine when posttimbering levels would equal pretimbering levels.

The pattern of change over time for the number of *P. hubrichti* at reference sites was not significantly different from shelterwood cut sites (repeated-measures ANOVA for treatment \times time interaction: $F_{6, 36} = 1.5$, Huynh-Feldt $P = 0.2$). Both treatments showed a significant, but similar, time effect (repeated-measures ANOVA for time: $F_{6, 36} = 1.5$, Huynh-Feldt $P = 0.001$), and the polynomials that accounted for most of the change over time were quadratic and cubic ones, 67.3% and 24.3%, respectively. Counts on shelterwood cut sites were stable for most of the study (Fig. 1). Between 1994 and 2001, counts ranged from a decline of 16% to an increase of 7%, and then in 2005, counts rose by 68% relative to 1993 counts. Although counts of salamanders at reference sites were more cyclical than those for shelterwood cut sites, long-term they both followed a similar pattern with higher counts of salamanders in 2005 relative to the first year of the study (Fig. 1). Differences in counts between 1993 and 2005 were not significantly lower for shelterwood cut sites relative to reference sites ($t_6 = 0.7$, $P = 0.26$; mean differences = 1.8 and 3.0 for reference and shelterwood cut sites, respectively).

Only means and medians of counts of surface-active salamanders were significantly

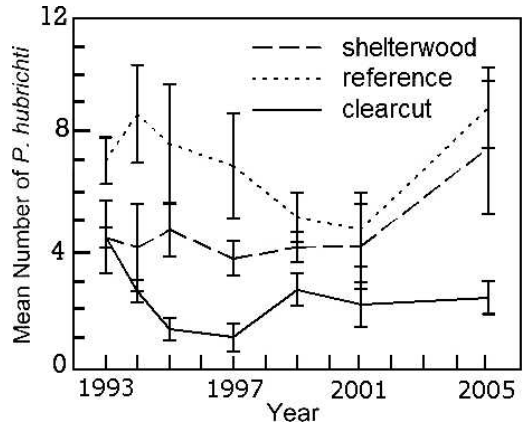


FIG. 1. Mean number (± 1 SE) of surface-active *Plethodon hubrichti* collected during night surveys conducted prior to timbering (1993, $N = 10$ per plot for each of four sites per treatment) and over a 12-yr period after timbering ($N = 8$ per plot per site except for years 1997 and 2001 where $N = 7$) for reference, shelterwood cut, and clearcut sites.

correlated with our population estimates ($r = 0.960$ and 0.956 , respectively). The linear regression fit to the data relating mean number surface-active salamanders to the population estimates in a 25-m² area is shown in Figure 2. Densities, based upon population estimates derived from this regression model, for non-timbered sites (reference and pretimbering data for shelterwood and clearcut sites) averaged 2.7/m² and ranged from 0.5–7.7/m². For these same sites, using counts of surface-active salamanders, densities averaged 0.21/m² and ranged from 0.08–0.50/m². Using only the reference site plots, the mean number of surface-active salamanders was 0.28/m² and ranged from 0.19–0.35/m² during the 13 yr of this study.

Temporal variability was high for surface counts of *P. hubrichti*. During the last year of the study, counts for two sites ranged from 1–29 and 3–31. The typical coefficient of variation (CV) for a site in a given year was 0.5 (Sattler and Reichenbach, 1998). The only weather variables tested that were significantly correlated ($P < 0.05$, $N = 84$) to surface counts of *P. hubrichti* were ones associated with no rain during the days prior to the survey day. For individual sites, the correlation coefficient ranged from ones that were not significantly different from zero to a high of 0.94. For all sites, the two highest correlation coefficients were 0.52 and 0.50 for number of dry days four and 12 days before the survey day, respectively. Essentially these variables are assessing how dry the conditions were prior to the survey day, which was conducted during rainy weather.

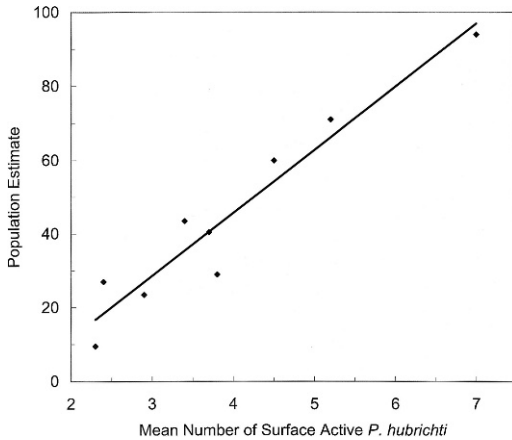


FIG. 2. Mean number of surface-active *Plethodon hubrichti*/25 m² in relation to population estimates from plots in reference, clearcut, and shelterwood cut sites during 1993, 1994, and 1995. Population estimate = $-22.543 + 17.071$ (mean surface-active *P. hubrichti*/25 m²; $N = 9$, $r^2 = 0.92$, $P < 0.001$)

Reference and shelterwood cut sites were distinguishable from the clearcut sites using bivariate plots of the first and second PCA factors (Fig. 3). This first factor ($\lambda = 4.5$, variance explained = 41.4%) was a contrast of parameters (parameter followed by component loading) associated with a canopy: trees with large dbh (0.90), closed canopy when viewed from a 3-m height (0.84) and dead leaves on the forest floor (0.86) versus bare soil on the forest floor (-0.87; all other component loadings ≤ 0.58). Relative to clearcut sites, reference sites and shelterwood cut sites had large trees (mean dbh = 52.2 cm), high percent of canopy closure (84.4%), high percent of cover of the forest floor by dead leaves (69.8%), and low percent of bare soil (14.8%; Table 1). Values for clearcut sites were 12 cm for mean dbh, 35.5% for canopy closure, 37.2% cover of the forest floor by dead leaves, and 39.5% bare soil (Table 1). The second factor ($\lambda = 2.4$, variance explained = 21.5) was a contrast of soil moisture (0.91) and pH (-0.93; all other component loadings ≤ 0.59). As soil moisture increased, soil pH decreased. The timbering treatments were not distinguishable on the bivariate plots using the second PCA factor.

Two hundred seventy-four and 364 *P. hubrichti* were marked in two reference and two clearcut transects, respectively, which were used to assess salamander movements in response to timbering. The two reference and two clearcut transects were homogeneous with regard to number of salamanders that stayed and moved (reference transects $\chi^2_1 = 0.17$, $P =$

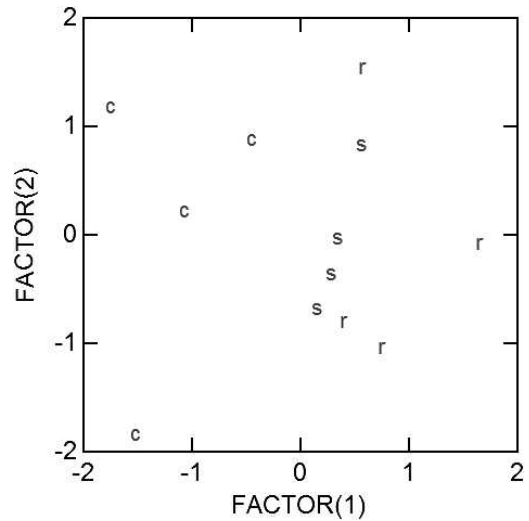


FIG. 3. Factors 1 and 2 from the principal components analysis of the habitat data. Factor 1 is a contrast of parameters associated with a canopy (large diameter at breast height, closed canopy at 2-m height, and dead leaves on the forest floor vs. bare soil on the forest floor). Factor 2 is a contrast of soil moisture and pH. The symbols represent data for the plots associated with clearcut (c), shelterwood cut (s), and reference (r) sites.

0.67; clearcut transects $\chi^2_1 = 0.22$, $P = 0.64$). The data were then pooled across transects per treatment, and the number of salamanders that moved and stayed were compared across treatments. Ninety-four salamanders from reference transects were recaptured. Ninety-three stayed in the reference transects and one moved to the clearcut transects. Sixty-eight salamanders were recaptured from the clearcut transects. Forty stayed in the clearcut transects, and 28 moved to the reference transects. The differences in the numbers that stayed or moved was not homogeneous for the two treatments ($\chi^2_1 = 43.2$, $P < 0.001$) with 41% of the salamanders moving from clearcut transects to reference transects during the year timbering occurred.

DISCUSSION

Within its limited range in the Blue Ridge Mountains, *P. hubrichti* dominates the terrestrial salamander community (e.g., it made up 94.8% of the species observed in this study). Densities, using counts of surface-active salamanders, averaged 0.21/m² and ranged from 0.08–0.50/m². These density estimates are similar to a previous estimate for *P. hubrichti* from a 10 × 10 m plot (0.24 ± 0.1 salamanders/m²; Kramer, et al., 1993).

TABLE 1. Habitat data (mean \pm 1SD) for the 12 sites used to assess the effects of timbering on *Plethodon hubrichti*.

Habitat parameter	Reference sites	Shelterwood cut sites	Clearcut sites
Leaves (%)	68.9 \pm 13.1	70.7 \pm 12.3	37.2 \pm 7.6
Rock (%)	1.2 \pm 1.6	3.1 \pm 4.9	9.4 \pm 7.2
Bare soil (%)	16.0 \pm 13.5	13.5 \pm 4.5	39.5 \pm 9.8
Branches (%)	13.9 \pm 7.2	10.7 \pm 7.3	10.9 \pm 7.4
Stumps (%)	0.0 \pm 0.0	2.1 \pm 2.5	3.1 \pm 6.3
pH	5.3 \pm 0.2	5.3 \pm 0.1	5.3 \pm 0.3
Canopy closure viewed from ground level (%)	93.8 \pm 12.5	83.3 \pm 20.5	77.3 \pm 17.4
Canopy closure viewed from 3-m height (%)	87.5 \pm 10.8	81.3 \pm 23.9	35.5 \pm 14.2
Mean diameter at breast height	58.7 \pm 15.4	45.8 \pm 10.3	12.0 \pm 0.9
Soil moisture (%)	17.0 \pm 7.1	16.8 \pm 2.1	16.8 \pm 6.2
Soil temperature ($^{\circ}$ C)	17.1 \pm 0.5	18.0 \pm 0.4	18.3 \pm 0.6
Air temperature ($^{\circ}$ C)	21.7 \pm 5.2	22.6 \pm 2.2	23.5 \pm 1.9

Surface counts explained a great deal of the variability found in our population estimates ($r^2 = 0.92$) and, therefore, was a good predictor of population size. Smith and Petranka (2000) found similar high correlations between mean surface catch and mark-recapture estimates of salamanders found in closed-canopy forests. Since our data include counts of surface-active *P. hubrichti* and population estimates one year prior and then two years posttimbering for reference, shelterwood cut, and clearcut sites, we found that mean surface counts can be used to estimate population size under both closed- and open-canopy forests.

Temporal variability for surface counts of *P. hubrichti* was high (CV per site = 0.5; Sattler and Reichenbach, 1998), and seven or more surveys were required to stabilize the means per site. Temporal variability is, in part, caused by the degree of dryness before the collection night. The more dry days four days before the collection night, the higher the number of surface-active salamanders ($r = 0.52$). Salamanders have low energy requirements and are susceptible to desiccation (Feder, 1983) and, hence, only periodically need to come to the surface to feed when the humidity is high. At the surface, they will forage in the leaf litter or sit on vegetation where they wait for prey (Kramer, et al., 1993). The greatest number of surface-active salamanders was found when our collection day was preceded by several dry days, there was soaking rain during the collection day, and the rain ended before the evening collection started. If more than a light rain fell while we were collecting, salamanders would often abandon their positions on vegetation and would no longer be visible. The impact of rain during the collection period would have to be measured for each site during the collection period in order to assess its impact on the number of surface-active salamanders.

Clearcuts had a significant and long-lasting impact on *P. hubrichti*, with counts of surface-active salamanders declining by 75% two years after timbering. The counts of salamanders began to show signs of recovery five years after clearcutting but then stabilized at 45% below pre-timbering levels for the duration of the study. In contrast, shelterwood cuts did not have any significant long-term impacts on salamander abundance. Sattler and Reichenbach (1998) noted that, during the first two years post-timbering, the fraction of juvenile to adult animals was similar between clearcut and shelterwood cuts and both were lower than in the reference sites. We suggest that this effect may be the reason why salamander abundance at shelterwood cut sites did not increase like those at the reference sites immediately following timbering (Fig. 1). Longer-term, from 2001–2005, when salamander abundance rose in reference sites, counts at shelterwood cut sites paralleled those from reference sites (Fig. 1).

Qualitatively, canopy and ground cover for sites receiving the shelterwood cut treatment were similar to reference sites. Five years after timbering our quantitative assessment of the habitat confirmed the similarity between reference sites and shelterwood cut sites with regard to canopy closure (both averaging 84.4%) and dead leaf cover on the forest floor (both averaging 69.8%). Clearcut sites were easily distinguished from the reference and clearcut sites in having less canopy closure (35.5%) and only 37.2% dead leaf cover on the forest floor. The reduction in canopy closure for clearcut sites relative to the reference and shelterwood cut sites would likely increase exposure of the forest floor to sun and wind. This along with the reduced dead leaf cover would decrease habitat quality for salamanders. Because of the impact clearcutting has on not only the Peaks of Otter Salamander but also the forest in general

(Covington, 1981; Seastedt and Crossley, 1981; Duffy and Meier, 1992), the George Washington and Jefferson National Forest Service no longer permits clearcutting on the land they manage (George Washington and Jefferson National Forests, U.S. Fish and Wildlife Services, and Blue Ridge Parkway National Park Service, Habitat conservation assessment for the Peaks of Otter Salamander [*Plethodon hubrichti*], 1997).

The losses noted above on clearcut sites may be, in part, caused by emigration. Forty-one percent of the salamanders recaptured from transects that were clearcut moved to adjacent reference transects. Therefore, if the salamander's habitat is significantly degraded, a portion of the residents, even residents like the strongly philopatric Plethodontids (Merchant, 1972; Kramer, et al., 1993), which were living near the clearcut edge, may attempt to relocate to more favorable habitats. Whether salamanders living in the interior of a clearcut site would move longer distances to intact forests and whether any of the emigrating animals would be able to survive in their new location is unknown.

Although the adverse effects of clearcutting on salamander populations is consistent across different forest types and salamander species, the impacts from timbering treatments that do not completely remove the forest canopy such as shelterwood cuts are less consistent (see introduction). Our shelterwood cuts reduced the basal area per site by 33–64%. This would have left basal areas ranging from 9.1–18.3 m²/ha, which is comparable to the one shelterwood cut site used in the study by Harpole and Haas (1999: 12–15 m²/ha). They noted significant declines in salamander abundances, whereas we noted only short-term reductions in juveniles. Although clearcuts should not be recommended because of the adverse effects on forest ecosystems, forms of timbering that do not completely remove the canopy may be an acceptable compromise in areas like National Forests where timbering is permitted. If it can be demonstrated that the proposed timbering does not reduce salamander populations long-term, then, at least with regard to salamander populations, this type of timbering could be permitted.

Changes in the reference sites are of interest to discerning declines in amphibian populations. If we only looked at the data from 1994 through 2001, we would have determined that the Peaks of Otter Salamander had experienced a 33% decline over an eight-year period. Others have seen declines in amphibian populations since the 1950s (Houlahan et al., 2000). Reanalysis of data used by Houlahan et al. (2000) by Alford et al. (2001) indicated that evidence for global declines in amphibian populations was

evident only in the 1990s. Had we stopped our study in 2001, we might have added the Peaks of Otter Salamander to the list of amphibian species showing declines. But in 2005, our populations rebounded to levels exceeding pretimbering levels. It may be that salamander populations oscillate even in stable, mature forests. Counts of surface active *P. hubrichti* at our reference site plots show one full oscillation around a mean of 0.28/m² and a range of 0.19–0.35/m² during the 13 yr of this study.

Our study took place in the core of the Peaks of Otter Salamander's range. If the mature hardwood forests persist in this area, *P. hubrichti* appears secure since it is the most common terrestrial salamander in the area and since clearcutting is not permitted in the core of its range. The major concern is with the populations at the boundary of its range where it comes in contact with *P. cinereus*, a widespread species and potential competitor. Limited information exists that suggests that the contact zone is static in areas where timbering has not occurred (Wicknick, 1995; Aasen and Reichenbach, 2003). A question for future research is whether this balance is disturbed in areas where timbering occurs.

Overall, our data show that mean counts of surface-active *P. hubrichti* at reference and shelterwood cut sites followed similar long-term trends. In contrast, mean counts at clearcut sites remained below pretimbering levels and full recovery was not evident 12 yr after timbering. Clearcuts degraded salamander habitat since, relative to reference and shelterwood cut sites, clearcut sites had less canopy closure and dead leaf cover. Some of the declines at the clearcut sites were likely caused by emigration since immediately after timbering 41% of the salamanders moved from the edge of clearcuts to nearby reference transects. Therefore, clearcuts are not recommended for harvesting timber because of their adverse effects on salamanders. In contrast, shelterwood cuts could be used to harvest timber in areas where *P. hubrichti* is allotopic with *P. cinereus* since in these areas we showed this type of timbering did not reduce *P. hubrichti* populations long term.

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