Recovery of Salamanders after Clearcutting in the Southern Appalachians: A Critique of Ash's Estimates

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Based on data gathered on regenerating clearcuts, Ash (1997) concluded that populations of salamanders are almost completely eliminated from plots in southern Appalachian forests within 2 years of timber harvesting and that "linear regressions estimate that salamander numbers on clearcut plots will equal or exceed numbers on forested plots by 20–24 years after cutting." The former finding is consistent with other studies showing that local populations undergo severe population crashes after clearcutting (Ash 1988; Petranka et al. 1993, 1994). The estimate of full recovery time, however, is less than other estimates for the southern Appalachians (50–70 years for forests at similar elevations; Petranka et al. 1993). Although recovery rates vary with local site conditions, studies to date suggest that populations of plethodontid salamanders in the eastern United States require 30–60 years to recover to postcut levels after mature hardwood forests are clearcut (deMaynadier & Hunter 1995). I critique Ash's estimates of recovery times and discuss potential biases that may explain discrepancies between this and previous studies.

Ash's basic protocol involved sampling salamanders (mostly *Plethodon jordani*) on 225-m^2 plots established in three clearcuts and in matching control areas in nearby forests. Each clearcut contained either a single plot (site RK in all years and site BC in 2 of 5 sample years) or two plots (site BC in 3 of 5 years and site RMS in all years). Matched plots at the sites (either one or two per site) were established in nearby forests and served as controls. At two of the sites (RK and BC), precut censuses revealed that salamanders were more abundant on future clearcut plots than control plots (for BC 22% higher on clearcuts than controls; for RK 58% higher on clearcuts than controls). Control plots were 40 and 70 m from clearcuts at RMS (Ash 1988), but distances were not reported for other sites (overall, plots were estimated to be 30–150 m from the edge; A. Ash, personal communication). Clearcut plots were 40–120 m from the forest edge (Ash 1988, 1997).

Ash monitored recovery by calculating an abundance index (AI), which expresses the number of salamanders on clearcuts as a percentage of the number on matching control plots. For clearcuts with two plots, he calculated a separate AI for each clearcut plot by dividing the number of salamanders on each plot by the mean number of salamanders on the two control plots; each AI was used as an independent data point in statistical analyses. Clearcuts and matching control plots were sampled at different intervals after timber removal as follows: RMS, years 1, 2, 4, 13, 14, and 15; RK, year 1 only; BC, years 1, 6, 7, and 8. Data collected from the same plot in different years were used as independent data points in statistical tests. Estimates of recovery time were based primarily on a regression analysis using data collected from two clearcut sites during 3 consecutive years. In this analysis, data collected from adjoining plots on the same clearcut, or data collected from the same plot in different years, were used as independent data points in the regression. Recovery was measured as the percentage of salamanders on clearcut plots relative to that on control plots.

I have reservations about these methodologies because the experimental design exhibits pseudoreplication, because Ash failed to use data from precut censuses to estimate recovery times, and because biases associated with the use of the abundance index may exist. There are numerous instances of pseudoreplication, and most data used in the statistical tests violate the assumption of independence of data points. The basic sampling unit is a clearcut ($n = 3$) along with the adjoining forest ($n = 3$). Pseudoreplication occurred because Ash used data from plots located in the same clearcut (or adjoining forest) and from the same plot in different years as independent data points. Standard statistical procedures require that mean values be used in statistical tests whenever data are collected from two or more subunits within the same sampling unit. Similarly, when repeated measures are made of the same sampling unit

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(plot in this case), these data cannot be used as independent measures of treatment effects if there is evidence of autocorrelation.

Because most statistical tests used by Ash (1997) are based on pseudoreplication and inflated degrees of freedom, meaningful statistical inferences cannot be made from the results. For example, in his Table 2 Ash used analysis of variance (ANOVA) to compare forested plots during the disappearance phase and concluded that population size does not differ significantly among sites. His sample size is eight, based on repeated samples on the same four plots during 2 consecutive years. In reality, there was no true replication at two of the three sites (only one control plot at each site). Consequently, there is no independent measure of within-treatment variation at each site, and ANOVA cannot be used legitimately to compare sites during the disappearance phase.

The regression analysis from which Ash estimates recovery periods suffers from similar problems of pseudoreplication. One assumption of regression analysis is that the data points are independent of one another. Ash shows 12 data points in each of his two regressions that come from only two sampling units (clearcuts). Most of these clearly violate the assumption of independence because they reflect either samples of adjoining plots on the same clearcut (spatial autocorrelation) or samples of the same plot during consecutive or nearly consecutive years (temporal autocorrelation). In the latter case, unless Ash can make a forceful argument that there is a near complete turnover of salamanders on clearcuts annually, which is highly unlikely, then he has violated the assumption of independence. A legitimate analysis would require that each data point come from either a separate clearcut or that the same plot be sampled a sufficient number of years apart to assure that the data points are independent. Because the mean generation time of *P. jordani* is nearly 10 years (Hairston 1983*a*), data from repeated sampling at 1- or 2-year intervals clearly would not be independent (Pechmann & Wilbur 1994). Ash could legitimately use yearly data to conduct trend analyses for individual clearcuts if autocorrelations could be detected and the appropriate corrections made. Unfortunately, a maximum of only 3 consecutive years of data are available for any site; neither tests for autocorrelation nor predictions of recovery times are feasible given these small sample sizes.

Ash conducted precut censuses of plots established in two of the three future clearcuts and in adjoining forest plots (control sites). Because treatments (clearcut or not clearcut) could not be assigned randomly at each site, the potential for an initial bias existed. Precut censuses indicate that this was the case: clearcut plots had markedly higher numbers of salamanders than control sites (22% and 58% higher; Ash's Table 3), with corresponding abundance indices of 122% and 158%. Because of strong evidence of a significant difference in the number of salamanders on clearcut and control plots before timber removal, recovery of salamanders could only be legitimately analyzed either by expressing postcut numbers as a percentage of precut numbers or by using the precut abundance indices as the baseline to gauge recovery rates. Rather than use these approaches, Ash expressed numbers on clearcuts as a percentage of control plots and assumed full recovery to have occurred when the abundance index equaled 100%. This significantly underestimates recovery periods. If we assume that the regressions in Ash's Fig. 1 are valid (they are not), then Ash's estimate of recovery for *P. jordani* would be 28 years (BC) and 35 years (RK) if return to precut population levels or precut abundance indices are used as the basis for measuring recovery (and populations on control sites are assumed to be stable).

The use of a relative abundance index based on the ratio of salamanders on clearcut versus control plots provides another source of bias that could underestimate recovery times. In particular, if factors associated with clearcutting resulted in a decline of salamanders on control plots relative to precut levels, this would produce a biased (conservative) estimate of recovery times.

Ash located his control plots as close as 30 m to clearcuts where edge effects and population source-sink phenomena could result in underestimates of recovery time. Because of habitat drying, salamander populations decline significantly in forest edge habitats after clearcutting. We are only beginning to estimate edge effects for plethodontid salamanders, but edge effects (reduced litter moisture, reduced litter depth, reduced humidity) within 30–50 m seem likely based on studies of microenvironment changes that occur near forest edges after timber extraction (e.g., Matlack 1993) and on censuses of salamanders (DeGraaf & Yamasaki 1992). Because some of Ash's plots were placed where edge effects are likely to occur, the abundance index may have been inflated. Ash did not report changes in salamander numbers in control plots. In his earlier study at RMS (Ash 1988), however, salamanders in one control plot declined 45% over a 3-year period after timber removal; this is consistent with the hypothesis of significant edge effects.

A second factor that could reduce numbers on control plots is the net dispersal of salamanders from forest to clearcuts as revegetation proceeds. Local losses of salamanders from clearcutting in the southern Appalachians in terms of absolute numbers are large. Using RMS as an example, Ash (1988) estimated the density of *Plethodon* to be roughly 0.20 salamanders/m^2 or 2000 salamanders/ha on forested plots. Thus, the 15-ha clearcut at this site resulted in a loss of about 30,000 salamanders. If the return of salamanders to clearcuts during early successional stages primarily reflects dispersal of salamanders from nearby forest, as Ash's (1997) data strongly suggest, then clearcuts would act as significant population sinks and adjoining forests as sources. This could potentially deplete numbers in control plots that were located close to

clearcuts. As with edge effects, this biases the abundance index and underestimates recovery time. The only way to demonstrate edge effects or population sinks convincingly would be to compare data for controls near clearcut edges versus those in interior areas of forests (say, several hundred meters away). Because no data are available for interior sites, the extent to which the AI was biased by these factors cannot be determined.

Ash and I have used different approaches to studying the effects of clearcutting on southern Appalachian salamanders. We strongly agree that local populations undergo major population crashes after clearcutting, although we disagree about the fate of the animals (Ash & Bruce 1994; Petranka 1994). One hypothesis—that salamanders move beneath ground for several years and reemerge as vegetative recovery proceeds—seems untenable given that plethodontids are surface foragers that generally cannot maintain a positive energy budget when underground. A second hypothesis—that most salamanders evacuate clearcuts and become successfully established in nearby forests—seems unlikely given that populations of plethodontid salamanders in mature forests tend to be stable and near carrying capacity (Hairston 1987). Resident adults are territorial, and intruders rarely drive residents from their home territories (Mathis et al. 1995). These factors explain why attempts to introduce salamanders into existing communities have failed or have proven to be exceedingly difficult (e.g., deMaynadier & Hunter 1995; Hairston 1983*b*, 1987).

Although Ash's data suggest that some animals may move from clearcuts into surrounding forest, there is no evidence that they become successfully established. Based on our knowledge of the physiology and ecology of terrestrial plethodontid salamanders, population crashes after clearcutting in all likelihood reflect mortality from both the loss of critical forest floor microhabitat on clearcuts and the failure of animals that disperse from clearcuts to become successfully established in adjoining forests where conspecific populations are near equilibrium.

Ash and I have criticized each other's methodologies for assessing the recovery of salamanders after clearcutting (Ash & Bruce 1994; Petranka 1994). Both approaches—intensive studies of local populations versus landscape studies that use spatial variation to estimate recovery rates—have advantages and disadvantages, and the combined use of both is advantageous. Nonetheless, we may never be able to fully resolve issues concerning salamander recovery after clearcutting because of the difficulty of designing studies that examine long-term population trends in salamanders that inhabit complex landscapes (Petranka 1994; deMaynadier & Hunter 1995). Ash believes that I overestimated recovery periods by using relative abundance estimates from area-constrained searches of cover objects, whereas I believe that he underestimated the same. As with all scientific inquiries, the story always proves to be more complex than initial investigations suggest. My interpretation of the existing data is that 30–60 years may be required for the full recovery of southern Appalachian salamanders inhabiting mesic hardwood forests at intermediate elevations. Even longer recovery periods may be needed in drier, low-elevation forests that have mid-successional stages dominated by pines (Petranka et al. 1994).

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