

Effects of Stand Age, Size, and Juxtaposition on Abundance of Western Redback Salamanders (*Plethodon vehiculum*) in Coastal British Columbia

Abstract

Terrestrial-breeding amphibians live at high densities, show strong site fidelity, and have relatively stable populations, long life spans, and high vulnerability to dehydration. These traits make them potentially useful indicators of effects of canopy removal during logging. We compared the relative abundance of western redback salamanders (*Plethodon vehiculum*) in old-growth and managed second-growth stands on Vancouver Island, and found significantly more individuals in old-growth stands. Salamanders were more abundant in larger stands of old growth, but showed no relationship with stand or patch size among mature second-growth stands. Managed stands contained more salamanders when old growth was adjacent. Juvenile:adult ratios within managed stands were significantly higher in stands not adjacent to old growth, suggesting poor survivorship to adulthood in younger stands.

Introduction

Several studies have documented greater abundance of terrestrial salamanders in old-growth stands than in younger stands (Raphael 1988; Aubry and Hall 1991; Corn and Bury 1991; Dupuis et al. 1995). These observations have been interpreted as evidence that at least some recent amphibian declines are a result of habitat loss to forest practices (Welsh 1990; Johnson 1992). The rationale is simple. Terrestrial salamanders are susceptible to dehydration (Ray 1958; Spotila 1972; Feder 1983). Forest removal increases the risk of dehydration by increasing wind speed and radiation (Geiger 1965), and by reducing amounts of downed wood used as foraging and breeding sites (Bury et al. 1991; Welsh and Lind 1992; Dupuis 1997). Habitats that become unfavorable, even for short periods of time, are recolonized only slowly because of the low vagility or high philopatry exhibited by amphibians (Ovaska 1988; Welsh 1990). Thus, we expect to find greater amphibian abundance in relatively closed stands containing abundant downed wood; that is, in older stands.

Although there are differences between old-growth and young forests in the Pacific Northwest, few studies reveal strong trends in salamander numbers with stand age (Bury and Corn 1988; Bury et al. 1991; Gilbert and Allwine 1991).

Bunnell et al. (1997) noted three possible reasons for differing results among studies: 1) variable amounts of critical elements such as downed wood or understory; 2) differences in regional macroclimates that determine importance of sheltering structures, such as overstory, understory, or downed wood; and 3) differences in the forest mosaic surrounding the study sites. Edenhann et al. (1992), for example, suggested that patch size and isolation were critical factors governing effects of habitat fragmentation on amphibians. Here we examine potential effects of the forest mosaic; specifically, effects of stand age and size, and proximity of favored habitat. We report the relative abundance of amphibians in different sized stands of older forest, and in younger, managed stands with or without adjacent old growth.

Study Area

The study area was in the Coastal Western Hemlock Biogeoclimatic Zone near Port Alberni (49° 03'N and 125° 3'W), central Vancouver Island, Canada. This region receives more than 250 cm of precipitation annually (mainly in spring and fall), has a mean summer temperature less than 16° C, and a mean of 180 frost-free days per year (Meidinger and Pojar 1991). Stands were located in a 500 km² area and varied in elevation from 150 to 550 m above sea level.

We chose low to mid-slope, moist, nutrient rich, south-facing or flat sites that supported mixed

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TABLE 1. Characteristics of the sampling scheme.

Site ¹	Age (years)	Years Sampled	Number Plots ²	Patch Size (ha)	Adjacent Old Growth ³	
OG1	380+	'91 & '92	3	2500	extensive, contiguous	(Y)
OG2	330+	'91 & '92	3	800	extensive, contiguous	(Y)
OG3	500+	'91 & '92	3	90	> 10 km distant	(N)
M1	54	'91 & '92	3	1000	extensive, contiguous	(Y)
M2	60	'91 & '92	3	131	extensive, contiguous	(Y)
M3	72	'91 & '92	3	2000	ca 50 ha, > 300 m distant	(N)
Y1	17	'92	3	150	ca 750 ha, contiguous	(Y)
Y2	18	'92	3	50	extensive, contiguous	(Y)
Y3	18	'92	3	107	> 2 km distant	(N)
CC1	5	'92	2	58	extensive, contiguous	(Y)
CC2	5	'92	2	510	> 2 km distant	(N)

¹ OG = Old Growth; M = Mature, managed; Y = Young, managed; CC = Clearcut

² Each plot includes 45, 1x2 m quadrats (90 m²)

³ Y = Yes, old growth adjacent; N = no, old growth not adjacent for analyses of juxtaposition

stands of Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). In 1991, we sampled old-growth (undisturbed) stands and 54 to 72-year-old (mature), managed second-growth stands to evaluate methodologies. In 1992 surveys were also conducted in 17- and 18-year-old (young) managed stands and in 5-year-old clearcuts. To avoid local microclimatic influences, all sites were located at least 30 m from temporary water bodies, 75 m from lakes and rivers, and 50 m from forest edges. Age and distance from water or forest edge were dominating criteria in site selection; the habitat mosaic permitted a range of stand sizes and some differences in isolation (Table 1). The mature stands were prescribed burned within 5 years of harvesting, and had regenerated naturally. The young stands were burned, planted, and subsequently mechanically treated to remove alder and smaller conifer stems.

Methods

From mid-May to mid-June 1991, we evaluated area-constrained searches over a range of plot sizes using Wiegert's two-term local quadrat variance methods (Krebs 1989:68; Ludwig and Reynolds 1988:43). Optimal plot size for assessing terrestrial salamander abundance proved to be 1 x 2 m (Dupuis et al. 1995); mean times for a thorough search of a 1 x 2 m plot were 9.3 minutes in old

growth and 8.7 minutes in managed, mature second growth. In 1992, the optimal plot size was extended to young managed stands and clearcuts. Three study sites for each forest age class were selected, and studies were carried out in three, 2-ha plots (400 x 50 m) within each site or age-class replicate. Each plot consisted of 45, 1 x 2 m quadrats randomly placed, for a total sample area of 90 m² per plot. Total sample area within each study site was thus 270 m² (Table 1). We sampled one plot of 90 m² every 2 weeks from mid-April to late-May in 1992. We could sample only two recent clearcuts, each with 2 replicates.

Two people searched for salamanders, while a third handled the captures and recorded data. Searchers looked under all cover objects (logs, bark and rocks) and vegetation (ferns and moss), and probed all crevices. Captured salamanders were identified, sexed, weighed (± 0.05 g) and measured (total and snout-vent length). Salamander age class was based on length distributions in Ovaska and Gregory (1989), who employed mark-recapture techniques with the same species (*Plethodon vehiculum*). We recognized three classes: hatchlings (<26 mm), yearlings or juveniles (26-35 mm), and mature (>35 mm).

To examine potential effects of stand age or habitat juxtaposition, analyses were site-specific and used the 3 plots per site as replicates. Where

2 years of data were available, two-way analyses of variance were initially performed to evaluate potential year effects as well as effects of forest age or patch size. Year effects were never significant, and subsequent analyses of relative density combined years. Potential differences among proportions of salamanders in different size/age classes were evaluated by Hicks' test of proportions. Fisher's exact test was used to test for potential influences of adjacent old growth on the relative numbers of juveniles and adults in younger stands.

Results

Average calculated densities (number/ha) of *Plethodon vehiculum* were 1519 ± 145 (SE) and 1346 ± 196 in old growth and 247 ± 41 and 482 ± 156 in mature second-growth during 1991 and 1992, respectively. Young stands and clearcuts were measured only in 1992, and yielded average densities of 247 ± 90 and 28 ± 28 ($n = 4$ plots), respectively. Because of high inter-plot variability (Figure 1a) there was no significant difference between sample years ($p > 0.15$). Density estimates for old growth were significantly higher ($p < 0.05$) than for the other three age classes. Only one salamander was found in the clearcuts; the 17-18 and 54-72 year-old age classes did not differ significantly.

Analysis of variance indicated a difference with patch size among old-growth stands ($p < 0.08$). Across both years mean relative densities in stands 800 and 2,500 ha in size, were 1611 ± 174 and 1630 ± 206 salamanders per ha, respectively (Figure 1b). The smaller stand (90 ha) had a relative density of 1056 ± 178 salamanders per ha. Within mature, second-growth stands, there was no difference across stand sizes ranging from 131 to about 2,000 ha (Figure 1b). Nor were differences with size evident in young managed or clearcut stands.

There was little difference among proportions of hatchlings, juveniles, and adults with forest age class (Figure 2a). Across all years and forest ages, hatchlings represented 13% to 23% of the sample and juveniles usually comprised 11% to 26% (in 1992 they represented 40% of the mature second-growth sample). Tests of proportions revealed no significant differences in age class distribution with either forest age class or patch size ($p > 0.3$). There was, however, an apparent effect of stand adjacency. In 1991, mature managed stands with adjacent old growth had 13.2% young



Figure 1. a) Relative densities of *Plethodon vehiculum* in stands of different ages. Values plotted are means and standard errors of 9 replicates (3 2-ha plots at each of 3 sites per age class). Recent clearcuts had only 4 replicates (Table 1). CC = clearcut (5 yrs), Y = young (17-18 yrs), M = mature (54-72 years), OG = old growth (300+ yrs).

b) Relative densities of *Plethodon vehiculum* in stands of different size and age. Means calculated as for a). Only 1 salamander was found in clearcuts. Old Growth 1991 (■), Old Growth 1992 (□), Mature 1991 (●), Mature 1992 (○).

(hatchling plus juvenile) salamanders, while mature managed stands without adjacent old growth had 75% young salamanders in the sample. The pattern was similar in 1992 (53% young with old growth adjacent; 88% young when not adjacent), though not as pronounced as in 1991 (Figure 2b). Two-tailed, Fisher's exact tests of the equality of proportions of young salamanders in mature, managed stands with and without adjacent old growth showed significant differences ($p < 0.04$). Of the young, second-growth stands (17 to 18 years

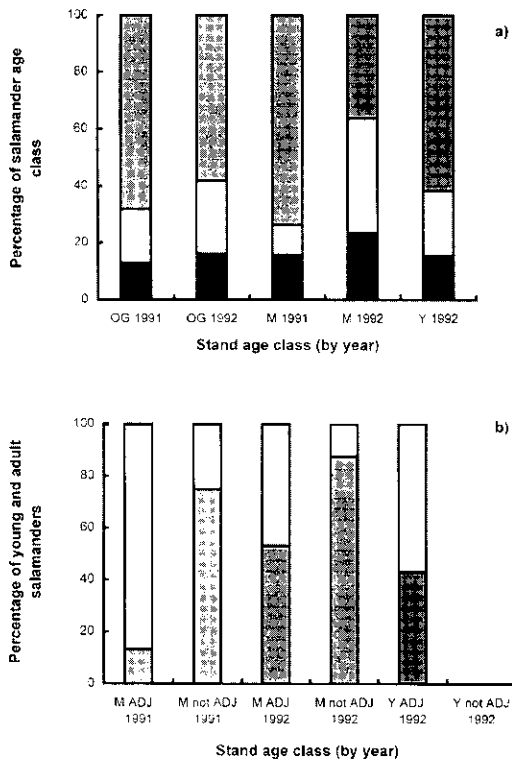


Figure 2. a) Percentages of adult, juvenile and hatchling salamanders in old growth (OG), mature (M; 54-72 years old), and young (Y; 17-18 years old) stands. Definitions of salamander age classes follow Ovaska and Gregory (1989). Grey bars represent the percentage of adults, white represent juveniles, and black represent hatchlings. b) Proportions of adult and young (juveniles and hatchlings combined) salamanders in mature (M; 54-72 years) and young (Y; 17-18 years) managed stands with and without adjacent old growth. No salamanders were encountered in young stands without adjacent old growth. White bars represent the percentage of adults, and dark bars represent young salamanders.

post-logging), only those adjacent to old growth contained salamanders, of which 43% were young salamanders. Only one salamander was encountered in clearcuts; an adult was found in the clearcut with adjacent old growth.

Discussion

We found a three- to six-fold difference in relative abundance of western redback salamanders between managed stands and old growth, with

the lowest numbers in the youngest managed stands (Figure 1a). Although there are no consistent trends in relative densities of terrestrial amphibians with stand age (Bury et al. 1991; deMaynadier and Hunter 1995), in several studies individual species were more abundant in unmanaged or old-growth stands than in younger, managed stands (e.g., Means et al. 1996; Bunnell et al. 1997). In the Pacific Northwest these include: clouded salamanders (Corn and Bury 1991; Gomez and Anthony 1996); ensatinas (Raphael and Barrett 1984; Welsh and Lind 1988; Corn and Bury 1991); Del Norte salamanders (Raphael 1988; Welsh and Lind 1988, 1995); Dunn's salamanders (Vesely 1996); northwestern salamanders (Aubry and Hall 1991); western redback salamanders (Corn and Bury 1991; Vesely 1996; Dupuis 1997); and Larch Mountain salamanders (Herrington and Larsen 1985). Most of the plethodontid salamanders of the Pacific Northwest are more abundant in habitats common in old-growth forests (Blaustein et al. 1995). These salamanders may be particularly sensitive to canopy removal because they are less resistant to desiccation than many amphibians and require terrestrial breeding sites (often downed wood).

The adult densities we observed in old growth were similar to those obtained by Ovaska and Gregory (1989), also in old growth on Vancouver Island. They employed mark and recapture in two plots (100 m² and 200 m²). The total numbers they captured during their 2-year study were naturally much higher than we obtained during area-constrained searches (single search period). Extrapolating their more comparable, quadrat-based estimate of 28 salamanders on the 200-m² plot yields 1400 per ha; we estimated 1356 and 1519 per ha. In both years on our plots, numbers were markedly lower in managed stands, even those 54-72 years of age, than in old growth (Figure 1a). Current conditions do not appear to explain the large difference. There was little difference in amounts of downed wood across stand age (Dupuis 1997), and all sites were classified as "moist" or "very moist" in the same biogeoclimatic subzone (Meidinger and Pojar 1991). Moreover, by age 50 overstory effects on near-ground microclimate should differ little from old-growth stands. Combined, these observations suggest some prior, but long-lasting effect reduced salamander abundance in managed stands. Working in unmanaged stands of fire origin, Aubry and Hall (1991) found that western redback salamanders

were more abundant in young, than in mature or old growth stands. We cannot evaluate whether the different findings are a product of scale of initial opening (Aubry and Hall's stands were much smaller than ours), different structural legacies after fire than after logging, or some other influence.

Forest practices have altered the age structure of forests in the Pacific Northwest dramatically (e.g., Harris 1984; Wallin et al. 1994; McGarigal and McComb 1995). It was difficult for us to find low-elevation, old-growth stands on Vancouver Island in which to conduct this study and spatial distribution of stands could not be controlled. As a result, both old and young stands differed in their degree of isolation from nearby old growth (Table 1). We chose to group young stands as those with adjacent old growth and those without (the closest old growth was >300 m away). The smallest old-growth stand (90 ha) was also the most isolated (no other old growth within 10 km). Despite this natural variability and sparse data, some relations were statistically significant.

The effect of patch size among old-growth stands appears curvilinear (Figure 1b), as would be expected if some microclimatic or edge-related phenomenon were acting as an influence on populations. Changes in radiation and wind regimes induced by clearcutting extend about 50-100 m into adjacent forest (review of Bunnell et al. 1998). In even the smallest stand, there should be an unmodified area of about 50 ha in the stand core (where our study plots were located). It is thus unclear why there should be an apparent effect of stand size in our sample. Two influences are plausible: local microhabitat variation among stands, and broad-scale influences related to salamander movement. In terms of microhabitat the smallest old-growth patch contained the highest volume of downed wood, but was subject to flooding. Soil profiles contained considerable sand that would not favor plethodontid salamanders. This stand also was the most isolated from other old growth (Table 1). Bunnell et al. (1997) argued that movements of amphibians are often underestimated. Some species may depend on movement across larger areas than has been supposed, thus requiring larger areas of suitable habitat. If that is true, more isolated stands should appear as population sinks.

Older managed stands without adjacent old growth had significantly greater proportions of young salamanders than did stands with adjacent old growth (Figure 2b). A high proportion of young salamanders could be consistent with a thriving population, but not when densities are as low as they were in mature, managed stands (Figure 1a). Managed stands may be "sinks" with moderate reproductive success but poor survival to adulthood. Recolonization by adults from adjacent old growth may be important, but is likely to be slow given the low vagility of salamanders. This suggestion is supported by findings in young managed stands without adjacent old growth (no salamanders) and recent clearcuts (one salamander). The smallest and most isolated patch of old growth (90 ha) displayed both the lowest abundance and lowest amphibian richness of all old-growth patches (Dupuis 1993). We cannot separate fine-scaled microhabitat effects from broad-scaled habitat juxtaposition. Both are likely acting, but findings are more consistent with broad-scale effects.

Lehmkuhl et al. (1991) also attempted to evaluate broad-scale effects on western redback salamanders. They noted that their findings were somewhat contradictory in that salamander abundance was positively correlated with dominance of late-successional stages at the landscape level, but negatively correlated with the abundance of old growth in the "buffer" surrounding the stands they sampled. Broad-scale results are invariably difficult to interpret. Findings of Lehmkuhl et al. (1991) could reflect species packing in stands when surrounding old growth was less abundant (in which case they are similar to ours), or a preference by western redback salamanders for younger stands as documented by Aubry and Hall (1991) who worked in the same area (in which case they are contrary to ours).

Our data suggest that clearcutting greatly reduces the abundance of western redback salamanders, and that these effects are long lived. Adults are present in stands 17-18 and 54-72 years after clearcutting, which indicates that harvest practices did not locally eliminate the species. Adults represented a greater proportion of the population in stands adjacent to old growth, and recolonization did not occur readily unless there was old growth nearby. That suggests two options for retaining higher densities of terrestrial

salamanders: 1) extensive tracts of unmanaged forests (about 100 ha), or 2) retention of small patches of older forest within harvested areas. We could not separate potential impacts of reduction in downed wood and altered microclimate, so can offer no recommendations on patch size. In moist, coastal areas it seems likely that breeding sites are more important than microclimatic effects, so even small, undisturbed patches would be helpful provided they were not too distant from each other.

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