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Abstract. There is little known about how timber harvest practices have affected terrestrial amphibians in the northern Rocky Mountains. Especially lacking is information on the effects of revised harvest methods that fall within the framework of environmental or New Forestry. We estimated the relative abundance of a common forest amphibian, the long-toed salamander (*Ambystoma macrodactylum*) captured in pitfall arrays on intact, environmentally harvested, and overstory-removal harvested sites in mixed-conifer forests of western Montana. Pitfall data from 1994 through 1996 showed that previously logged sites contained significantly fewer long-toed salamanders regardless of harvest method used. The number of salamanders captured on intact sites (3.1 salamanders·[array]$^{-1}$·[100 d]$^{-1}$) was nearly three times the number captured on logged sites (1.2 salamanders·[array]$^{-1}$·[100 d]$^{-1}$). Habitat conditions measured in conjunction with trapping efforts indicated that lower amphibian abundance was associated with decreased numbers of large live trees. Declines in amphibian abundance occurred in the absence of changes in understory vegetation that typically occur when forest canopy is reduced. Our findings suggest that long-toed salamanders responded to changes in the physical environment, probably increased temperatures and decreased moisture. That salamanders should respond so dramatically indicates that immediate changes in physical conditions may profoundly alter habitat quality even when other components of the habitat are unaffected.

Key words: Ambystoma macrodactylum; amphibian; disturbance; environmental forestry; forest management; habitat associations; long-toed salamander; Montana; New Forestry; overstory removal; Rocky Mountains; salamander.

INTRODUCTION

Despite the importance of amphibians in terrestrial ecosystems (Burton and Likens 1975, Hairston 1987) and their sensitivity to environmental change (Wyman 1990, Blaustein and Olson 1991, Blaustein 1994, Corn 1994, Blaustein et al. 1995), the status of amphibian populations has only recently become a concern of forest management and monitoring programs (Gibbons 1988, Szaro et al. 1988). Many amphibians depend on the temperature, moisture, and cover characteristics provided by undisturbed mature forests (Stiven and Bruce 1988, Welsh 1990, Corn and Bury 1991). Consequently, excessive harvesting of old-growth forests has been suggested as one cause for the broad declines that are occurring in a number of North American amphibians (Walls et al. 1992).

Past logging practices in western forests paid little concern to the broader issues of forest ecosystem sus-

tainability and conservation of biological diversity. Until recently, preferred harvesting practices promoted nearly complete logging of selected stands, accompanied by the burning of all residual woody debris, including snags and deadfall. Deep scarification of soils typically followed to promote tree seedling establishment and to speed stand regeneration. Recognition of the cumulative harmful effects of forest canopy removal and understory habitat destruction stimulated important research into ecologically sustainable forestry practices (Franklin and Forman 1987, Hansen et al. 1991, Franklin et al. 1997). Implementation of research findings has produced several new approaches to timber harvesting commonly labeled environmental or New Forestry. These revised forestry practices are being implemented throughout the Pacific Northwest and the northern Rocky Mountains. As yet, however, research documenting the effectiveness of these practices in conserving vertebrate communities, especially amphibians, is not generally available.

Although it is less diverse than the herpetofauna in other regions of North America, there is growing concern about the status of the Rocky Mountain herpetofauna and the effects that intensive land management is having on the viability of native amphibians (deMaynadier and Hunter, Jr. 1995). Unfortunately, ecological research on the herpetofauna of the northern Rocky Mountains is limited, with little emphasis on

forest management practices (e.g., Wishard 1977, Daugherty and Sheldon 1982, Corn 1994).

Of the 13 amphibian species presumed to occur in western Montana, the western long-toed salamander (*Ambystoma macrodactylum*) is perhaps the most common. Its range includes much of the northern Rocky Mountains and the Pacific Northwest. Adults measure ~9 cm total length and weigh ~2.5 g. Western long-toed salamanders are a semiaquatic species. Metamorphosed adults are fossorial in terrestrial habitats, sheltering and foraging in burrows, beneath rocks or logs in a variety of habitats from sagebrush to alpine meadows up to elevations of 2700 m (Anderson 1967, Howard and Wallace 1985, Petranka 1998). Adults return to water to breed as soon as open water appears in ponds and lakes from late February through April. Larvae typically mature within the same season the eggs are laid, but may require two years to mature in high-elevation habitats (Howard and Wallace 1985).

In this paper we report on the responses of western long-toed salamanders to forest management practices in mixed conifer forests of western Montana. We present findings on the overall effects of timber harvesting on the abundance of terrestrial populations. We also compare traditional overstory-removal timber harvests to lower-impact New Forestry harvests aimed at conserving biological diversity.

METHODS

Stand selection and treatments

We conducted our study on U.S. Forest Service, Plum Creek Timber Company, and Montana state lands in the Swan Valley (47°35' N, 114°45' W), ~100 km northeast of Missoula, Montana, USA. We chose sites in Douglas-fir (*Pseudotsuga menziesii*) dominated mixed coniferous forest at ~1200 m elevation. Historically, lower elevation forests in the Swan Valley often were dominated by pines (*Pinus* spp.) and western larch (*Larix occidentalis*), but 50 years of fire suppression has allowed Douglas-fir to become dominant over much of the region (Antos and Habek 1981).

Four sites, referred to hereafter as Gordon Ranch, Bucksnort, Gravel Pit South, and Gravel Pit North, were selected along a 30-km north–south axis. The total area of each site subjected to logging ranged from 7 to 28 ha and the proximity of neighboring sites ranged from 0.25 to 16 km. Similarity of habitat and proximity of treatment plots to intact state, federal, and Plum Creek lands were the principal criteria that guided site selection. Each site was divided into three treatment plots which were designated as either (1) intact (control); (2) overstory removal; or (3) New Forestry. Intact plots were located on state or federal land; harvested plots were on Plum Creek land. Cutting and skidding on harvested sites occurred during the winter of 1992–1993 when the ground was frozen and had sufficient snow cover to reduce soil disturbance by logging ma-
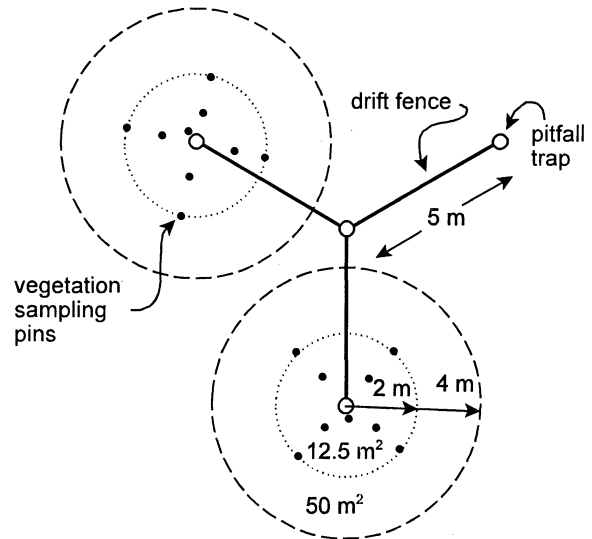

FIG. 1. Design of pitfall arrays used to capture salamanders, together with the sampling scheme used to measure habitat attributes at each array. Array construction used four number-10 cans buried flush to the ground at the center and vertices of a triangle. A 5-m polyethylene sheeting fence 25-cm high extended from the center to each marginal can. Understory vegetation was sampled using nine pins placed systematically within 2-m radius, 12.5-m² circular plots (dotted circles). Canopy vegetation was measured in larger, 4-m radius, 50-m² circular plots (dashed circles). Two sets of plots were sampled at each array.

chinery (Zasada et al. 1987, Martin 1988, Williams and Buckhouse 1993). Overstory-removal harvests removed all trees >25 cm diameter. Logging debris was piled and burned on the periphery of harvested plots. New Forestry harvests were cut according to environmental forestry guidelines implemented by Plum Creek Timber Company. On the New Forestry plots all trees >25 cm diameter were removed except for 10–15 dominant or codominant trees per ha. Left trees were selected without respect to species in order to retain preharvest proportions in affected plots. Harvested trees were limbed at felling sites, and branches were scattered. All nonmerchantable trees and snags were retained on both overstory-removal and New Forestry plots.

Salamander sampling

We constructed three pitfall arrays containing four pitfalls per array on each of the 12 treatment plots in 1994. In 1995, two additional arrays were added per plot. Each array consisted of three, 5 m long fences made from 15 cm high plastic sheeting radiating from the center of the array at 120° angles (Fig. 1). Number-10 metal cans set flush with the surface of the ground were placed at the center of each array and at the distal end of each fence. We put small drain holes in the cans to prevent water accumulation. Arrays were placed at least 100 m apart and more than 100 m from the edge

of each plot. The area covered by each array from the center to the outer edge of the distal cans was 86 m², and the combined area occupied by arrays was <1% of the total area of each plot.

Pitfalls were opened from 7 June to 15 August 1994, 28 May to 15 August 1995, and 29 May to 28 September 1996. Arrays were checked daily; amphibians taken from pitfalls were identified to species and measured (total length). In 1994 captured amphibians were removed 50 m from the arrays to minimize recaptures. In 1995, all captures were marked for identification by clipping one toe to the middle joint (C. R. Petersen, *personal communication*) and released immediately adjacent to the array. Because of extremely low recapture frequency (<2%), marking was abandoned for 1996.

Habitat attributes

Habitat information for each array was collected in 1994 using a two-staged design consisting of nested small (12.5 m²) and large (50 m²) circular plots (Fig. 1). At each array, two samples were collected using two randomly selected pitfalls as plot centers. Data from both samples within an array were pooled to provide a single description of the habitat within the immediate vicinity of each array. Within the small plots, nine, 1 m tall pins were placed in a crossing pattern at 1-m intervals to estimate coverage of understory vegetation classes. All contacts with vegetation were tallied in 1-dm intervals along each pin. Vegetation classes included forb, graminoid, shrub, litter (dead herbaceous and decomposed organic debris), and woody debris (logs and dead branches >1 cm diameter). Understory data for 12.5 m² plots, up to 1 m height, included mean percentage volume for each vegetation class and mean percentage volume of woody debris and litter. Overstory data collected by species within the 50 m² plot included number of trees, number of snags, and diameter at breast height for both live and dead trees.

General habitat changes caused by logging were measured on 1-ha subplots located near the center of each experimental plot. Systematic placement of 20 points assured homogeneous sampling within the subplots. At each point, tree and understory sampling followed the same methods described above with one difference. Understory vegetation data were collected from just one 12.5-m² circular quadrat centered on each sampling point within the subplots. Sampling for general habitat changes was conducted yearly from 1992 to 1994.

Statistical analysis

We converted the cumulative catch of salamanders on each plot in each year to catch per unit effort (CPUE) of pitfall trapping to estimate the relative abundances of long-toed salamanders:

$$\text{CPUE} = \frac{C_i}{A_i T_i} \cdot 100$$

where C_i = total number of salamanders captured in the ith sample, A_i = the number of arrays in the sample, and T_i = number of days effort in the sample. Catches per unit effort were multiplied by 100 to avoid rounding errors during analysis, then were square-root transformed to equalize variances among site and year groups. Levene's statistic calculated for the transformed data did not reject the hypothesis that the transformed data were homoscedastic (Levene$_\text{sites}$ = 0.301, P = 0.824; Levene$_\text{years}$ = 0.220, P = 0.804). We used analysis of variance (ANOVA) to test for differences in salamander abundances among harvest treatments and among years. Our experimental design included four different locations (blocks). Each block was divided into three plots (intact, New Forestry, and overstory removal). All plots were trapped for three years (subplots). We analyzed the data as a randomized block design with repeated measures. The P value for significance of all tests was set at 0.05.

We used multivariate analysis of variance (MANOVA) to test for differences in habitat attributes among sites and treatments. Canonical discriminant function analysis was used with MANOVA to determine the relative importance of habitat attributes in distinguishing among sites and treatments (Johnson and Wichern 1982). We applied square-root transformations to habitat variables as necessary to achieve homoscedasticity among treatment groups prior to analysis. Salamander abundance and habitat analyses were performed using the GLM procedure in SPSS for Windows 7.5 (SPSS Inc. 1997).

RESULTS

Logging effects

At the beginning of the project in 1992 all 12 experimental plots were similar in tree density and species composition. Douglas-fir (*Pseudotsuga menziesii*) was dominant on all sites. It comprised 40% of both total density and basal area (Table 1). Other species that were common included, in order of abundance, lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmanni*), and ponderosa pine (*Pinus ponderosa*). Most sites showed some evidence of prior limited timber harvest. There were few trees >60 cm diameter, and occasional large stumps dispersed through the stands indicated that selective tree harvesting had occurred within the past 50 years. Portions of the Gordon Ranch plots were more intensively harvested but were at rotation age for the most part. It was apparent that the combination of timber harvesting and fire suppression over the past half century promoted the establishment and dominance of *P. douglasii* in the stands (Antos and Habeck 1981, Habeck 1988).

Final log hauling and site cleanup were completed

TABLE 1. Tree densities (no./ha) of principal merchantable species (>10 cm dbh), all species (>10 cm dbh), and snags (>20 cm dbh) before and after harvest on control and harvested plots.

Harvest type	Period	Mean number of trees per hectare (1 SD)						
		Merchantable species					Snags >20 cm diameter	Basal area (m²/ha)
		Larix occidentalis	Picea engelmanni	Pinus ponderosa	Pseudotsuga menziesii	All species		
Intact		93 (450)	130 (77)	3 (5)	235 (193)	525 (84)	40 (2)	43 (13)
New Forestry	preharvest	60 (29)	68 (15)	23 (33)	150 (148)	453 (19)	30 (2)	43 (7)
	postharvest	50 (29)	43 (21)	3 (5)	80 (22)	230 (24)	10 (1)	19 (2)
Overstory	preharvest	100 (37)	33 (52)	18 (24)	182 (22)	488 (80)	0	51 (6)
removal	postharvest	43 (19)	13 (19)	20 (34)	108 (22)	240 (82)	1 (1)	21 (8)

Note: Data were collected from 20 50-m² circular quadrats systematically sampled within 1-ha plots in harvest units.

during the first part of the field season in June 1993. New Forestry harvests removed 35% of the trees from treated stands, while overstory-removal harvests reduced tree density by 43% (Table 1). In addition to the differences in total number of trees harvested, the distribution of size classes harvested was different as illustrated for *P. douglasii* and *L. occidentalis* (Fig. 2). New Forestry harvests retained the general size distribution of trees within affected stands with the exception of *L. occidentalis*. All *L. occidentalis* >30 cm diameter were harvested on the New Forestry plots. On the overstory-removal plots the size distribution was sharply truncated for all species, leaving only trees <30 cm diameter following harvest. Despite the density differences that resulted from the two harvest treat-

ments, tree basal area in merchantable size classes on both New Forestry and overstory-removal sites was reduced by ~50% and became nearly equal between harvest treatments (Table 1). Changes in snag densities on the harvested sites was due to removal of some of the smaller diameter snags, 30 cm diameter or less. Larger diameter snags were not removed.

Understory vegetation did not show substantial response to the timber harvests (Table 2). Through 1994, we observed no change in the percentage composition of forbs and shrubs on the sites. Woody debris increased slightly immediately after harvest, due to logging activities. The only obvious change in the understory composition that we observed on harvested sites was an increase in grasses, presumably due to increased sunlight, higher temperatures, and drier conditions that resulted from logging. Combined vegetative biomass, indicated by total percentage of volume 1 m above the ground, remained nearly constant. Dry conditions caused a drop in understory biomass in 1993, but by 1994 when the amphibian study began, understory biomass was at preharvest levels on all plots.

Salamander abundance

In 1994, we captured 75 salamanders on all arrays (total trapping effort = 2484 array days). In 1995, we caught 128 salamanders with only two subsequent recaptures (4740 array days). The total catch in 1996 was 121 salamanders (7320 array days). The increase in captures in the second and third years reflects both the increased number of arrays on each plot and longer sampling seasons in 1995 and 1996. The paucity of recaptured animals during 1995 increased our confidence that few, if any, of the animals we captured and displaced in 1994 and 1996 were recaptured later in the season. It also suggests that the population of salamanders was very large, that turnover was high, or both.

Mean CPUE among years was highly variable but declined from 2.9 to 0.5 salamanders. Overall, however, the CPUE on intact plots was nearly three times greater than on harvested plots (Fig. 3). Differences in the relative abundances of salamanders between years were not statistically significantly different ($P > 0.10$),

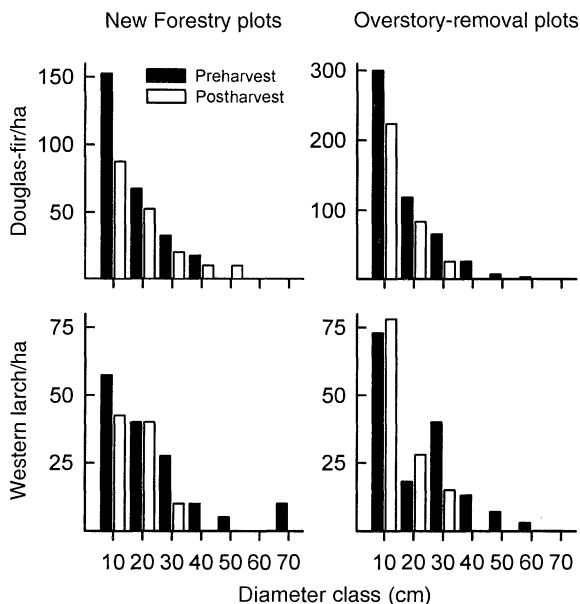FIG. 2. Size distribution of Douglas-fir (*Pseudotsuga menziesii*) and western larch (*Larix occidentalis*) before and after logging on New Forestry and overstory-removal treatment plots. The broader range in tree sizes for *P. menziesii* after logging occurred because some plot boundaries were changed during logging operations, which necessitated establishment of new sampling points in those plots.

TABLE 2. Percentage volume occupied by understory vegetation on intact and harvested plots in the Swan Valley from 1992 through 1994.

Harvest treatment	Year	Mean percentage (± 1 SD) $n = 20$		
		Forb	Grass	Shrub
Intact	1992	6.9 (2.2)	8.5 (3.0)	10.5 (0.7)
	1993	5.6 (1.7)	7.4 (1.7)	9.7 (0.4)
	1994	5.0 (2.7)	8.3 (0.6)	10.8 (0.6)
New Forestry	1992	5.2 (2.9)	11.8 (3.8)	10.7 (0.5)
	1993	5.4 (0.3)	7.6 (2.0)	9.9 (0.9)
	1994	3.2 (0.6)	10.6 (2.4)	11.1 (1.6)
Overstory removal	1992	3.4 (0.7)	12.5 (1.4)	10.2 (0.2)
	1993	3.2 (0.9)	7.4 (1.3)	10.3 (0.7)
	1994	3.1 (0.8)	13.3 (5.5)	10.9 (0.8)

Notes: Data for 1992 are preharvest conditions. Estimates were made from the number of hits on groups of nine 1-m long pins sampled at 20 points in each of four treatment plots.

but differences in relative abundances among treatments were highly significant ($P < 0.01$; Table 3). No interaction between year and harvest type was detectable. Scheffé a posteriori comparisons between treatments indicated that mean CPUE of long-toed salamanders was significantly greater on the control sites than on the New Forestry and overstory-removal sites (Fig. 3). We could not detect any difference in the relative abundance of long-toed salamanders between New Forestry and overstory-removal sites.

Habitat attributes

Tree and understory analysis yielded measurements on a number of vegetation attributes that we considered important descriptors of salamander habitat quality. In general, harvested sites differed from intact sites in that total basal area of trees and mean basal area per tree were reduced (Table 4). As described earlier, loss of larger older trees was less pronounced on New Forestry plots. Timber removal was associated with slight re-

FIG. 3. Western long-toed salamander (*Ambystoma macrodactylum*) capture rates on intact and logged sites in the Swan Valley of western Montana, USA. Means + 1 SD are plotted for four sites per treatment which were resampled each year of the study. Three arrays per plot were sampled in 1994; five arrays per plot were sampled in 1995 and 1996.

duction of forbs and a complementary increase in grasses in the understory. The harvested sites also showed increased woody debris as a consequence of logging activities.

Multivariate analysis of variance revealed a significant interaction between site and treatment effects (Table 5). Univariate F tests of group differences suggested that the interaction effect was significant only for mean percentage shrub cover. The Gravel Pit New Forestry South (mean ± 1 SD = 3.23% ± 1.46%), Bucksnort Control (3.06% ± 1.69%), Bucksnort Overstory Removal (2.81% ± 0.12%) and Gravel Pit New Forestry North (2.74% ± 0.76%) plots all had percentage understory shrub cover that was substantially higher than the overall mean (mean = 1.95% ± 1.14%). The absence of a consistent pattern among sites and treatments suggests that the significance of the interaction is attributable to inherent differences in shrub cover that existed on certain plots from the beginning of our study. Also, the lack of concordance between shrub cover and treatment increased our confidence that preexisting habitat conditions did not bias our observations of salamander responses to the different harvests. There were also significant differences in habitat attributes among the three treatments and sites (Table 5). Univariate statistics suggested that mean basal area of trees and mean grass cover were the only attributes that differed among harvest treatments.

Subsequent canonical discriminant function analysis of habitat variables among treatment groups confirmed the relative importance of tree basal area and grass cover in distinguishing among harvest treatments (Table 6). One significant function, based on six variables, resulted and accounted for ~91% of the among-treatment variance. Standardized canonical coefficients confirmed the MANOVA results. Mean tree basal area and mean grass coverage were the highest weighted variables in the function. Tree basal area obviously was greater postharvest on intact plots; increased grass cover probably indicates a response to increased light that accompanied tree removal on harvested plots. The absence of any other significant changes in habitat struc-
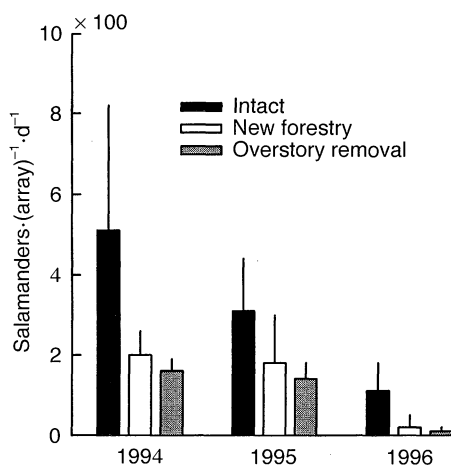
TABLE 3.   Summary of ANOVA for differences in mean numbers of western long-toed sal-
amanders (*Ambystoma macrodactylum*) captured on intact and harvested forest sites, Swan
Valley, Montana.

Source	SS	df	MS	F	P	Power (α = 0.05)
Site	6.09	3	2.03			
Harvest	28.17	2	14.09	17.34	0.003	0.98
Harvest × site	4.88	6	0.81			
Year(site)	6.43	6	1.07	1.29	0.39	0.25
Harvest × year	1.12	4	0.21	0.34	0.85	0.10
Residual	9.93	12	0.83			

Notes: Catch per unit effort (salamanders·[array]$^{-1}$·d^{-1}) was analyzed. Data were coded by
multiplying by 100 and then square-root transformed prior to analysis. A randomized complete
block with repeated-measures design was analyzed by the split-plot method using sites as
blocks, harvest treatments as main plots, and years as subplots.

ture following harvest indicates that changes in the
canopy was the principal correlate with differences in
salamander abundance that we observed. The under-
story vegetation remained mostly unchanged, and dif-
ferences were not statistically significant (Table 4).
Among-site differences identified by canonical dis-
criminant function analysis also confirmed MANOVA
findings described above. Once again one function was
significant, but accounted for only ~62% of the among-
group variance in the data set. Mean shrub and litter
cover dominated the function and indicated that, over-
all, the Bucksnort plots had higher shrub coverage and
less litter coverage than the other plots.

DISCUSSION

One potential weakness in our study is the absence
of prelogging estimates of salamander abundance from
all plots. It is possible that the differences we observed
stem from preexisting differences in salamander pop-
ulations unrelated to logging. We believe that this is

unlikely for two reasons. First, during site selection we
matched plots among and within sites as closely as
possible to minimize site specific differences that could
influence animal populations. Second, the consistency
in population trends among all four replicates, which
spanned 32 km between the two most widely separated
sites, argues strongly that the logging treatments, rather
than site characteristics, produced the salamander re-
sponses that we observed.

Long-toed salamanders are the most widespread of
all salamanders in Washington, Oregon, Idaho, and
western Montana. The variety of habitats in which they
occur and the geographic range they occupy (Petranka
1998) suggest tolerance for broad environmental var-
iation. Given their broad ecological amplitude it would
be logical to assume that harvested forest stands also
fall within the limits of long-toed salamander tolerance.
That assumption is supported by observations in sev-
eral amphibian communities that amphibian abundance
was only weakly correlated with old-growth habitat

TABLE 4.   Habitat variables measured at intact (*n* = 12), New Forestry (*n* = 12), and overstory-
removal (*n* = 12) pitfall arrays in 1994.

Habitat characteristic	Harvest treatment		
	Intact	New Forestry	Overstory removal
Tree species percentage composition			
Larix occidentalis	10.0 (11.4)	2.7 (4.5)	10.0 (10.0)
Pseudotsuga menziesii	28.6 (18.6)	34.5 (39.1)	65.0 (80.2)
Picea engelmanni	27.1 (43.6)	2.7 (6.4)	3.0 (5.4)
Pinus ponderosa	1.4 (2.9)	5.5 (15.5)	1.0 (2.7)
Pinus contorta	13.6 (19.3)	40.9 (65.5)	7.0 (12.6)
Abies lasiocarpa	2.1 (3.6)	0	5.0 (10.8)
snags	17.1 (13.6)	16.4 (24.5)	7.0 (9.0)
Trees per hectare	2800 (1540)	2200 (2980)	2000 (2220)
Total basal area (m²) per	108.5 (82.6)	27.1 (48.0)	20.1 (28.0)
hectare	228 (207)	65 (74)	55 (51)
Basal area (cm²) per tree	1.8 (1.0)	0.7 (0.5)	1.4 (1.0)
Forbs			
Grasses	2.7 (1.5)	4.3 (1.0)	3.9 (1.4)
Shrubs	2.3 (1.2)	2.2 (1.4)	2.0 (0.8)
Total live	6.8 (2.4)	7.2 (2.3)	7.3 (2.0)
Woody debris	0.3 (0.4)	0.4 (0.4)	0.6 (0.4)
Litter	4.5 (1.2)	4.4 (1.1)	4.1 (0.6)

Notes: Data are means, with 1 SD in parentheses. Total basal area is the summed basal area
of all trees within a plot averaged across the 12 plots within each treatment. Mean basal area
per tree is averaged within plots then across plots.

TABLE 5. Multivariate analysis of variance for habitat differences at salamander pitfall arrays among treatments and sites.

Source	Value	F	df	Error df	P	Power $\alpha = 0.05$
Site	0.24	2.01	18	54.23	0.03	0.92
Treatment	0.21	3.72	12	38.00	0.00	0.99
Site × treatment	0.11	1.56	36	86.20	0.05	0.86

structure (Corn and Bury 1991) or even increased in clearcuts and regeneration stands (Harris 1984). The absence of correlation between old-growth character- istics and amphibian abundance led Corn and Bury (1991) to conclude that important microhabitat con- ditions for amphibians may be supplied by young as well as intact forests.

Other research suggests, however, that amphibians have specialized microclimate and habitat require- ments, and that physical and biotic conditions found in different aged forests limit the distribution and abun- dance of forest amphibians (Welsh 1990). Surveys con- ducted in the Pacific Northwest have documented de- clines in amphibian abundance in second-growth man- aged stands, especially where significant understory habitat disturbance has occurred (Bury 1983, Welsh and Lind 1988, Dupuis et al. 1995). In contrast to Bury (1983) and Dupuis et al. (1995), we did not detect any significant changes in the understory vegetation after logging. In fact, logging was conducted in a manner intended to minimize understory disturbance. Never- theless, we documented a 70% reduction in long-toed

salamander abundance on the newly harvested New Forestry and overstory-removal stands in 1994 and 1995.

We found that the loss of an intact overstory, re- flected in decreased abundance and mean basal area per tree of dominant species, was the critical factor asso- ciated with decreased abundance of long-toed sala- manders. Amphibians have a low tolerance for hot, dry conditions. Removal of the canopy resulted in a mean 1.8°C increase in daily summer temperatures (intact mean = 8.4°C, New Forestry mean = 10.2°C, over- story-removal mean = 10.2°C; McGraw 1997) on har- vested sites that probably increased moisture stress on long-toed salamanders (Dupuis et al. 1995). Harris (1984) summarized findings that older, taller, and more structurally complex forests have more daily and sea- sonal microclimatic stability than younger forests. Du- puis et al. (1995) found soils of young and mature postharvest stands were less moist than those of old growth. High ambient air temperatures, low soil mois- ture, and wind have been shown to cause dehydration (Hutchinson 1961, Heatwole 1962a, Petranka et al.

TABLE 6. Summary of discriminant analysis for habitat differences among sites and harvest treatments.

Statistic	Treatment		Site		
	Function 1	Function 2	Function 1	Function 2	Function 3
Standardized discriminant function coefficients					
Mean forb	0.43	0.80	0.64	0.25	−0.42
Mean grass	−0.67	−0.26	−0.16	1.35	0.03
Mean litter	0.06	−0.49	−1.10	0.42	−0.32
Mean shrub	0.39	0.49	1.16	−0.77	0.89
Mean wood	−0.46	0.54	−0.15	0.22	0.57
Mean basal area	0.78	−0.21	−0.20	0.37	0.35
Mean discriminant scores					
Intact	1.43	−0.04			
New Forestry	−0.81	−0.43			
Overstory removal	−0.63	0.47			
Gordon Ranch			−1.02	0.54	−0.28
Bucksnort			0.52	0.43	0.51
Gravel Pit S.			−0.61	−0.81	0.17
Gravel Pit N.			1.11	−0.16	−0.40
Function summary					
Eigenvalue	1.56	0.15	0.81	0.37	0.13
Percentage discriminating variance	91.20	8.80	61.80	27.90	10.30
Canonical correlation	0.78	0.36	0.67	0.52	0.34
P	0.00	0.51	0.03	0.22	0.44

Notes: Extraction of discriminant functions was performed after multivariate analysis of variance indicated significant ($P < 0.05$) habitat differences among sites and treatments. Stepwise selection of variables was performed based on Mahalanobis distance and was fol- lowed by varimax rotation of the pattern matrix (coefficients).

1993). Thus, the harvested sites may have become less suitable for the long-toed salamanders. The reduction in canopy cover may also have indirectly affected the distribution of long-toed salamanders by changing the temperature and moisture of cover objects (Heatwole 1962b; Pough et al. 1987). Exposed logs may be 3.5–5× warmer than shaded ones (Heatwole 1962b).

Our observations lead us to conclude that microclimate protection under New Forestry cuts was not sufficient to safeguard long-toed salamander populations on affected sites. That may be partly a consequence of the similarity in canopy retention between New Forestry and overstory-removal sites. Recall that, although a proportion of all size classes were retained after New Forestry cuts, the mean basal area of remaining trees on overstory-removal and New Forestry sites were not very different. Nearly equivalent opening of the canopy under both harvest methods would be expected to produce similar responses if canopy closure influences habitat suitability for long-toed salamanders. Added to that, the care that was taken to protect understory microhabitats in both methods minimized differences between them. On both New Forestry and overstory-removal sites, winter logging and retention of snags and coarse woody debris protected vegetation and conserved understory habitat structure. Despite these efforts to conserve understory habitats, long-toed salamander numbers declined on harvested sites. It appears that only by conserving substantially more of the canopy can tolerable microclimates be retained. We think this is unlikely to occur, given the current economic realities of timber management on private and public lands.

What then can be done to promote conservation of long-toed salamanders and other amphibians that inhabit Rocky Mountain forests? Stand replacing disturbance, most often fire, was common in naturally regulated forests in western Montana (Arno 1980, Antos and Habeck 1981). Amphibians, like other terrestrial species adapted to periodic disturbance, either retreated to intact habitats or repopulated disturbed habitats from unaffected neighboring habitats. The disturbance created by both timber harvesting methods in our study was much less severe than that caused by stand replacing fire, and it is probable that many long-toed salamanders in the affected habitats retreated into adjacent unharvested stands. That makes the relative area of harvested and intact forest, the continuity between unharvested patches, and their connections to breeding sites critical to continued persistence of long-toed salamanders in managed forests. To that end we see the emergence of sound landscape management philosophies as vital to conservation of amphibian diversity in Western forests.

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