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Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in Northwestern California

N.E. Karraker, H.H. Welsh Jr.*

Pacific Southwest Research Station, U.S. Forest Service, 1700 Bayview Drive, Arcata, CA 95521, USA
Department of Wildlife Management, Humboldt State University, Arcata, CA 95521, USA

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ABSTRACT

Conservation needs for amphibians in managed timberlands may differ based upon the species present and the timber harvesting methods employed. Clearcuts have been documented to be detrimental to amphibians but the impacts of associated silvicultural edges and alternative harvesting treatments are not well understood. The primary objective of this study was to determine if amphibian abundances and body condition differed in thinned forests and intact forests, and in clearcuts and associated silvicultural edges. We also examined which environmental attributes were important in explaining observed differences. We sampled clearcuts, silvicultural edges, and adjacent late-seral forests at 10 sites in northwestern California from October 1999 to July 2002. Clearcuts at these sites ranged in age from 6 to 25 years. Five of these forest stands were intact and five had been commercially thinned at least 10 years prior to our study. Amphibian abundances were similar in thinned and unthinned forests, but body condition of the most common species was lower in thinned forests. Abundances of amphibians were nearly twice as high in forests and at silvicultural edges than in clearcuts. Clearcutting at these sites appears to have affected amphibian numbers up to 25 years post-harvest, however, silvicultural edges were suitable habitats for amphibians. While commercial thinning did not reduce amphibian numbers, it is an intermediate treatment followed by clearcutting. Where conservation of amphibians is a concern, even-aged silvicultural systems may not provide the most appropriate method for maintaining viable populations on managed forestlands in the northwestern US.

1. Introduction

Amphibians play keystone roles in forest ecosystems, influencing vital ecosystem processes and contributing to system resilience-resistance (=stability) (Davic and Welsh, 2004). Declines and extinctions of amphibians have been reported globally since the 1970s (Blaustein and Wake, 1990; Alford and Richards, 1999; Corn, 2000). These declines have been attributed to factors such as habitat disturbance, exotic species introductions, toxicants, and pathogens (reviewed by Collins and Storfer, 2003). Of these mechanisms, habitat alteration is considered the primary cause of declines (Blaustein and Wake, 1990; Collins and Storfer, 2003). In both the eastern and western United States, documented declines in terrestrial

* Corresponding author: Present address: State University of New York, College of Environmental Science and Forestry, Department of Environmental and Forest Biology, 250 Illick Hall, Syracuse, NY 13210, USA. Tel.: +1 315 470 6754.
E-mail address: nekarrak@syr.edu (N.E. Karraker).
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amphibian populations have been associated with habitat loss from timber harvesting (reviewed by deMaynadier and Hunter, 1995; Cushman, 2006). Many terrestrial amphibians have narrow temperature and moisture tolerances due to their respiratory physiology (Spotila, 1972; Feder, 1983), and moist, cool, and stable microclimatic conditions are essential to the viability of these species. Timber harvesting reduces canopy cover, which can increase air and soil temperature (Chen et al., 1995). Reductions in coarse woody debris and leaf litter, resulting from timber harvesting, eliminate climate-ameliorating cover used by many species. Loss of both canopy cover and cover objects on the forest floor can result in dramatic changes in the microclimatic regime necessary for the survival of terrestrial amphibians (Welsh, 1990; deMaynadier and Hunter, 1998).

In most studies, clearcutting has been demonstrated to reduce amphibian abundances in forests in the eastern and northwestern United States (reviewed by deMaynadier and Hunter, 1995). In Maine, abundances of both anurans and salamanders were significantly higher in mature forests than in clearcuts aged 2, 5, 9–11, and 25 years (deMaynadier and Hunter, 1998). Western Red-backed Salamanders (*Plethodon vehiculum*) were 3–6 times less abundant in young stands (17–18 years) than in mature (380–500+ years) stands on Vancouver Island, Canada (Dupuis et al., 1995). Contrasting with these studies, however, abundances of Peaks of Otter Salamanders (*Plethodon hubrichti*) in Virginia were not significantly different between either recent clearcuts (4–5 years) or older clearcuts (12–18 years) and mature forests (>80 years) (Mitchell et al., 1996).

While much previous research has been conducted on the effects of clearcutting on amphibians, relatively less is known about the impacts of other silvicultural methods. Selection harvesting, used to maintain an uneven-aged stand, entails harvesting either individual trees, creating many small canopy gaps, or groups of trees, creating fewer larger gaps. Salamander densities were similar between plots located within canopy gaps and plots within closed canopy forests in the first year following selection harvesting in New York (Messere and Ducey, 1998). Significant decreases in salamander abundance were reported 3 years following group selection harvesting when compared with pre-treatment abundance in the southern Appalachian Mountains of the US (Harpole and Haas, 1999). Commercial thinning, another partial-harvesting method, generally reduces basal area by up to 50%, with the goal of creating an even-aged stand made up of healthy, evenly spaced trees. In one previous study on this topic, thinning had no significant effect on the abundance of Eastern Red-backed Salamanders (*Plethodon cinereus*) in New Hampshire and Massachusetts, on sites treated 12–21 years prior to the study (Brooks, 1999). Given the paucity of previous research it is not clear if partial harvesting treatments, such as selection harvesting and commercial thinning, are detrimental to amphibians to the degree that clearcutting can be. However, there is an important distinction to be made between the two treatments. Selection harvesting is a silvicultural system, whereas commercial thinning is an intermediate treatment usually conducted 20–40 years prior to clearcutting. Where even-aged management is the goal, it is not clear if it is the intermediate step, commercial thinning, or the final step, clearcutting, that causes the declines in amphibian numbers reported following harvesting. Few studies on amphibians have focused on the effects of silvicultural practices other than clearcutting, and further efforts are needed to examine how the range of these forestry practices and the extent and duration of their effects on amphibians may vary geographically. In addition, previous research on the effects of timber harvesting on amphibians has evaluated these effects by examining changes in abundance or density or amphibians. While some studies have demonstrated changes, it is likely that more subtle effects to individuals and populations also occur. To our knowledge, only one previous study has examined other impacts on amphibians, such as changes in body condition. In Brazil, males of *Phyllomedusa tarsius* were of smaller body size (snout-urostyle length) in previously cleared forest than in intact forest (Neckel-Oliveira and Gascon, 2006). This result signals a need for further examination into the indirect effects of timber harvesting on amphibians.

Recently cut forests adjacent to late-seral forests create high-contrast edges that may be less permeable to species' movements (Stamps et al., 1987; Yahner, 1988). Such edges are more likely to create significant effects (Saunders et al., 1991), including changes in vegetative composition, increases in air and soil temperature, and decreases in humidity. In most studies, edges have been found to affect biotic and abiotic factors up to 50 m into the adjacent forest (Murcia, 1995). However, silvicultural edges, associated with clearcuts less than 11 years old, affect forest microclimate up to 240 m from the edge (Chen et al., 1990, 1995). The effects of silvicultural edges on amphibians have not been well documented. In Maine, salamanders avoided 11 year-old clearcuts and associated silvicultural edges more than most anurans, and anuran abundance increased with increasing proximity to forest interior locations (deMaynadier and Hunter, 1998). In contrast to this study, however, distance to forest edge showed no relationship with abundance of terrestrial salamanders in Oregon (Biek et al., 2002).

Intensive timber harvesting occurs on both public and private forests in the Pacific Northwest and in other regions of the US and has the potential to cause significant declines in terrestrial amphibian populations over large areas. With timber rotation ranging from 20 to 30 years in southern US pine (*Pinus* sp.) forests (Mitchell and Ford-Robertson, 1992) to 50–70 years in Pacific Northwest coast redwood (*Sequoia sempervirens*)/Douglas-fir (*Pseudotsuga menziesii*) forests (Aubry, 2000), permanent losses of amphibian populations are possible. In order to prevent such extirpations in northwestern California, we sought to understand how commercial thinning, clearcutting, and associated silvicultural edges affect amphibian abundances and important habitat attributes. With this information, land managers, environmental regulators, and others interested in protecting these species can make informed decisions to better conserve populations of terrestrial amphibians. The objectives of this study were to determine: (1) how clearcutting, silvicultural edges, and commercial thinning affect the abundances and body condition of terrestrial amphibians, particularly over the long term; and (2) which environmental attributes best explain observed differences in amphibian abundances between sites and between silvicultural treatments.

2. Methods

2.1. Study sites

This study was conducted on the Six Rivers National Forest in northwestern California. The study area is located within the Klamath River drainage, approximately 50 km inland from the Pacific Ocean. Elevation at the study sites ranged from 585 to 1264 m above sea level, with moderate to steep slopes. The study area was characterized by a mixed conifer-hardwood forest made up primarily of Douglas-fir (*Pseudotsuga menziesii*) with a tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) understory. Clearcuts contained dense vegetation composed primarily of young Douglas-fir and several shrub species including *Ceanothus* spp. and *Arctostaphylos* spp. Climate within the study area was characterized by hot, dry summers, heavy rainfall during spring and fall, and heavy winter snowfall. Average annual minimum and maximum temperatures in the area were 6.3 and 21.6 °C, and mean annual precipitation was 135.2 cm (Western Regional Climate Center, 2002).

Using forest inventory maps and field reconnaissance we located 18 unthinned late-seral forest stands adjacent to clearcuts aged 6–25 years, and 25 thinned late-seral forest stands, harvested at least 10 years prior, adjacent to clearcuts aged 6–25 years, all within a 625 km^2 area. After evaluating both sets of sites, we determined that there were 8 unthinned forest/clearcut sites and 10 thinned forest/clearcut sites sufficiently similar in aspect (easterly-facing) and slope (range 35–64%) to control for variation in these characteristics. We randomly selected five sites from each of these subsets, for a total of 10 sites. At all sites, silvicultural edges were oriented perpendicular to the topographical contour. Sites were distributed over a broad area, with sites closest to each other located approximately 1.5 km apart and the farthest sites located approximately 19 km apart.

2.2. Animal sampling

Within each site, two 150-m long pitfall trap transects were installed approximately 20 m apart, perpendicular to and centered on the forest edge (Fig. 1). Each transect contained seven trap stations for a total of 14 stations per site. A trap station consisted of a drift fence and four pitfall traps (Fig. 1). Drift fences were constructed with 5 m lengths of fiberglass window screen and wooden stakes, and the lower edge of each fence was buried. Two pitfall traps were positioned directly adjacent to the fence, one on each side at each end of the fence. Each trap was covered with a wooden coverboard, and an additional coverboard, with no pitfall trap, was positioned next to each drift fence to increase sampling effort at each trap station. Moist soil and leaf litter were maintained in all pitfall traps to reduce stress on amphibians. Jute twine was attached to coverboards and allowed to hang down into pitfall traps so that trapped mammals could escape (Karraker, 2001). Traps were closed with plastic lids when not in use.

Pitfall traps and coverboards were checked weekly during the sampling periods from October to December and April to June 2000, 2001, and 2002. Amphibians in traps and under coverboards (hereafter 'captured animals') were identified to species, weighed, measured (snout-vent length, posterior angle of vent), and marked by toe-clipping, following Twitty (1959). Anurans are rarely captured in the type of pitfall traps

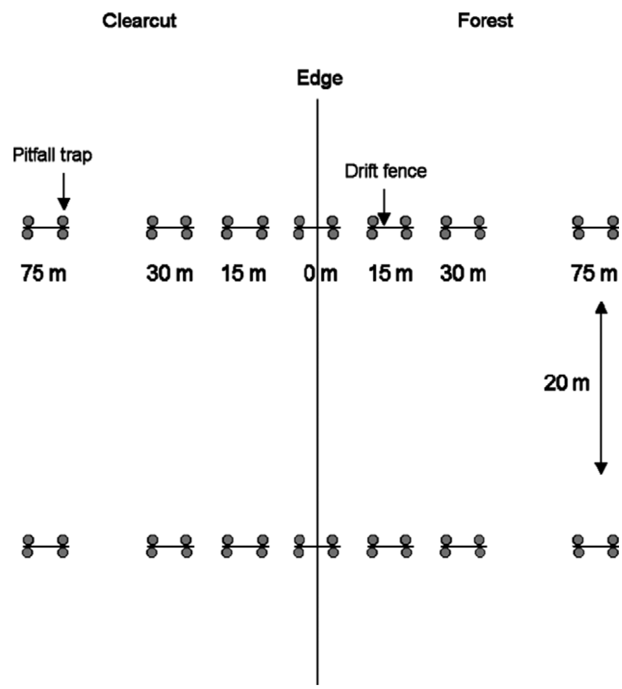

Fig. 1 – Schematic representation of one site, with 2 150 m-long transects, each extending from 75 m in a clearcut, through the edge, and 75 m into the adjacent late-seral forest, and associated pitfall trap stations.

Table 1 – Amphibian species and total number captured (excluding recaptures) by silvicultural treatment in northwestern California, October 1999–June 2002

Silvicultural method	Species							
	Ensatina eschscholtzii	*Plethodon elongatus*	*Bufo boreas*	*Dicamptodon tenebrosus*	*Taricha granulosa*	*Rhyacotriton variegatus*	*Ascaphus truei*	Total
Clearcut	159	25	10	1	0	0	0	195
Edge	73	30	8	1	0	0	1	113
Thinned forest	148	62	3	1	0	1	0	215
Unthinned forest	106	6	0	0	1	0	0	113
Total	486	123	21	3	1	1	1	636

used in this study, so only salamanders were marked. Length and weight measurements were used to identify the few Western Toads (*Bufo boreas*) that were captured. Gender was recorded for those species for which it could be determined in the field. We released animals approximately 2 m from the trap in which they were captured and perpendicular to the drift fence.

2.3. Environmental sampling

Measurements of environmental attributes were made during October 2000. Overstory canopy cover, litter cover, rock cover, and duff depth were measured in 5 m-diameter circular plots located adjacent to each trap station within each transect, such that 14 circular plots were assessed at each site. Canopy cover was measured from the center of each plot using a convex spherical densiometer. Visual estimates were made of litter and rock cover within each plot. To measure duff depth, a soil sampling tube was rotated into the ground to a depth of approximately 25 cm in three different locations within each plot. We measured the depth of duff (to the nearest cm) in each soil core, and the three measurements were averaged. We measured coarse woody debris along 20-m transects associated with each pitfall trap station, and calculated downed wood volume for the area around each pitfall trap station.

2.4. Data analyses

We pooled amphibian detections at similar distances along the paired transects within forests, edges, and clearcuts because of low capture rates. Animal captures from pooled trap stations were then converted to captures per 1000 trap nights to balance unequal sampling effort due to factors such as periodic inaccessibility of some sites due to snow and trap disturbance by large mammals. Recapture data were omitted from the primary analyses and used only to assess movements by amphibians.

To test the effects of silvicultural type (clearcut, edge, and forest) and thinning type (thinned or unthinned forest) on total amphibian abundance, we conducted a split-plot analysis of variance (ANOVA) (Underwood, 1997), with silvicultural type as the whole-plot factor and thinning type as the split-plot factor. The response variable was amphibian captures/1000 trap-nights. We conducted an additional split-plot ANOVA on data for Ensatina (*Ensatina eschscholtzii*) only, which was considerably more abundant than other amphibians. We made pairwise comparisons of significant main effects using Waller–Duncan tests (Day and Quinn, 1989).

We captured *E. eschscholtzii* and the Del Norte Salamander (*Plethodon elongatus*) in sufficient numbers to examine differences in use of clearcuts and forests for each species. We also examined the use of clearcuts and forests by gender and age class for *E. eschscholtzii* with split-plot ANOVAs. Gender of *P. elongatus* could not be determined easily in the field (but see Ollivier and Welsh, 2003) and too few sub-adults were captured to conduct similar analyses for this species.

To evaluate the importance of measured environmental parameters in explaining differences in amphibian abundance between clearcuts, edges, and forests, we used an information-theoretic approach and developed models a priori for subsequent testing (Burnham and Anderson, 1998). We constructed two topographic models to examine differences in amphibian detections between sites and seven habitat attribute models to examine differences in detections between clearcuts, edges, and forests and thinned and unthinned forests. The 10 models, containing only variables that were not highly correlated ($r < 0.70$), were tested using linear regression. We used the corrected form of Akaike's Information Criterion (AIC_c) to rank competing models and examined the R^2 (adjusted R^2 for models with multiple variables) to determine the strengths of relationships between independent variables and the response variable (Burnham and Anderson, 1998).

We evaluated body condition of *E. eschscholtzii* by silvicultural treatment and forest type and of *P. elongatus* by silvicultural treatment using the following formula:

$$\text{body condition index} = \text{weight (g)}/\text{total length (mm)}$$

Salamanders missing tails or parts of tails were excluded from this analysis, as were recaptured animals. Body condition indices were log-transformed and then compared using ANOVA.

Recapture data for *E. eschscholtzii* and *P. elongatus* were used to determine minimum, maximum, and mean distances moved for each species. Because animals were capable of moving between transects, we calculated straight-line distances between captures using the Pythagorean Theorem (Bennett, 1995). For *E. eschscholtzii*, we compared movement distances by gender using a Student's *t*-test.

3. Results

3.1. Amphibian abundance and silvicultural treatment

We captured 636 individuals of seven amphibian species (Table 1), with 56 recaptures of *E. eschscholtzii* and 26 of *P. elongatus*. Mean capture rates were nearly two times greater in forests and at edges compared with clearcuts ($F_{2,16} = 3.70$, $P = 0.048$) (Fig. 2), but they were more variable at edges compared with interior forests (Table 2). Total amphibian detections were higher in thinned than unthinned forest ($F_{2,16} = 8.43$, $P = 0.010$), and they were less variable in unthinned forest (Table 2). In the analysis of *E. eschscholtzii*, we found more *E. eschscholtzii* in forests than in edges or clearcuts, with significantly higher abundances in forests than in clearcuts ($F_{2,16} = 2.85$, $P = 0.087$). Abundances of *E. eschscholtzii* were similar between thinned and unthinned forests ($F_{1,8} = 1.07$, $P = 0.316$) (Table 2).

Table 2 – Mean capture rates for amphibians by silvicultural treatment

Silvicultural method	*n*	Mean capture rate [captures/1000 trap nights (SD)]
Clearcut	10	3.82 (0.66)
Edge	10	6.62 (1.76)
Forest	10	6.44 (0.97)
Thinned forest	5	6.84 (1.00)
Unthinned forest	5	3.85 (0.45)

E. eschscholtzii were four times more abundant than *P. elongatus* across all sites. *E. eschscholtzii* were six times more abundant than *P. elongatus* in clearcuts than in forests, but this difference was highly variable across sites and therefore was not statistically significant ($F_{1,8} = 2.37$, $P = 0.126$). Relative abundances of the two species were similar between thinned and unthinned forests ($F_{1,8} = 0.01$, $P = 0.934$). We captured nearly two adults to every one subadult *E. eschscholtzii* across all sites. The two age classes were similar in their abundance in clearcuts and forests ($F_{1,8} = 0.01$, $P = 0.92$) and in thinned and unthinned forests ($F_{1,8} = 0.71$, $P = 0.42$).

3.2. *Body condition and silvicultural treatment*

The body condition index for *E. eschscholtzii* was similar in clearcuts, edges, and forests ($F_{2,406} = 0.003$, $P = 0.99$) but was approximately 10% higher ($F_{1,407} = 13.28$, $P < 0.001$) in unthinned than thinned forests (Table 3). We found similar body condition indices for *P. elongatus* in clearcuts, edges, and forests ($F_{2,97} = 0.008$, $P = 0.99$) (Table 3).

3.3. *Amphibian movements*

The 56 recaptured *E. eschscholtzii* and 26 recaptured *P. elongatus* yielded recapture rates of 12% and 21%, respectively. For all recaptures, including those in which no movement occurred, *E. eschscholtzii* moved an average of 10.5 m (SD = 20.3, $n = 56$, range = 0–90) and *P. elongatus* moved an average of 5.1 m (SD = 11.8, $n = 26$, range = 0–45). For the recaptures in which movement occurred, *E. eschscholtzii* moved an average of 32.7 m (SD = 23.7, $n = 18$, range = 15–90). Movement distances in male ($\bar{x} = 36.4$, SD = 22.5, $n = 9$, range = 15–75) and female ($\bar{x} = 29.0$, SD = 25.6, $n = 9$, range = 15–90) *E. eschscholtzii* were similar ($t = 0.64$, df = 17, $P = 0.53$). For those recaptures in which movement occurred, *P. elongatus* moved an average of 26.5 m (SD = 11.7, $n = 5$, range = 15–45). Of the 82 recaptures, 75 salamanders remained in the silvicultural treatment in which they were originally captured, and seven salamanders moved from one silvicultural treatment to another. Of those, two moved from forest to clearcut, none moved from clearcut to forest, and five moved between edge and either forest or clearcut.

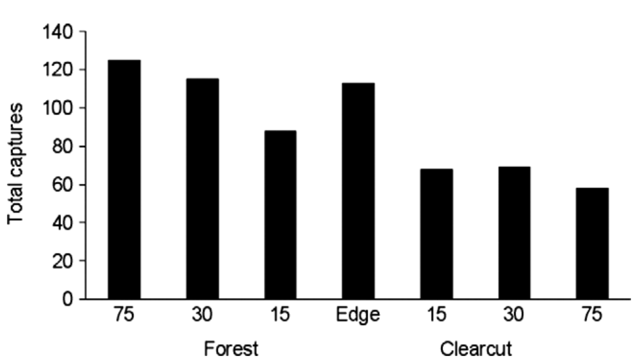

Fig. 2 – Total amphibian captures (excluding recaptures) at silvicultural edges and distances (in m) into adjacent clearcuts and forests for all 10 sites.

3.4. *Environmental variables and silvicultural treatment*

Percentage canopy cover, downed wood volume, and duff depth generally increased along a gradient from clearcuts, through edges, and into forests, while other measured parameters varied little (Table 4). Canopy cover explained 11% of the variation in amphibian abundance between clearcuts, edges, and forests (Table 5). Measured environmental variables were similar between thinned and unthinned for-

Table 3 – Quantities of environmental variables measured by silvicultural treatment

Silvicultural treatment	Environmental variables (mean ± SD)			
	Canopy closure (%)	Litter cover (%)	Downed wood volume (m^3)	Duff depth (cm)
Clearcut	62 (24)	90 (11)	69 (115)	18 (7)
Edge	72 (15)	91 (14)	115 (108)	18 (13)
Forest	93 (3)	99 (2)	236 (252)	26 (8)
Thinned forest	93 (1)	98 (1)	205 (74)	26 (2)
Unthinned forest	93 (1)	99 (1)	268 (55)	26 (2)

Table 4 – Environmental and topographical models tested to explain differences in amphibian abundances between clearcuts, edges, and forests and between sites

Variable(s)	R^2	P	AIC_c
Environmental			
Canopy cover	0.11	0.004	206.9
Canopy cover, duff depth	0.09	0.014	208.8
Canopy cover, downed wood	0.09	0.017	209.2
Canopy cover, downed wood, duff depth	0.08	0.036	211.1
Downed wood	<0.01	0.431	214.8
Duff depth	<0.01	0.581	215.2
Downed wood, duff depth	−0.02	0.692	217.0
Topographical			
Elevation	0.51	<0.001	166.1
Elevation, slope	0.50	<0.001	167.0
Slope	0.14	0.001	204.9

The dependent variable for each model is amphibian capture rate. Adjusted R^2 is given for models with two or more variables. AIC_c is Akaike's Information Criterion corrected for small sample sizes.

Table 5 – Body condition indices for *E. eschscholtzii* and *P. elongatus* by silvicultural treatment

Silvicultural treatment	Body condition index (mean ± SD)			
	n	*E. eschscholtzii*	*n*	*P. elongatus*
Clearcut	137	0.031 (0.010)	19	0.021 (0.007)
Edge	58	0.031 (0.011)	22	0.021 (0.006)
Forest	212	0.031 (0.010)	56	0.021 (0.007)
Thinned forest	128	0.030 (0.010)	–	–
Unthinned forest	84	0.033 (0.010)	–	–

Body condition indices for *P. elongatus* were not compared for thinned and unthinned forests due to small sample sizes.

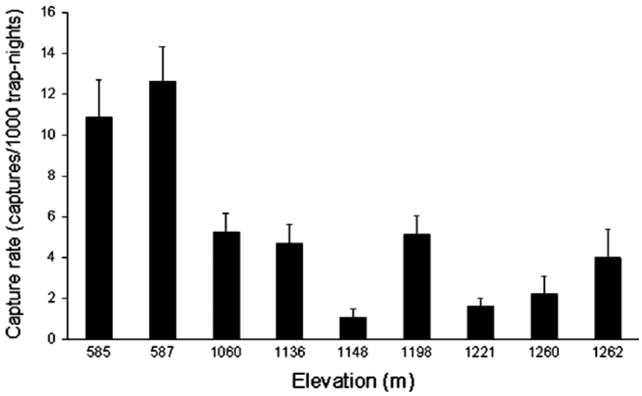

Fig. 3 – Amphibian capture rates (excluding recaptures) by elevation.

ests, with the exception of downed wood volume, which was approximately 25% greater in unthinned forests (Table 5). Elevation, which ranged from 585 to 1264 m above sea level, explained 51% of the variation in amphibian abundances between sites (Table 5), with higher capture rates occurring at lower elevations (Fig. 3).

4. Discussion

Forest resources are important to the economies of many countries throughout the world. However, timber harvesting can be a significant form of habitat disturbance in many ecosystems, and understanding the impacts of timber harvesting and the associated legacy of silvicultural edges on terrestrial amphibians remains an important conservation issue.

4.1. *Commercial thinning and amphibians*

Little research has been previously conducted on the impacts of commercial thinning on terrestrial amphibians. In the northeastern US, commercial thinning did not reduce abundance of *P. cinereus*, yet in Washington capture rates of *P. vehiculum* were lower following thinning of forests (Grialou et al., 2000). Commercial thinning of the late-seral forests at our sites did not reduce numbers of terrestrial amphibians. Our results suggest that changes in environmental attributes caused by commercial thinning were not so severe as to affect amphibian abundances. In fact, while not statistically different, abundances of amphibians were greater in thinned than unthinned forests. However, body condition in thinned forests was significantly lower for the most abundant species, *E. eschscholtzii*. Higher abundance of amphibians in thinned stands may result in increased competition for resources, such as cover objects, resulting in lower body condition in *E. eschscholtzii*. There may be some evidence for this explanation in that downed wood volume was 25% higher in unthinned forests in our study, and downed wood is the primary cover used by this species (Stebbins, 1954). Future research should attempt to understand the relationship between abundance and body condition relative to the availability of resources for amphibians in harvested forests.

4.2. *Clearcutting and amphibians*

Results of our study and most other studies (reviewed by deMaynadier and Hunter, 1995) have shown that clearcutting reduces amphibian abundances, yet equivocal results exist, particularly when researchers have examined the responses of individual species. In Washington, abundances of Northwestern Salamanders (*Ambystoma gracile*) and Western Red-backed Salamanders (*P. vehiculum*) were not affected by clearcutting, but numbers of *E. eschscholtzii* were lower in clearcuts than in mature forests (Aubry, 2000). We found that numbers of both *E. eschscholtzii* and *P. elongatus* were lower in clearcuts than in late-seral forests, and that clearcuts affected these species differently. *E. eschscholtzii* was four times more abundant than *P. elongatus* across all sites, but six times more abundant within clearcuts. This result suggests that clearcuts in northern California may have a greater effect on *P. elongatus* than on *E. eschscholtzii*. In contrast to our study, abundances of these two species were similar in clearcuts and adjacent mature forests in Oregon (Biek et al., 2002), an effect that was attributed to the large amounts of woody debris remaining following clearcutting. More *E. eschscholtzii* occur in late-seral than young forest, but also greater numbers at drier inland sites compared with sites in the moist coastal zone of northwestern California (Welsh and Lind, 1988), suggesting that this species may be more tolerant of xeric conditions, either natural or human-caused. However, our results suggest that while they may be more resilient/resistant than some other plethodontids, such as *P. elongatus,* they are clearly not immune to the effects of timber harvesting. Geographic variation in climatic regimes, timber harvesting prescriptions, topography (elevation), vegetation composition and structure, and life requisites of terrestrial amphibians may contribute to differences between these studies and complicate interpretations of their results.

4.3. *Silvicultural edges and amphibians*

The effects of silvicultural edges on abundance of terrestrial amphibians in our study (see Fig. 2) were different than those reported in a study conducted in the eastern US (deMaynadier and Hunter, 1998). In Maine, salamander abundance increased significantly with increasing proximity to interior forest locations (deMaynadier and Hunter, 1998). In forests of the northwestern US greatest extremes and variability in microclimate existed at silvicultural edges rather than in clearcuts or interior forests (Chen et al., 1995). Daytime air temperature was higher and relative humidity was lower at silvicultural edges than in clearcuts, probably because of decreases in wind at edges (Chen et al., 1995). Such conditions would theoretically make silvicultural edges relatively inhospitable for terrestrial salamanders. However, amphibian abundances were similar in silvicultural edges to that in forests in our study, suggesting that these edges contained suitable cover habitat and equable microclimatic conditions for terrestrial salamanders. Similarly, silvicultural edges did not affect the abundance of *E. eschscholtzii* or *P. elongatus* in Oregon (Biek et al., 2002). However, variation in capture rates at edges in our study was nearly two times greater than in forests, and nearly two times greater than in clearcuts (Fig. 2), suggesting that greater differences in microclimatic instability at edges (Chen et al., 1999) may be a factor.

4.4. *Amphibian movements and timber harvesting*

We believe that both *E. eschscholtzii* and *P. elongatus* were most likely residents of the areas (clearcut, edge, or forest) in which they were detected. In our study, *E. e. oregonensis* moved a mean distance of 10.5 m over 3 years. By contrast, *P. elongatus* moved 5.1 m over the same time period at these sites (see also Welsh and Lind, 1992). Earlier research found that *E. e. xanthoptica* moved a mean distance of 7.7 m for over 4 years in northern California (Stebbins, 1954) and *E. e. platensis* moved 22.0 m over 3 years in the Sierra Nevada Mountains of California (Staub et al., 1995). Based on our results and those of others (Stebbins, 1954; Staub et al., 1995), it appears unlikely that salamanders are making regular movements between clearcuts and forests. In fact, in 82 recaptures in our study, only seven were made in which salamanders moved from one silvicultural treatment (clearcut, edge, or forest) to another. Only two of those moved from forest to clearcut and none moved from clearcut to forest. Similarly in Brazil, no movements of the hylid frog *Phyllomedusa tarsius* occurred between ponds in intact forests and those in disturbed habitats, suggesting that the populations in the latter are not sinks for the populations in intact forests (Neckel-Oliveira and Gascon, 2006). Detections of individuals of all ages of *E. eschscholtzii* and *P. elongatus* within clearcuts at our sites coupled with short movement distances determined by this and other studies (Stebbins, 1954; Staub et al., 1995) indicate that reproduction, foraging, and estivation by these salamanders is occurring in clearcuts within the study area.

4.5. *Duration of effects of timber harvesting on amphibians*

Differences in results obtained in studies on the impacts of timber harvesting on amphibians may be related to differences in the timing of the study relative to the time of harvesting. For example, capture rates of *P. vehiculum* were lower within 5 years following thinning of forests in Washington (Grialou et al., 2000), yet in the eastern US commercial thinning had no effect on abundance of *P. cinereus* in stands that had been thinned 12–21 years prior (Brooks, 1999). Similarly in our study, commercial thinning of late-seral forests at our sites occurred more than 10 years prior to sampling of amphibians and we found no reduction in numbers of terrestrial amphibians. Similar examples can be found in the research on clearcutting and amphibians. Many of these studies (Enge and Marion, 1986; Harpole and Haas, 1999; Herbeck and Larsen, 1999; Knapp et al., 2003) were conducted less than 5 years after harvesting and found that clearcut harvesting significantly affected abundance of terrestrial salamanders. One study demonstrated the long-term impacts of timber harvesting on lotic amphibians. In northern California, species richness and abundance remained significantly lower in streams 37–60 years after timber harvesting, compared with streams in late-seral forests (Ashton et al., 2006). We studied clearcuts older than 5 years, and while our results support those mentioned above, we also ensured that the focus was on the longer-term habitat changes following clearcutting.

By studying the impacts of timber harvesting on amphibians in recently harvested forests, results potentially reflect only the immediate, short-term effects on amphibians. These effects may be direct and devastating, including soil compaction due to log skidding methods, displacement or removal of cover objects, reduction of herbaceous and wood cover due to prescribed burning, and soil contamination due to application of herbicides. Such studies would not provide information on long-term effects of harvesting as the immediate habitat changes and adverse microclimatic conditions ameliorate over time. The temporal scale over which investigations on this topic are conducted has important implications for understanding the trajectory of impacts and their ultimate long-term consequences.

4.6. *Effects of elevation on amphibians*

Elevation explained over 50% of the variation in amphibian abundance between sites, with greater capture rates occurring at lower elevations (Fig. 3). Lower abundances of amphibians at higher elevations in northwestern California probably result from longer periods of cold temperatures and snow cover reducing the time when salamanders can be active on the forest floor. Elevation is a particularly important variable influencing salamander distributions because it affects life history parameters such as age and size at metamorphosis and sexual maturity (Bruce, 2003). Careful consideration of timber harvesting methods may be necessary to maintain viable and functional (sensu Conner, 1988) amphibian populations, especially at higher elevations.

4.7. *Management implications*

Our study has important implications for management of terrestrial salamanders in northwestern California and considerations for salamanders on managed lands in other regions of the world. *E. eschscholtzii*, while more abundant in late-seral forests (Welsh and Lind, 1988, 1991), occurs in a wide range of habitats, including moist meadows, mature forests, and even residential areas. Their generally robust bodies may allow *E. eschscholtzii* to exploit environments with microhabitats or microclimatic conditions unsuitable for smaller salamanders. In fact, one study (Bury and Corn, 1988) reported that *E. eschscholtzii* were more abundant in young and late-seral stands than in mature stands. This species is relatively common in northwestern California and receives no state or federal protection. Contrarily, *P. elongatus* has a well-documented association with late-seral forests (Welsh and Lind, 1988, 1991, 1995), except in the cooler, moister coastal zone where the species occurs in younger forests (Diller and Wallace, 1994). In suitable habitat *P. elongatus* can occur at high densities (Welsh and Lind, 1992), but at most sites abundances are low. *P. elongatus* is listed as a species of special concern by the State of California (Jennings and Hayes, 1994). Under the Northwest Forest Plan (USDA et al., 1994), regulations were in place on federal land until recently (USDA/USDI, 2001) that required surveying for, and then protecting, the species prior to ground-disturbing operations in suitable habitat.

The results of our study suggest some clear patterns with regard to the longer-term effects of even-aged timber management on terrestrial amphibians, particularly two species of plethodontid salamanders, in northwestern California. Clearcutting appears to be the primary harvest method causing reductions in amphibian numbers in forests subjected to even-aged management. In addition, clearcutting has a greater effect on *P. elongatus* than on *E. eschscholtzii*. Within the range of *P. elongatus* land managers might consider the use of uneven-aged management practices such as selection harvesting in order to conserve populations of this sensitive species. While commercial thinning does not appear to reduce amphibian numbers, thinning is usually an intermediate treatment in an even-aged management regime, which eventually will be followed by clearcutting. Where conservation of amphibians is important, even-aged silvicultural systems may not represent an appropriate method for maintaining viable, ecologically functional populations of amphibians on managed timberlands in northwestern California and possibly other regions.

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