Abundance and Movements of Terrestrial Salamanders in Second-Growth Forests of Southwestern British Columbia

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ABSTRACT

There is a lack of quantitative work on amphibian communities located in second-growth forests in British Columbia. The relative abundance, variation in capture rates, and movement patterns of terrestrial salamanders were investigated in 6 second-growth sites located in the University of British Columbia's Malcolm Knapp Research Forest. These data indicate that while amphibian species richness is similar among sites, total abundance is highly variable both within and among species between sites, with coefficients of variation in capture rates ranging from 44.2% to 245%. This high natural variation in amphibian abundance between forested sites of similar age and structure emphasizes the importance of collecting baseline data before drawing conclusions about the impacts of forest harvesting on amphibians. In addition, aquatic-breeding salamanders (*Ambystoma gracile* and *Taricha granulosa*) moved significantly greater distances and their direction of movement was generally parallel to the stream, while terrestrial-breeding salamanders (*Plethodon vehiculum* and *Ensatina eschscholtzii*) moved less and randomly with respect to stream location. These results suggest breeding biology (i.e., aquatic vs. terrestrial) may be a useful predictor of species' responses to timber harvesting.

Key words: *Ambystoma gracile*, amphibian, *Ensatina eschscholtzii*, forestry, movement, *Plethodon vehiculum*, riparian, salamander, second-growth, *Taricha granulosa*.

The physiological characteristics of amphibians limit them to specific microhabitats and/or microclimates within forest ecosystems; changes to these conditions via timber harvesting may influence population and community-level attributes. Numerous correlative studies have shown the density of many amphibian species to be lower in clearcuts compared to mature forests. Terrestrial salamanders, in particular, appear to be reduced by harvesting practices, with a median 3.5-fold difference in abundance between clearcut and forested sites (deMaynadier and Hunter 1995). However, the reasons for the observed lower densities are unknown.

One particular habitat component within forest ecosystems that may provide optimal habitat for terrestrial amphibians is the riparian zone. The riparian zone, defined as the interface between terrestrial and aquatic ecosystems, has a unique set of environmental conditions that may favour amphibian species, unlike those conditions found in upslope areas (Brosofske et al. 1997). A few studies have shown that riparian areas may be very important to amphibian populations (e.g., McComb et al. 1993, Gomez and Anthony 1996); however, it is unknown whether this is a broad pattern across regions and seasons, or if it is restricted to specific sites and/or environmental conditions.

Limited quantitative research has been conducted on British Columbia's terrestrial amphibian communities, and next to nothing in second-growth forest, the seral stage dominating southwestern British Columbia's landscape, where high densities of terrestrial amphibians are found. Therefore, the purpose of this study was to establish baseline conditions of abundance and movement patterns in riparian areas for terrestrial amphibian communities in 6 second-growth sites slated for harvesting. The specific objectives were: 1) to compare variation in abundance within and between 4 terrestrial salamanders among 6 second-growth sites; 2) to compare and contrast the movement patterns of aquatic-breeding salamanders with terrestrial-breeding salamanders; and 3) to determine if stream proximity affected the spatial distribution of terrestrial salamanders.

STUDY SITES

This study was conducted in the University of British Columbia's Malcolm Knapp Research Forest (122°34'W, 49°16'N), located approximately 60 km east of Vancouver.

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Table 1. General description of 6 second-growth sites in the Malcolm Knapp Research Forest.

Site	CWD[a]	Understory	Proximity of pond
Mike	large	present	<500 m
Spring	small	present	>1 km
H	medium	present	>1 km
Sck	medium	absent	>1 km
B	small	present	>1 km
I	large	absent	<500 m

[a] CWD = amounts of coarse woody debris at each site relative to each other.

This location is within the Coastal Western Hemlock biogeoclimatic zone, characterized by rainy, cool winters and dry summers. Six sites were selected in naturally regenerated 70-year-old second-growth forests, all of which were logged in the early part of the century and then burned in a stand-replacing fire. General characteristics of each site are described in Table 1. Each site will receive one of 3 treatments: control, 30-m buffer, and clearcut. The data presented in this paper include pretreatment results only.

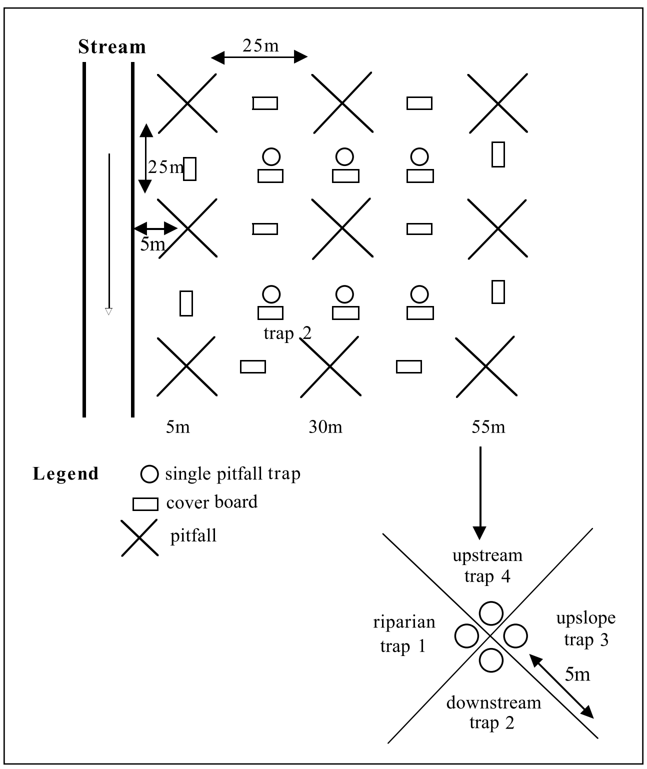

Figure 1. Arrangement of trapping grids designed to determine terrestrial amphibian abundance, direction of movement, and spatial distribution relative to the stream. Enlargement at bottom right illustrates design of a single array and arrangement of pitfall traps.

METHODS

Trapping and Marking

A combination of pitfall arrays, single pitfall traps, and cover boards were set up in a grid encompassing an area of approximately 50 X 50 m at each site (Fig. 1). Nine arrays consisting of 4 pitfall traps and drift fences were installed such that 1 trap each was oriented both downslope (trap 1) and upslope (trap 3) of the stream, as well as in the downstream (trap 2) and upstream (trap 4) direction (Fig. 1). The traps were intersected by a total of 20 m of drift fencing arranged in a cross, with the length of each arm equal to approximately 5 m. This X-arrangement of the pitfall arrays was designed to determine the direction of movement of the amphibians captured relative to the stream. Sixteen cover boards and 6 single pitfall traps were installed in the spaces between the arrays to increase amphibian capture probabilities.

Trapping was initiated in September 1997, with traps open for a total of 3 days at each site. In October and November, traps were opened for 2 or 3 days, alternating every 2 weeks and totalling 5 days of monitoring per month at each site. Trapping recommenced in February 1998, with grids monitored for 3 days, alternating every 2 weeks, for a total of 6 trap-nights per month. On 21 April 1998, traps were open continuously until 29 June 1998, when they were closed due to low trapping rate. Traps were opened a final time in July for a period of 4 trap-nights during a rain event.

Two marking techniques were used, depending on the species and weight of the individual captured. All salamanders and frogs with a weight of <8 g were marked in the field using a unique combination of elastomer dyes and toe clips. PIT (passively induced transponder) tags were used to individually mark 2 species of amphibians: northwestern salamander (*Ambystoma gracile*) and adult rough-skinned newt (*Taricha granulosa*). Animals to be PIT-tagged were taken back to the lab and anaesthetized using MS222; a small incision was then made in the lower abdomen, a PIT tag was inserted, and, finally, measurements were taken. The animals were kept overnight in a refrigerator to ensure their full recovery and then returned to their point of capture the following day. The following information was recorded for each amphibian captured: species, date, location of capture, snout–vent length, total length, mass, sex (if possible), age (juvenile or adult), individual mark, and whether the animal was newly caught or a recapture. Following processing, each individual was released approximately 1 m from the array on the opposite side from where it was captured, assuming the animal was moving in that direction.

RESULTS

Species Composition and Relative Abundance

A total of 1,247 amphibians were captured, including 5 salamander species and 3 anurans (Table 2); chorus frogs were

Table 2. Summary of total number of amphibians captured at all 6 sites combined.

Species	Common name	No. captured	No. of sites where captured
SALAMANDERS		979	
Ambystoma gracile	Northwestern salamander	327	6
Ambystoma macrodactylum	Long-toed salamander	15	3
Ensatina eschscholtzii	Ensatina	265	6
Plethodon vehiculum	Western redback salamander	232	6
Taricha granulosa	Rough-skinned newt	140	6
ANURANS		268	
Ascaphus truei	Tailed-frog	67	5
Bufo boreas	Western toad	167	6
Rana aurora	Red-legged frog	34	5
TOTAL		1,247	

present on at least 1 site but not captured. Although species composition was similar among sites, the relative abundance of each species was variable between sites and seasons (Figs. 2a–d). The aquatic breeders, northwestern salamander and rough-skinned newt, had similar patterns of abundance and seasonal activity, but differed from terrestrial-breeding salamanders in both respects. Both species were most abundant at Site I, with Mike Creek also having high numbers of northwestern salamanders. The timing of the activity patterns of the 2 aquatic breeders was slightly staggered. The northwestern salamanders' peak of activity occurred in the winter and spring, corresponding with their seasonal breeding migration. The rough-skinned newts' capture rate peaked slightly later than that of the northwestern salamanders in the spring, with movement frequency declining only slightly with the onset of summer. These salamanders had high coefficients of variation in capture rates between sites by season, ranging from 76.1% to 188.4% for the northwestern salamander, and from 64.5% to 162.2% for the rough-skinned newt.

Terrestrial-breeding salamanders, ensatina (*Ensatina eschscholtzii*) and western redback salamander (*Plethodon vehiculum*), responded similarly to site differences as reflected by their relative abundance at each site, as well as having similar patterns of seasonal activity. The abundance of terrestrial-breeding salamanders was highest at the same sites (Sck, B, and H) during the fall, contrary to the aquatic salamanders, which were most active in the winter and spring. Both the ensatina and western redback salamander were almost completely inactive in the winter, with another peak of activity occurring in the spring. There was a general decline of activity with the onset of the summer months at most sites for these 2 species. The coefficient of variation of capture rates between sites by season range from 57.5% to 245% for the ensatina, and from 44.2% to 154.9% for the western redback, reflecting the high site-to-site variation. The winter has the most variation in capture rates for the northwestern salamander, ensatina, and western redback salamander.

Movement and Spatial Distribution Relative to the Stream

For each species, the direction of movement was analyzed relative to the stream. The aquatic-breeding salamanders moved significantly more in the upstream/downstream direction of the stream: northwestern salamander: $\chi^2 = 16.12$, $P < 0.001$; rough-skinned newt: $\chi^2 = 14.33$, $P < 0.002$ (Fig. 3). No significant difference was detected in the movement direction for either the ensatina or western redback salamander.

The minimum average distance moved was calculated for each species based on recapture data (Fig. 4). The mean minimum distance moved by northwestern salamanders and rough-skinned newts was 32.1 m and 43.0 m, respectively. Ensatinas moved an average of 6.4 m and western redbacks an average of 0.64 m. Aquatic breeders moved significantly greater distances than terrestrial-breeding salamanders (1-way ANOVA, $F_{1,87} = 80.64$, $P < 0.001$).

The number of amphibians captured at 3 distances (5 m, 30 m, and 55 m) from the stream was analyzed both within and between seasons to determine if stream proximity affected the salamanders' spatial distribution (Figs. 5a–d). Within seasons, the northwestern salamander was captured significantly more often at 30 m from the stream during both the fall ($\chi^2 = 7.52$, $P < 0.02$) and winter ($\chi^2 = 9.08$, $P < 0.01$) than at either 5 m or 55 m. There was no significant difference in the number captured between the 3 distances for any other species. Between seasons, there was a trend toward increased capture rates near the stream during the summer for all species, but this was not significant.

DISCUSSION

Numerous studies conducted in the Pacific Northwest have found amphibian abundance to be highly variable within and among stand ages ranging from clearcut to old-growth forests (e.g., Aubry and Hall 1991, Corn and Bury 1991). Experimental results from studies using this chronosequential approach are confounded because variation in amphibian abundance across stand ages due to site-specific differences cannot be distinguished from variation induced by treatment effects. Conclusions may be further limited by the lack of information on the movement patterns of amphibian species both within "natural" systems and in human-altered landscapes (Gibbs 1998). There is some debate as to whether amphibians emigrate from the disturbed sites or migrate vertically into the substrate, aestivating and eventually dying due to the altered environmental conditions. While death and emigration are 2 mechanisms explaining the pattern of lower abundance in clearcut sites versus forested areas, management strategies for terrestrial amphibians might be quite different depending on the process actually responsible for the patterns observed. Therefore, the collection of pretreatment data, including information on life history parameters and movement patterns, are critical in determining the response of terrestrial amphibians to forest harvesting.

The variation in capture rates, movement patterns, and minimum distance moved for aquatic-breeding salamanders is expected based on their life history. The spatial distribution of northwestern salamanders and rough-skinned newts is dependent upon the proximity of suitable breeding sites. Site I and Mike Creek have large ponds within a few hundred meters of the study sites; the high number of aquatic breeders captured at these sites reflect the large population of salamanders these ponds are capable of producing and supporting. High variation in capture rates between forested sites of similar ages were also observed by Aubry and Hall (1991) and Corn and Bury (1991), and postulated to be a function of distance from suitable breeding sites and not a response to forest age per se. In addition, both species conduct annual breeding migrations in the late winter, spring, and early summer in which direction of movement is nonrandom, but oriented towards or away from breeding ponds (Blaustein et al. 1995). The pattern of movement of both salamanders parallel to the stream in this study is a reflection of these migrations. Both species are capable of moving several hundred meters from their terrestrial refuges to breeding ponds and, therefore, can easily move through the

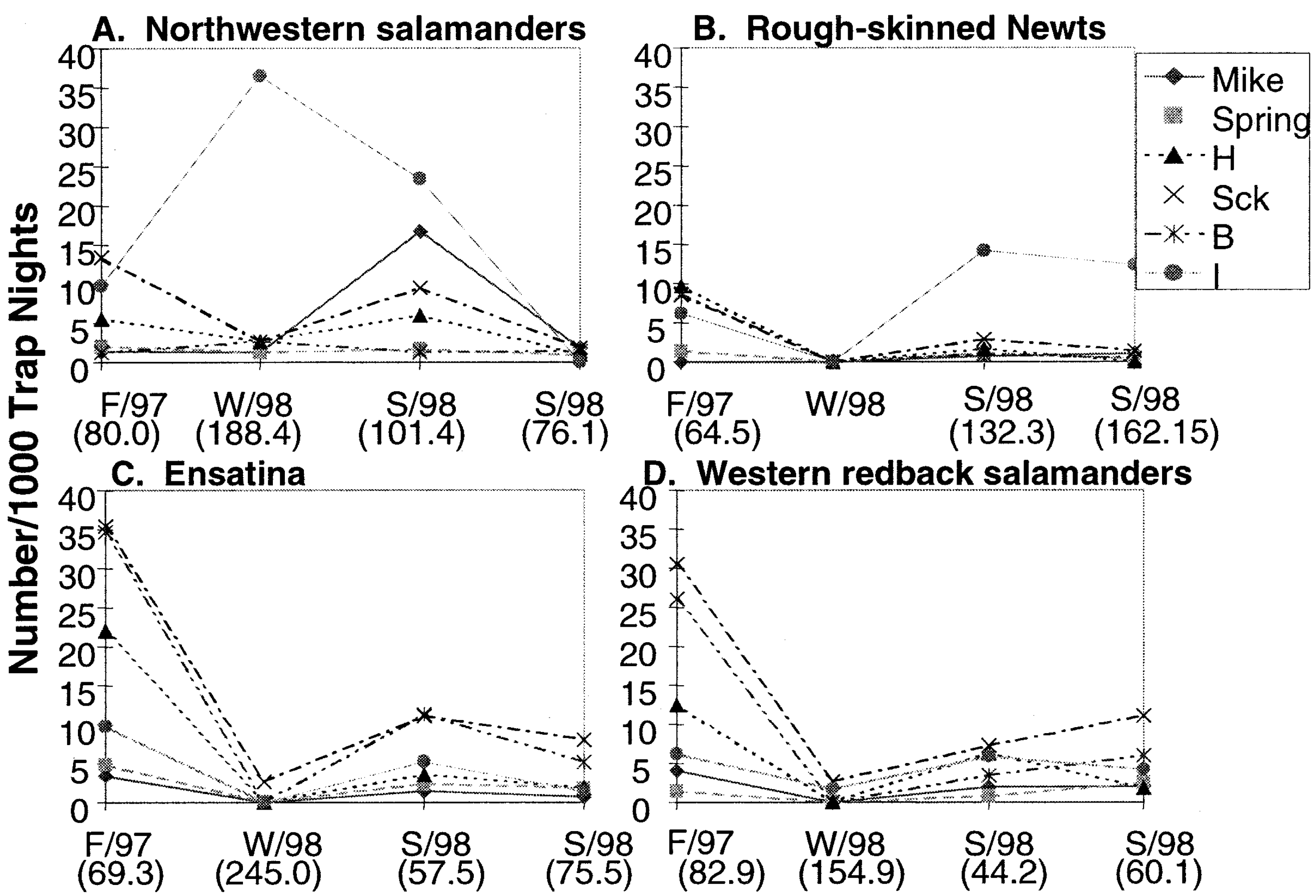

Figure 2a–d. Relative abundance of 4 terrestrial salamanders at 6 sites by season. Coefficient of variation between sites by season is included in brackets.

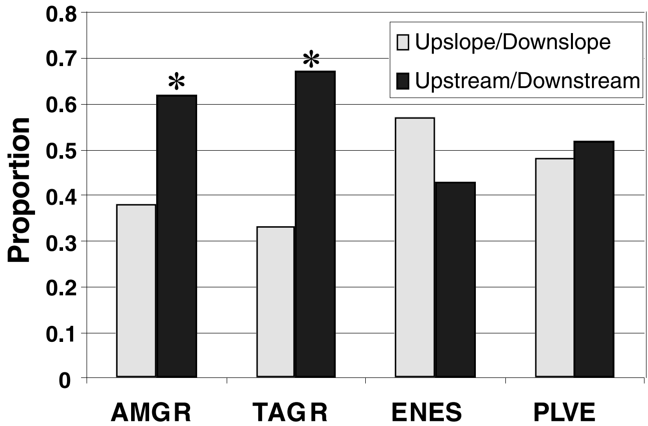

Figure 3. Comparison of the parallel versus perpendicular movement of 4 terrestrial salamanders. (Aquatic breeders: AMGR - northwestern salamander; χ^2 = 16.12 , P < 0.001; TAGR - rough-skinned newt, χ^2 = 14.33 , P < 0.002. Terrestrial breeders: ENES - ensatina, χ^2 = 7.09, P > 0.05; PLVE - western redback salamander, χ^2 = 0.14, P > 0.05.).

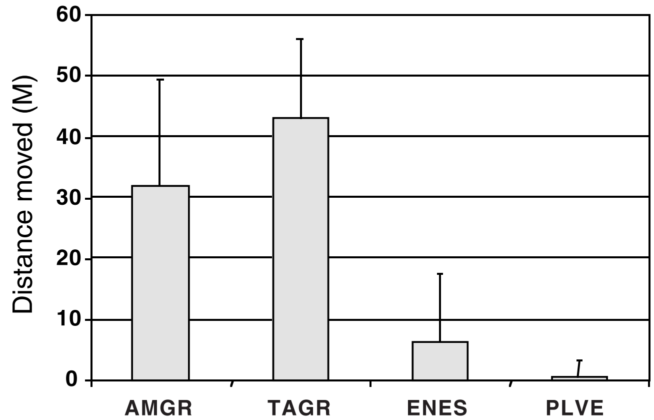

Figure 4. The minimum average distance moved for the 4 terrestrial salamanders. (Aquatic breeders: AMGR - northwestern salamander, and TAGR - rough-skinned newt. Terrestrial breeders: ENES - ensatina, and PLVE - western redback salamander).

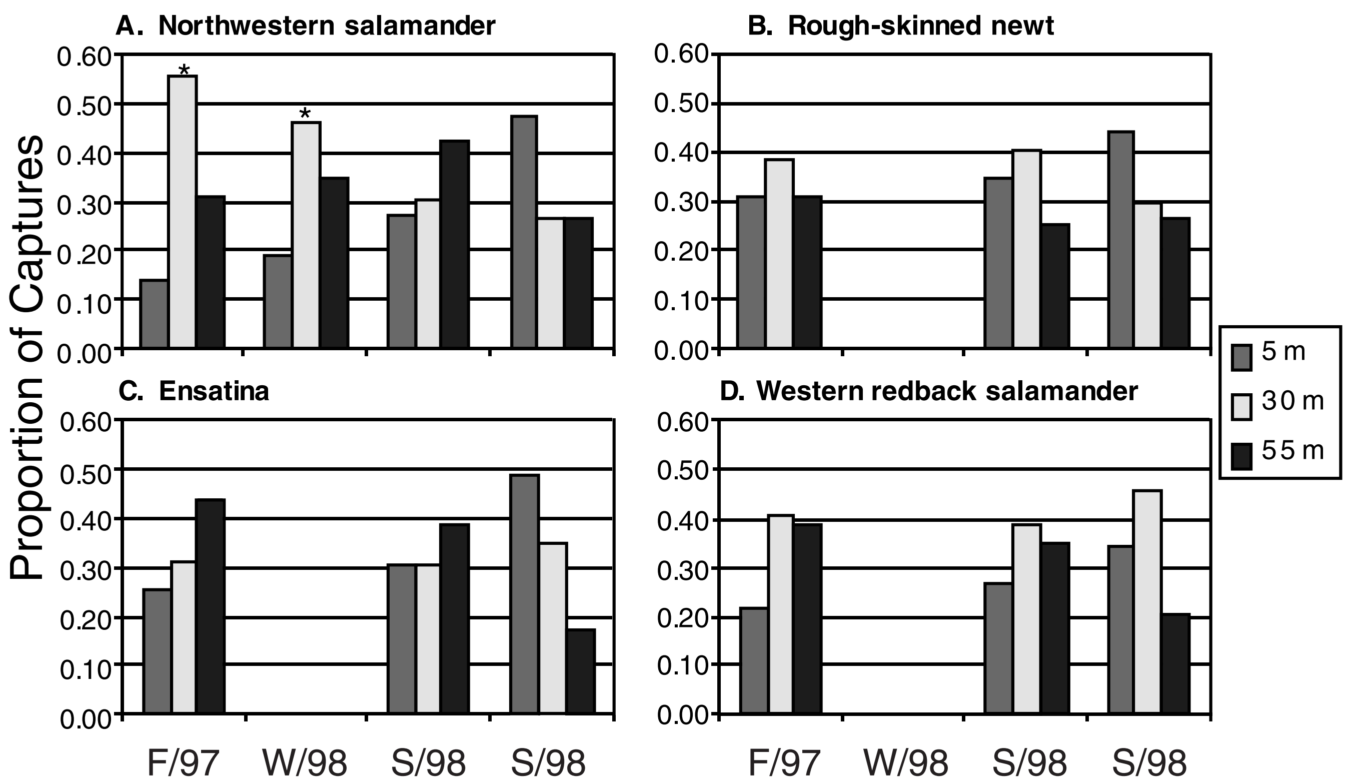

Figure 5a–d. Proportion of captures with increasing distance from the stream. Within seasons there was a significant difference in the proportion captured at the 3 distances from the stream for northwestern salamander in Fall 1997 (χ^2 = 7.52, P < 0.02) and Winter 1998 (χ^2 = 9.08, P < 0.01). No other species showed a significant pattern of abundance relative to distance from the stream between seasons (χ^2 test, all with P > 0.05).

50-m grids used in this study, as indicated by the high minimum average distance recorded for each species.

The apparent random movement of terrestrial-breeding salamanders, ensatina and western redback, and the low average distances moved are also expected based on their life histories; the high site-to-site variation in abundance is more difficult to explain. Both the ensatina and western redback salamander are members of the family Plethodontidae, which is characterized by its completely terrestrial existence. Both species breed terrestrially, laying their eggs in burrows or decayed wood, or on talus slopes, in the spring. Development occurs through the summer with hatchlings emerging in the fall as miniature adults (Blaustein et al. 1995). Moist substrate conditions are required for successful reproduction, but standing water is not necessary for either salamander and, therefore, they make no annual breeding migrations. Habitat requirements for each species may be met in a much smaller area than for the aquatic breeders. The observed mean minimum distance moved of 0.64 m for western redback salamanders is similar to the distances observed by Ovaska (1988) who calculated the home range size of western redback salamanders to be approximately 2.5 m^2, with 8.5 m being the maximum recorded distance moved by 1 individual. The mean distance of 6.4 m recorded for ensatinas is less than that observed by Staub et al. (1995), who calculated mean movement distances of 21.7 m and 22.2 m for males and females, respectively. This discrepancy in distance is likely an artifact of the different sampling designs used for both studies.

As there were no obvious differences between the 6 study sites, and because terrestrial-breeding salamanders require only 1 habitat to successfully survive and reproduce, the observed variation in capture rates between sites was not expected. However, there are 2 hypotheses potentially explaining the observed variation. One hypothesis is that competition and/or predation by the larger, aquatic-breeding salamanders may limit the abundance of the terrestrial breeders on at least 2 of the study sites. Both the ensatina and western redback salamander are most abundant on sites where northwestern salamanders and rough-skinned newts are least abundant. Competition and predation have both been experimentally determined to affect the distribution of terrestrial salamanders in eastern North American amphibian communities (Hairston 1996) and, therefore, cannot be ruled out as mechanisms structuring amphibian communities on these study sites. A second hypothesis explaining the site-to-site variation may be inherent differences in site quality, such as soil moisture or productivity, which limit the density, reproductive rates, and/or survival rates of salamanders. For example, eastern redback salamanders (*Plethodon cinereus*) can sense low soil pH and move away from areas where pH is too low (Wyman and Hawksley-Lescault 1987). Salamanders could be responding to such environmental factors, limiting their abundance on certain sites in this study.

Importance of Riparian Areas

Due to the physiological requirements of amphibian species, riparian areas have been suggested to provide optimal habitat for amphibians (deMaynadier and Hunter 1995). Humidity and temperature are 2 important factors determining the distribution of many amphibian species; higher humidity and lower temperatures are often associated with stream presence (Brosofske et al. 1997). In this study, however, stream proximity did not appear to affect the spatial distribution for any of the salamanders. These results are contrary to those of McComb et al. (1993) and Gomez and Anthony (1996), who both observed higher capture rates along streams versus upslope areas within Pacific Northwest coniferous forests. This discrepancy in results may reflect a difference in the size of the streams used in the various studies. Larger streams have greater influence on the surrounding terrestrial environment than do smaller streams. McComb et al. (1993) and Gomez and Anthony (1996) both worked on second- to fourth-order streams averaging >2 m in wetted width. These streams are larger than those used in this study and, therefore, amphibians may not have had a strong trans-riparian gradient to respond to. Secondly, the scales of the studies are much different. Riparian captures were within 10 m of the stream and upslope captures were 200 m from the stream for Gomez and Anthony (1996), and 400 m for McComb et al (1993). Upslope in this study is only 55 m from the stream, which may also explain the discrepancy.

Although terrestrial salamanders are not considered obligate riparian users, they still may benefit from the retention of buffer strips along headwater streams. As indicated by previous comparative studies (e.g., Aubry and Hall 1991, Corn and Bury 1991), all 4 salamander species found on our study sites may respond negatively to forest harvesting. The non-random movements of both northwestern salamanders and rough-skinned newts, parallel to the stream, indicate buffer strips may potentially be used as corridors, although whether they will be preferentially selected over clearcut areas is unknown, but hopefully will be elucidated with our posttreatment data. In the case of terrestrial-breeding amphibians, buffer strips may act as refuge areas for the population. Leave strips may allow the population to persist until the adjacent clearcut has recovered to provide suitable habitat. A nearby population source may be especially important due to their limited movement capabilities and high site fidelity, particularly for western redback salamanders. Plethodontids have evolved under the stable, moderate conditions that old-growth forests provide. Density-independent perturbations, such as clearcutting, make it difficult for salamander populations with low fecundity and vagility to recover following the disturbance.

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