

Plethodontid Salamander Distributions in Managed Forest Headwaters in Western Oregon, USA

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PLETHODONTID SALAMANDER DISTRIBUTIONS IN MANAGED FOREST HEADWATERS IN WESTERN OREGON, USA

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Abstract.—We examined terrestrial amphibians in managed headwater forest stands in western Oregon from 1998 to 2009. We assessed: (1) temporal and spatial patterns of species capture rates, and movement patterns with distance from streams and forest management treatments of alternative riparian buffer widths and upland thinning; (2) species survival and recapture probabilities; and (3) artificial cover object (ACO) sampling utility. We captured over 1,300 animals, primarily *Ensatina eschscholtzii*, *Plethodon vehiculum*, and *P. dunni*. We found spatial and temporal variation in capture rates over time for *P. vehiculum*, but these patterns appeared unrelated to forest management treatments. Although captures were evenly distributed between near-stream (< 15 m from stream edge) and upland (> 15 m) ACO arrays, species distributions differed with distance from stream. Most movements were short (< 10 m), near streams, and between adjacent ACOs. Using mark-recapture methods (2006–2009) we found no difference in apparent survival among the three species. ACOs were effective, but we offer caveats on their utility. Our results suggest that riparian corridors are highly used by both semi-aquatic and upland salamanders, and movements among surface cover objects occur on the order of a few meters. Headwater riparian areas may act as habitat ‘funnels’ for these animals, where movements are concentrated within and along narrow stream-side zones. Positioning of upland down wood in ‘chains’ extending out from riparian area funnels is proposed to facilitate overland habitat connectivity for salamander dispersal. At larger spatial scales, landscape chains of connectivity may be designed with log links connecting riparian and upland areas.

Key Words.—amphibians; artificial cover objects; dispersal; *Ensatina*; movements; *Plethodon*

INTRODUCTION

Recent recognition that amphibians are a significant part of the developing crisis of global biodiversity loss, having some of the highest documented rates of decline worldwide among faunal groups (Stuart et al. 2004; IUCN 2008; Wake and Vredenburg 2008), has renewed efforts to understand their basic ecology, identify threats to populations, and develop innovative conservation approaches. However, the cryptic tendencies of many forest-dwelling amphibians challenge researchers studying their general ecology or monitoring populations relative to potential threats. Lungless salamanders (family Plethodontidae) are especially difficult to study due to their fossorial tendencies and limited forest floor surface activity correlated with a narrow range of environmental conditions (e.g., Feder 1983; Olson 1999; species accounts in Lannoo 2005). For example, Taub (1961) estimated that only 2 to 32% of a New Jersey, USA population of *Plethodon cinereus* occurred at the surface of the ground at any one point in time. The remaining portion was assumed to be underground. In addition, several habitat factors can influence spatial and

temporal variability of plethodontid salamander detection at the ground surface, such as vegetation cover and elevation (e.g., Bailey et al. 2004a, b).

In northwestern North America, the challenges of studying plethodontids are exacerbated due to relatively few being captured on the ground surface when seasonal conditions appear to be suitable for surface activity (Olson 1999). Several factors likely contribute to this pattern. First, western plethodontids may have relatively low overall population abundances; they have been estimated to occur in abundances numbering tens to hundreds per hectare (Corn and Bury 1990, 1991), in contrast to the thousands per hectare estimated in some northeastern United States (US) forests (e.g., Burton and Likens 1975; Hairston 1987). However some northwest locations may have greater abundances; for example, Ovaska and Gregory (1989) reported up to 1.16 *Plethodon vehiculum* per square meter at a site in British Columbia, Canada. Second, many northwestern plethodontids appear to have relatively low average surface vagility over the timeframe of months to years, some with home ranges of only a few meters, for example: *Plethodon vehiculum*, < 1 m (Maxcy and

Richardson 2000) to < 3 m (Ovaska 1988); *Aneides ferreus*, < 2 m (Davis 1991); *A. vagrans*, < 2 m (Davis 2002); *Plethodon elongatus*, ~5 m (Karraker and Welsh 2006); *Ensatina eschscholtzii*, ~6 m (Maxcey and Richardson 2000) to ~22 m (Staub et al. 1995). Additionally, short or unpredictable periods of surface activity pose challenges to detection: multiple site visits during active seasons have been recommended to ascertain rare species presence at sites (Olson 1999). Lastly, forest amphibian use of surface cover objects that are difficult to sample reduces their detectability during surveys. Further, using survey methods that destroy microhabitats to detect down wood associated species can be problematic for rare species conservation or long-term monitoring because these methods can alter and reduce habitat suitability. Consequently, for many northwestern plethodontids only general habitat associations and species ranges are known. Many basic life history parameters (e.g., growth rates, longevity, age at maturation) and behavioral ecology components (home range size, movement ability, mating system) of these salamanders are poorly understood, and known threats are few, whereas potential, suspected threats are numerous (reviewed in species accounts: Blaustein et al. 1995; Jones et al. 2005; Lannoo 2005).

DeMaynadier and Hunter's (1998) review of studies examining timber harvest effects on amphibians, including several plethodontids in the eastern United States, supported generally adverse effects of clearcutting. Highton (2005) more recently compared relative abundances of > 200 populations of 38 plethodontid species in eastern North America over two time periods, 1951–1985 and in the 1990s, and found the vast majority (88%) to be lower in the latter years. He concluded that although the causes of the declines were unknown, timber harvest had degraded salamander habitat for many species. In northwestern North America, old-growth forest associations of northwestern plethodontids highlight their sensitivity to historic clearcut timber harvest practices (Blaustein et al. 1995). It should be noted that across-study comparisons or reviews such as those above are reporting general patterns, and if more specific analyses of such multi-study data were of interest, the inconsistent methodologies used to assess animal occurrences among studies would need to be addressed.

Specific forestry operations that potentially affect northwestern plethodontids include those altering salamander microhabitat and microclimate conditions from overstory removal, loss of down wood, road construction, ground disturbance, and soil compaction (Crisafulli et al. 2008; Olson 2008a, b; Clayton and Olson 2009). Timber harvest practices are a particular concern for species with restricted distributions (e.g., *Plethodon stormi*, Olson et al. 2009) and low vagility, if dispersal constraints affect post-disturbance

recolonization. However, logging effects on plethodontids are not straightforward and may vary with species and with timber harvest approaches, time-since-harvest, cumulative impacts of repeated harvests, and pre-existing site conditions (e.g., Grialou et al. 2000; Karraker and Welsh 2006; Kluber et al. 2008; Hawkes and Gregory 2012). Forest refugia provided by talus substrates (Kluber et al. 2008), hill-shading (Olson et al. 2009), landform measures such as slope gradient and basin lithology (Wilkins and Peterson 2000), riparian areas (Olson et al. 2007; Olson and Rugger 2007), down wood (Rundio and Olson 2007; Kluber et al. 2009), and leave islands (Wessell 2005) may play important roles in species persistence at site, stand, and landscape scales during disturbances such as the variety of current timber harvest practices. A greater understanding is therefore needed of the basic ecology of plethodontids in managed forest landscapes, and how interactions between species ecology and disturbances may be integrated into long-range planning for forest ecosystem integrity including biodiversity maintenance. To contribute to a greater understanding of plethodontid ecology, long-term monitoring of terrestrial salamander populations is needed (Welsh et al. 2008; Hawkes and Gregory 2012), but given these animals' fossorial tendencies and the down wood associations of many species, long-term monitoring is challenging without disrupting their microhabitats.

Recently, focused attention on amphibians occurring in headwater forests has contributed to our understanding of the ecology of a suite of northwest plethodontid species in unmanaged and managed systems. In unmanaged forests in western Oregon, US, Sheridan and Olson (2003) described amphibian assemblages in zero-order stream basins, the initiation points of streams and their surrounding hillslopes. They found that amphibians located in these zero-order stream basins were associated with certain geomorphic features, with some species occurring near streams (*P. dunni*), upland (*P. vehiculum* and *E. eschscholtzii*), or in headwalls (*A. ferreus*), and generally described headwater riparian areas as being spatially compressed. In managed forests of western Oregon, Olson and Weaver (2007) found evidence of two species occurring in association with headwater stream banks (*P. vehiculum* and *P. dunni*). Rundio and Olson (2007) and Kluber et al. (2009) further described associations of these species in managed forests with distance-from-stream and associated microhabitat conditions. A reliance on riparian corridors is an emerging theme for several amphibian species in managed forests (Olson et al. 2007; Hawkes and Gregory 2012). Using these species-habitat associations, Olson and Burnett (2009) developed a landscape model for forest habitat connectivity, applying the design to headwater-dwelling amphibians and their habitats, to connect spatially-

compressed headwater riparian areas over ridgelines. Over headwater drainage ridgelines is the shortest connection possible among discrete watersheds, and could provide the shortest path for less vagile species, especially those with riparian associations. However, an important question remains relative to this type of design: how effectively would headwater riparian corridors be used by plethodontids for habitat or dispersal?

We advance the understanding of terrestrial headwater forest salamanders relative to these questions in a case study spanning a decade at a managed forest site in western Oregon. Our overall goal was to characterize the basic ecology of terrestrial amphibians in three forest stands with different management treatments, and to address relevant management implications. From 2006 to 2009, we used capture-mark-recapture data collected from artificial cover object (ACO) arrays to explore life history attributes of individual salamanders. Artificial cover objects facilitate repeated sampling of forest amphibians that dwell in down wood or subsurface retreats (e.g., Fellers and Drost 1994; Davis 1997). Although the ACOs that we used were designed and used successfully in British Columbia (Davis 1997), and have been tested elsewhere (Pearce and Venier 2009), reports of their general efficacy in the northwestern United States are lacking. We also summarize plethodontid data available from area-constrained searches conducted at the site, in comparison to ACO data. Furthermore, following recent directions in the science of studying forest management effects on plethodontids (Karraker and Welsh 2006; Welsh et al. 2008; Hawkes and Gregory 2012), we examine a suite of population metrics (abundance, survival, recapture probability, movements) among stands with different forest management histories. Specifically, our study objectives include determination of the: (1) temporal and spatial variation in capture numbers, with data collected for different years, seasons, distances from stream, and forest management treatments; (2) apparent survival and recapture probability estimates of the dominant species captured, assessed using ACO capture data; and (3) general utility of ACOs to monitor terrestrial amphibian populations. From mark-recapture data, we also analyze individual movement distances and spatial patterns relative to our cover board arrays and stream proximity. Although our case study has limited inference, we feel it offers keen insights into further development of site-to-landscape management designs to help retain these ground-dwelling species with relatively low mobility in managed forests. We offer a ‘funnel and chain’ landscape design that may benefit forest habitat connectivity for these species.

MATERIALS AND METHODS

We deployed ACO arrays during summer 2000 at a forest study site on land managed by the US Bureau of Land Management, Salem District, in western Oregon (Green Peak site, Benton County; N 44.3667, W 123.4583; elevation 472–765 m). The site is in the Western Hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988) and is dominated by Douglas Fir (*Pseudotsuga menziesii*). The study site consisted of naturally regenerated timber following clearcut harvest in 1933–1935, followed by grazing for several years, and was burned by a forest fire in 1943 (Cissel et al. 2006). The relatively low volume (150 m³/ha) of legacy down wood at the site, and existing down wood in early decay stages, likely resulted from these activities (Olson et al. 2006; Rundio and Olson 2007). The site is now part of the Density Management Study being implemented by the US Bureau of Land Management in cooperation with the US Forest Service and Oregon State University. The dense second-growth forest, with 500 to 875 trees per hectare (tph), is undergoing a series of thinning phases to test approaches to accelerate development of late-successional forest conditions (Cissel et al. 2006). In October 1999 to February 2000, the 46-ha stand used in the current study (‘moderate density’ thinning unit) was thinned to 200 tph, and an adjacent 23-ha unthinned control stand was established (Fig. 1A).

Initiation points of several headwater streams occur within the thinned and unthinned forest stands. We deployed ACO arrays along 3 of these streams (Fig. 1A). One ACO array was located along a headwater stream in the unthinned control stand (managed forest, not an old-growth reference site). Within the thinned stand, alternative widths of riparian buffers were established along both banks, extending 110–150 m along stream lengths. We deployed ACO arrays along two of these buffered streams: one with a 6-m (slope distance) riparian buffer zone and one with a 70-m riparian buffer zone. The 6-m buffer provided a ‘streamside retention’ zone to retain trees to protect stream bank stability and provide shade over stream habitats. The 70-m buffer was a ‘one site-potential tree height’ distance implemented to examine the effects of the interim Riparian Reserve for the Northwest Forest Plan (USDA and USDI 1994) along non-fishbearing headwater streams on federal lands. This larger buffer was designed to provide down wood and litter inputs to streams, and to retain a variety of microclimate attributes (USDA and USDI 1993; Cissel et al. 2006).

Artificial cover object arrays were located along transects used by a companion study examining forest microclimate and microsite conditions, extending from

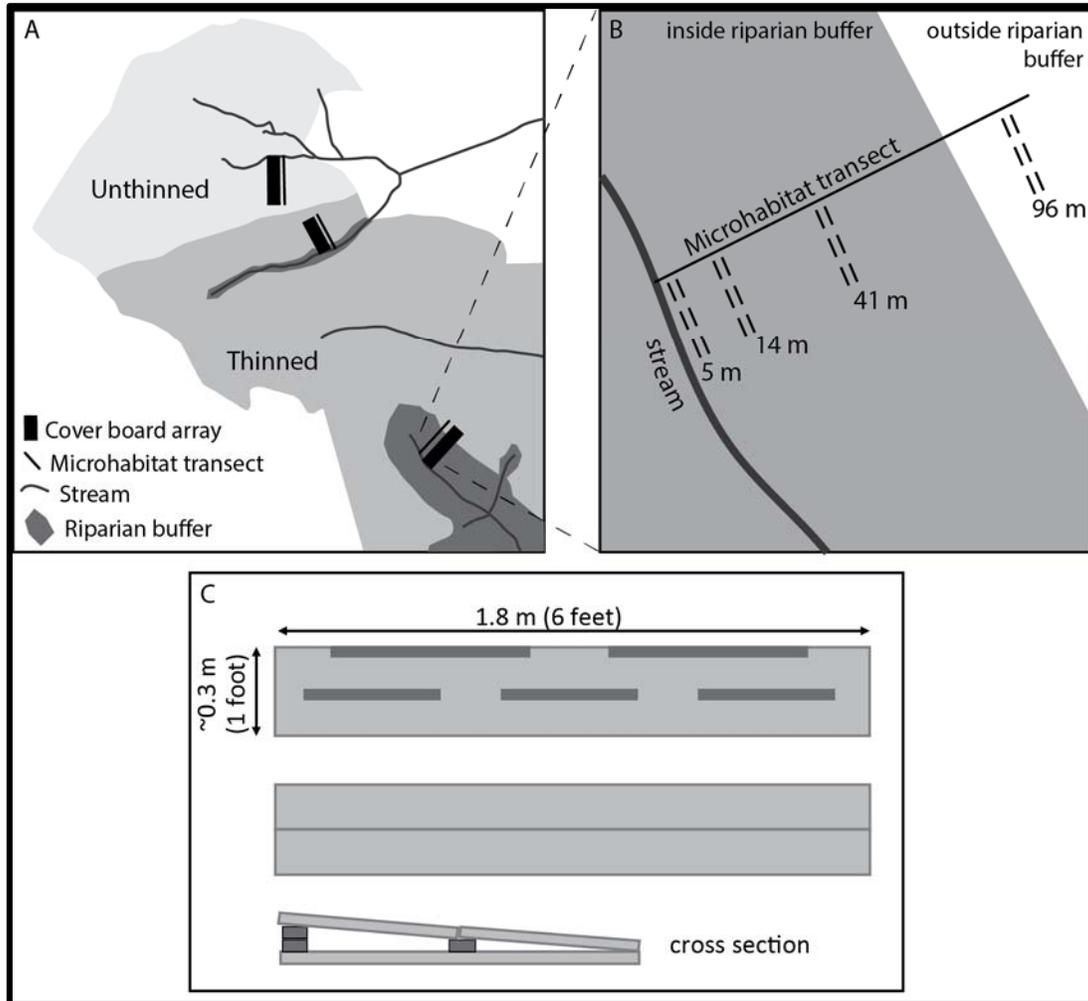


FIGURE 1. Artificial cover object (ACO) design used to sample terrestrial amphibians at Green Peak, Oregon, USA from 2001 to 2009. A) Location of ACO arrays and adjacent transects surveys (straight lines) along three headwater streams (curved lines) in forest stands undergoing three management scenarios: an unthinned control stand of ~65-year old second growth (top); a stand thinned in 2000 from 330 trees per hectare (tph) to 200 tph with a 6-m unthinned riparian buffer (middle); and a stand thinned in 2000 from 330 tph to 200 tph with a 70-m unthinned riparian buffer (bottom; diagram is not to scale). B) Along each stream, arrays of 6 ACOs were deployed at each of 3–4 distances from the stream: 5 m; 14 m; 41 m; and 96 m (this array was not included along the 6-m buffer stream due to area constraints; diagram is not to scale). C) ‘Davis boards’ were the ACOs used (Davis 1997), with each ACO consisting of two layers of wood (light shading) separated by lathe spacers (dark shading); top figure is from above showing spacers in bottom layer, middle figure is from above with top layer of two side-by-side boards, bottom figure is side view.

stream banks into uplands (Anderson et al. 2007; Anderson and Meleason 2009; Fig. 1B). We did not position these transects and the ACO array locations randomly. Rather, we aligned them to be central within treatment areas and to avoid bisecting circular clearcut gaps and leave-tree islands in the thinned forest matrix. We arranged six ACOs in a 3 × 2 grid, spaced 2–3 m apart, positioned as an array in conjunction with microhabitat plot locations. Four arrays were located along transects extending upland from the stream edges in the 70-m buffer and unthinned control stand, at 5 m, 14 m, 41 m, and 96 m from the streams (Fig. 1B). This layout resulted in only one array in the thinned forest

along the 70-m buffered stream, with the other three arrays within the unthinned riparian buffer zone. Along the stream with the 6-m buffer, we deployed three arrays of 6 ACOs each adjacent to a transect extending upslope from the stream at 5 m, 14 m, and 41 m from the stream edge. Hence, two of the three arrays were in the thinned forest, and one was in the riparian buffer. Due to the proximity of the boundary for the unthinned control stand, a 4th array at 96 m from the 6-m buffer stream was not possible (Fig. 1A). Limited resources constrained the number of ACOs and ACO arrays we were able to deploy; hence we note that our design is a subsample

TABLE 1. Artificial cover object (ACO) monthly sampling schedule from 2001–2002 and 2006–2009 and total numbers of amphibians captured per sampling event at Green Peak, Oregon, USA (overall total amphibians captured = 884).

| Year | Spring Wet Season | | | | Fall Wet Season | | | |
|------|-------------------|-------|-------|-------|-----------------|-------|-------|-------|
| | Mar | Apr | May | Jun | Oct | Nov | Dec | Jan |
| 2001 | ----- | ----- | 65 | ----- | 17 | ----- | ----- | ----- |
| 2002 | ----- | ----- | 99 | ----- | ----- | ----- | ----- | ----- |
| 2006 | ----- | 67 | ----- | 17 | ----- | 9 | ----- | ----- |
| 2007 | 72 | 76 | 31 | ----- | 43 | 21 | ----- | 8 |
| 2008 | ----- | 75 | 77 | 59 | ----- | 6 | 19 | ----- |
| 2009 | 35 | 48 | 18 | ----- | 17 | 5 | ----- | ----- |

that constrains our ability to fully detect animal occurrences and movements.

The ACOs (Fig. 1C) were constructed of untreated fir lumber, using the double-decker board designed by Davis (1997). This design allows for animals to be visually observed under each of two smaller top boards, as well as under the bottom base board that was in contact with the forest floor. Additionally, the wedge-shaped space between the top boards and the base board allowed rain water and needle litter to enter between the cracks of the two top boards creating a complex microhabitat over time (Davis 1997). We aligned boards parallel to the hillslope and placed them on bare soil by removing litter, rocks and down wood. Materials cost US\$8.99 per ACO at the time of initial construction in 2000, and were US\$9.60 per ACO in November 2009 when replacements were deployed due to decay of the original ACOs.

We monitored the ACOs on a monthly basis in spring (March to June) and fall (October to November) wet seasons (2–3 samplings per season), during a pulse of work in 2001–2002, and a second pulse in 2006–2009 (Table 1). These sampling intervals were initially timed to synchronize with other studies (Olson and Rugger 2007; Rundio and Olson 2007), and hence were not conducted every year within the span 2001 to 2009. We continued sampling opportunistically into December and January if above-freezing temperatures occurred during the timeframe of our monthly census interval. Upon capture, we identified amphibians to species, measured for snout-vent length (SVL) and total length (to nearest mm), and locations at ACOs were noted (under top board, under bottom board). In April 2006, we began giving each captured animal an individual mark using visible implant elastomers (Northwest Marine Technology, Inc., Shaw Island, Washington, USA). During each subsequent sampling event, we remeasured marked recaptures. After processing, we released all animals at the location of capture.

For comparison with other knowledge of amphibian assemblages at our forest stands, we also compiled data from area-constrained searches along transects positioned at these same stream reaches in 1998, 2000, and 2001. Within each of the three forest stands (unthinned, thinned with a 6-m stream buffer, thinned

with a 70-m buffer), we sampled four 2-m-wide transects extending from stream edges into upland forest. We aligned transects perpendicular to streams, parallel to habitat transects used in another study (Anderson and Meleason 2009), and transects were 18–28 m away from ACOs. We used a visual encounter survey (Crump and Scott 1994) to survey along transects, where we lifted or dismantled natural cover objects (litter, rocks, down wood) in our search of amphibians (Rundio and Olson 2007). We collected the 1998 transect data prior to the thinning treatment and installment of riparian buffers, and we conducted the 2000–2001 surveys post-thinning. We conducted one sampling effort per year in 1998, 2000, 2001.

Survival and recapture probability.—We used the 2006–2009 capture-mark-recapture data to estimate apparent survival (Φ) and recapture (p) probabilities of the most abundant species captured (*P. vehiculum*, *P. dumni*, *E. eschscholtzii*) using Cormack-Jolly-Seber (CJS) open population models in program MARK (version 5.1; White and Burnham 1999). Live-recaptures-only models, like CJS, generate estimates of apparent survival, Φ , the probability that animal has not died or emigrated from the study population, and recapture probability, p , the probability that an animal that is available for capture in the study is actually caught. In MARK, survival estimates in CJS models do not distinguish between death and permanent emigration, resulting in minimum estimates of true survival (Lebreton et al. 1992). We collected capture-mark-recapture data during 18 capture occasions between spring 2006 and fall 2009, resulting in 17 recapture occasions. Time between seasonal capture occasions ranged from 4 to 6 weeks, and 20 to 31 weeks between spring and fall sampling trips. Program MARK accounts for unequal time intervals between sampling events by taking the length of the time interval (L_i) as the exponent of the survival estimate (S_i) for the interval, i.e., $S_i^{L_i}$. For our study, analysis structure consisted of 17 recapture occasions and 3 groups based on the most abundant amphibian species captured.

We developed a set of *a priori* models to test hypotheses concerning effects of seasonality (fall, spring) and species (*P. vehiculum*, *P. dumni*, *E.*

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TABLE 2. Total number of amphibian captures, species richness (S), Shannon Index of diversity (H'), and evenness (E_{HT}) at Green Peak, western Oregon, USA, in each of three forest stands with differing management treatments along headwater streams (6-m buffer with upland thinning; 70-m buffer with upland thinning; unthinned control stand) during five different sampling periods: (1) 1998 pre-harvest area-constrained search along transects (one spring sampling occasion); (2) 2000 post-harvest area-constrained search along transects (one spring sampling occasion); (3) 2001 post-harvest area-constrained search along transects (one spring sampling occasion); (4) 2001 and 2002 artificial cover object (ACO) sampling (three total sampling occasions); and (5) 2006–2009 ACO sampling (eighteen total sampling occasions).

| Species | 1998 Transects (pre) | | | 2000 Transects (post) | | | 2001 Transects (post) | | |
|--------------------------------|----------------------|------|---------|-----------------------|------|---------|-----------------------|------|---------|
| | 6 m | 70 m | control | 6 m | 70 m | control | 6 m | 70 m | control |
| <i>Plethodon vehiculum</i> | 12 | 62 | 18 | 8 | 83 | 28 | 4 | 81 | 7 |
| <i>Ensatina eschscholtzii</i> | 26 | 29 | 10 | 17 | 21 | 17 | 10 | 21 | 6 |
| <i>Plethodon dunni</i> | 0 | 0 | 1 | 0 | 8 | 6 | 0 | 6 | 1 |
| <i>Taricha granulosa</i> | 4 | 3 | 2 | 3 | 0 | 3 | 4 | 1 | 1 |
| <i>Dicamptodon tenebrosus</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Rhyacotriton variegatus</i> | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 |
| <i>Ascaphus truei</i> | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 |
| <i>Ambystoma gracile</i> | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| <i>Aneides ferreus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 44 | 95 | 33 | 28 | 112 | 59 | 19 | 111 | 18 |
| Species Richness (S) | 5 | 4 | 6 | 3 | 3 | 6 | 4 | 5 | 6 |
| Shannon Index (H') | 1.06 | 0.80 | 1.18 | 0.90 | 0.72 | 1.21 | 1.15 | 0.82 | 1.49 |
| Evenness (E _{HT}) | 0.66 | 0.58 | 0.66 | 0.82 | 0.66 | 0.68 | 0.83 | 0.51 | 0.83 |

| | 2001-2002 ACOs | | | 2006-2009 ACOs | | | N |
|--------------------------------|----------------|------|---------|----------------|------|---------|------|
| | 6 m | 70 m | control | 6 m | 70 m | control | |
| <i>Plethodon vehiculum</i> | 4 | 35 | 32 | 23 | 79 | 169 | 633 |
| <i>Ensatina eschscholtzii</i> | 17 | 10 | 30 | 61 | 35 | 54 | 338 |
| <i>Plethodon dunni</i> | 1 | 36 | 11 | 2 | 171 | 88 | 331 |
| <i>Taricha granulosa</i> | 0 | 0 | 0 | 4 | 1 | 8 | 30 |
| <i>Dicamptodon tenebrosus</i> | 0 | 1 | 0 | 0 | 4 | 1 | 10 |
| <i>Rhyacotriton variegatus</i> | 0 | 4 | 0 | 0 | 1 | 1 | 11 |
| <i>Ascaphus truei</i> | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| <i>Ambystoma gracile</i> | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Aneides ferreus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Total | 22 | 86 | 73 | 90 | 291 | 322 | 1359 |
| Species Richness (S) | 3 | 5 | 3 | 4 | 6 | 7 | |
| Shannon Index (H') | 0.66 | 1.18 | 0.98 | 0.82 | 1.02 | 1.14 | |
| Evenness (E _{HT}) | 0.60 | 0.73 | 0.89 | 0.59 | 0.57 | 0.59 | |

eschscholtzii) on Φ and p . We used the program U-CARE to test our fully parameterized global model for goodness-of-fit (GoF) of this model to the assumptions of the CJS model (Choquet et al. 2005). U-CARE also provides directional tests for transience and trap-dependence (trap-happiness or trap-shyness). We examined our data for overdispersion in variance estimation and model selection by estimating the variance inflation factor (\hat{c}), which we obtained by dividing the combined χ^2 values by the combined degrees of freedom from Tests 2 (trap-dependence) and 3 (transience) in U-CARE (Choquet et al. 2005). We detected no evidence of overdispersion ($\hat{c} = 0.942$), indicating independence and heterogeneity of all individuals. Therefore, we did not adjust \hat{c} (Burnham and Anderson 2002).

Once we had identified an acceptable global model (the CJS standard time-dependent model), we progressively fitted simpler models using MARK. We modeled the effects of species and time with a seasonal constraint on time, where captures were grouped by season (spring vs. fall) for both Φ and p . We used the Akaike Information Criterion corrected for small sample

sizes (AIC_c) and Akaike weights to determine which model was best supported by the data (Burnham and Anderson 2002; Lebreton et al. 1992).

Movements.—We assessed individual movements between ACOs using recapture data of animals marked between 2006 and 2009. We calculated mean and maximum movement distances per species and for each riparian-upland management context. We estimated distance traveled by salamanders by measuring from ACO centers. Additionally, to see if there was a directional pattern to salamander movements, we examined movement direction (upslope vs. downslope; upstream vs. downstream) using a χ^2 test for equal proportions in SAS version 9.1 (SAS Institute 2004).

RESULTS

In our two ACO sampling pulses, from spring 2001 to fall 2002 and from spring 2006 to fall 2009, we captured 884 amphibians total, with 5 to 99 animals captured per sampling event (Table 1). Captures were dominated by three plethodontid species: *P. vehiculum* ($n = 342$), *P.*

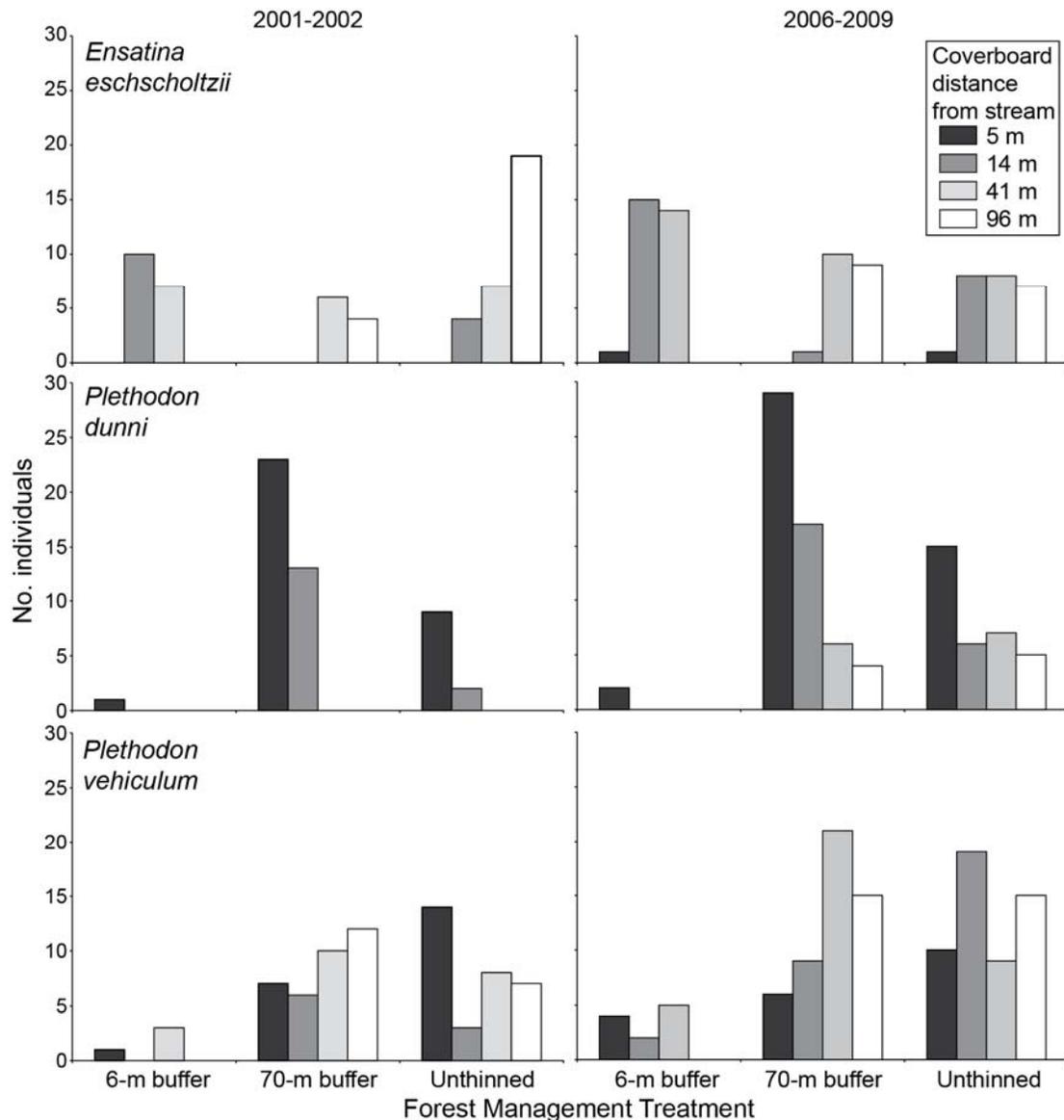


FIGURE 2. Occurrence of individually marked plethodontid salamanders, *Ensatina eschscholtzii*, *Plethodon dunni*, and *P. vehiculum*, in each of three forest management treatments: (1) 6-m buffer with upland thinning (no 96-m array); (2) 70-m buffer with upland thinning; and (3) unthinned control stand, per artificial cover object array by distance from stream at Green Peak, Oregon, USA, in two time periods, 2001–2002 and 2006–2009. Note that the two sampling time intervals had unequal survey efforts (Table 1).

dunni ($n = 309$), and *E. eschscholtzii* ($n = 207$). Additionally we captured six other species (Table 2). We found salamanders most frequently under the top boards of the two-tiered ACO design ($\bar{x} \pm \text{SE}$: $79.9\% \pm 0.02$). During transect surveys in 1998–2001, we captured 519 total animals, with *P. vehiculum* and *E. eschscholtzii* dominating captures, and only 22 (4%) *P. dunni* detected.

Species abundances varied with year, season, riparian-upland management treatment (Tables 1 and 2), and distance from the stream (Fig. 2). We observed greater numbers of animals and species richness in the ACO

arrays in the unthinned control stand and 70-m buffer thinned stand (Table 2). Most *P. dunni* captures under ACOs occurred within the 5-m arrays of the 70-m buffer stand, whereas most *P. vehiculum* were within the unthinned control arrays, with captures spread more evenly among distances (Fig. 2). We captured the greatest number of *E. eschscholtzii* in the 6-m buffer stand (Table 2), and the fewest within the 70-m buffer arrays with very few captures in the 5-m arrays (Fig. 2).

We observed differences in patterns of amphibian detection between transect sampling in 1998, 2000, and 2001, compared to ACO sampling in 2001–2002 and

TABLE 3. Recaptures of individuals of three plethodontid species (*Ensatina eschscholtzii*, *Plethodon dunni*, and *P. vehiculum*) at artificial cover objects (ACOs) in 2006–2009 at Green Peak, Oregon, USA.

| No. Recaptures | <i>E. eschscholtzii</i> | <i>P. dunni</i> | <i>P. vehiculum</i> | Total |
|----------------|-------------------------|-----------------|---------------------|-------|
| 0 | 40 | 33 | 59 | 132 |
| 1 | 16 | 16 | 22 | 54 |
| 2 | 7 | 17 | 9 | 33 |
| 3 | 5 | 9 | 9 | 23 |
| 4 | 5 | 7 | 4 | 16 |
| 5 | 0 | 4 | 6 | 10 |
| 6 | 1 | 3 | 2 | 6 |
| 7 | 0 | 0 | 2 | 2 |
| 8 | 0 | 2 | 2 | 4 |
| Total | 74 | 91 | 115 | 280 |

2006–2009 (Table 2). However, sampling efforts are difficult to compare between methods and effort differed among years for the ACO sampling (Tables 1 and 2), so that while patterns can be seen, we caution against comparing absolute numbers. The two survey methods appeared to have different efficacies for sampling some species. Most remarkable were the very few *P. dunni* recorded during any of the transect-sampling events. *Plethodon dunni* appear to have been recruited to ACOs in good numbers within the 70-m buffer stand and unthinned control stand, especially during the 2006–2009 timeframe (Table 2). For *P. vehiculum*, over 75% of captures occurred in the 70-m buffer stand during transect sampling in 1998–2001, whereas comparable numbers were seen in both the 70-m buffer and unthinned control stands in 2001 and 2002 using ACOs. We recorded a shift to generally more animals under ACOs in the control stand in 2006–2009. In contrast, we found about one-third as many *E. eschscholtzii* under ACOs in the unthinned control stand in 2006–2009. These differences with method and time affected species diversity indices (Table 2). We observed no apparent differences among treatments overall.

Between 26 April 2006 and 20 November 2009 (1304 d interval), we captured and individually marked 302 animals of 7 species. Three plethodontid species comprised 93% of marked animals (*E. eschscholtzii*: $n = 74$; *P. dunni*: $n = 91$; *P. vehiculum*: $n = 115$). We did not use uncommon species and individuals with apparent errors in individual marks (possible mark migration, misread marks, $n = 22$) in analyses. Of the remaining 280 animals analyzed, we recaptured 53% ($n = 149$) at least once, and we recaptured 63% ($n = 94$) of these at least twice (Table 3). We recaptured two *P. vehiculum* and two *P. dunni* on eight occasions each, and both *P. dunni* were captured under their same respective boards upon each capture occasion. The longest recapture interval was 1304 d (3.6 y), the length of the mark-recapture study. This individual was a *P. vehiculum* in the unthinned control stand; we recaptured it six times

and it moved 4 m between ACOs during that time interval.

Survival and recapture probability.—Component tests used to estimate goodness of fit for our fully parameterized Cormack-Jolly-Seber model (time-dependent apparent survival, Φ , and recapture probability, p) indicated that there was evidence of trap (ACO) dependence, or ‘trap-happiness,’ among species (UCARE global TEST, statistic for trap dependence = -2.765, $P = 0.005$). Likewise, tests of survival homogeneity or transience indicated a difference among species in the probability of newly marked and previously marked salamanders being re-encountered (UCARE global TEST, statistic for transience = 3.316, $P = 0.0009$). Upon further investigation, we determined that *E. eschscholtzii* showed no evidence of trap dependence (UCARE TEST2.CT, statistic for trap dependence = 0.0357, $P = 0.97$). However, both *P. dunni* and *P. vehiculum* showed signs of trap dependence (UCARE TEST2.CT, statistic for trap dependence, respectively = -2.422, $P = 0.02$; -2.233, $P = 0.03$). The negative value of the trap dependence statistic indicates that *P. dunni* and *P. vehiculum* were ‘trap-happy’ (ACO-happy); that is, previously captured animals had a higher recapture probability (i.e., under ACOs). When looking at individual species, we found that neither *E. eschscholtzii* nor *P. dunni* showed significant evidence of transience (UCARE TEST3.SR, statistic for transience, respectively = 1.220, $P = 0.2$; 1.54, $P = 0.12$). Conversely, *P. vehiculum* showed significant evidence of transience (UCARE TEST3.SR, statistic for transience = 2.879, $P = 0.004$), indicating a difference in the probability of being re-encountered at a later sampling trip between newly marked and previously marked individuals encountered at occasion i (Choquet et al. 2005). However, the results of TEST3.SR and TEST2.CT should be treated with caution, as they were based on relatively sparse data (682 total captures from 280 capture histories).

Our most parsimonious model suggested apparent survival was constant, whereas we saw an additive

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TABLE 4. Model selection results based on AIC_c for the 9 top models (and null model) of apparent survival (Φ) and recapture probability (p) of the three most abundant terrestrial salamanders species (*Ensatina eschscholtzii*, *Plethodon dunni*, and *P. vehiculum*) at Green Peak, Oregon, USA using the Cormack-Jolly-Seber approach in program MARK (White and Burnham 1999) with 2006–2009 data from artificial cover objects. Model variables include species (spp), time (t) and season (sea: spring vs. non-spring); * indicates interactions between variables; + indicates additive effects. (.) indicates blank entries indicating that a variable was not included in the model.

| Model | AIC _c | Δ AIC _c | AIC _c Weight | Likelihood | No. Est. Parameters | Deviance |
|------------------------------------|------------------|---------------------------|----------------------------|------------|------------------------|----------|
| 1 Φ (.) p (spp + t) | 1844.54 | 0.00 | 0.89038 | 1.0000 | 20 | 959.927 |
| 2 Φ (spp) p (spp + t) | 1848.82 | 4.27 | 0.10484 | 0.1177 | 22 | 959.923 |
| 3 Φ (.) p (t) | 1855.00 | 10.46 | 0.00476 | 0.0053 | 18 | 974.647 |
| 4 Φ (spp + t) p (spp + t) | 1865.50 | 20.96 | 0.00003 | 0.0000 | 38 | 941.311 |
| 5 Φ (t) p (t) | 1870.88 | 26.34 | 0.00000 | 0.0000 | 34 | 955.691 |
| 6 Φ (sea) p (spp * t) | 1877.70 | 33.16 | 0.00000 | 0.0000 | 53 | 918.677 |
| 7 Φ (.) p (spp * t) | 1881.79 | 37.26 | 0.00000 | 0.0000 | 52 | 925.149 |
| 8 Φ (spp + sea) p (spp * t) | 1882.40 | 37.86 | 0.00000 | 0.0000 | 55 | 918.600 |
| 9 Φ (spp * sea) p (spp * t) | 1884.56 | 40.02 | 0.00000 | 0.0000 | 56 | 918.355 |
| 10 Φ (.) p (.) | 2085.57 | 241.03 | 0.00000 | 0.0000 | 2 | 1238.299 |

TABLE 5. Model-averaged estimates and confidence intervals (95% CI) of recapture probabilities for the three most abundant plethodontid salamander species (*Plethodon dunni*, *P. vehiculum*, and *Ensatina eschscholtzii*) at Green Peak, Oregon, USA using the Cormack-Jolly-Seber approach in program MARK (White and Burnham 1999) with 2006–2009 artificial cover object data. Recapture estimates and confidence intervals are given for the 17 recapture occasions between 26 April 2006 and 20 November 2009.

| Recapture Occasion | <i>P. dunni</i> | <i>P. vehiculum</i> | <i>E. eschscholtzii</i> | Interval |
|--------------------|-------------------|---------------------|-------------------------|-----------------|
| 1 st | 0.16 (0.08–0.29) | 0.12 (0.06–0.23) | 0.08 (0.04–0.17) | 26APR06–01JUN06 |
| 2 nd | 0.02 (0.003–0.14) | 0.02 (0.002–0.10) | 0.01 (0.001–0.07) | 01JUN06–08JAN07 |
| 3 rd | 0.54 (0.40–0.67) | 0.46 (0.33–0.60) | 0.36 (0.23–0.50) | 08JAN07–26MAR07 |
| 4 th | 0.55 (0.44–0.66) | 0.47 (0.36–0.59) | 0.37 (0.26–0.49) | 26MAR07–26APR07 |
| 5 th | 0.23 (0.15–0.33) | 0.18 (0.12–0.27) | 0.12 (0.07–0.20) | 26APR07–24MAY07 |
| 6 th | 0.27 (0.18–0.38) | 0.21 (0.14–0.31) | 0.15 (0.09–0.23) | 24MAY07–11OCT07 |
| 7 th | 0.09 (0.05–0.17) | 0.07 (0.03–0.13) | 0.05 (0.02–0.09) | 11OCT07–20NOV07 |
| 8 th | 0.53 (0.40–0.61) | 0.45 (0.34–0.57) | 0.35 (0.24–0.47) | 20NOV07–14APR08 |
| 9 th | 0.50 (0.38–0.58) | 0.42 (0.33–0.53) | 0.32 (0.23–0.43) | 14APR08–08MAY08 |
| 10 th | 0.48 (0.37–0.58) | 0.40 (0.31–0.50) | 0.30 (0.22–0.41) | 08MAY08–11JUN08 |
| 11 th | 0.06 (0.02–0.13) | 0.04 (0.02–0.10) | 0.03 (0.01–0.07) | 11JUN08–06NOV08 |
| 12 th | 0.12 (0.06–0.21) | 0.09 (0.05–0.16) | 0.06 (0.03–0.11) | 06NOV08–04DEC08 |
| 13 th | 0.22 (0.13–0.33) | 0.17 (0.10–0.26) | 0.11 (0.07–0.19) | 04DEC08–26MAR09 |
| 14 th | 0.32 (0.23–0.44) | 0.26 (0.18–0.36) | 0.18 (0.12–0.28) | 26MAR09–27APR09 |
| 15 th | 0.09 (0.04–0.17) | 0.07 (0.03–0.13) | 0.04 (0.02–0.09) | 27APR09–29MAY09 |
| 16 th | 0.08 (0.03–0.17) | 0.06 (0.03–0.13) | 0.04 (0.02–0.09) | 29MAY09–27OCT09 |
| 17 th | 0.03 (0.006–0.10) | 0.02 (0.005–0.07) | 0.01 (0.003–0.05) | 27OCT09–20NOV09 |

species and time effect on recapture probability (Table 4). This model was strongly supported by the data, accounting for 89% of the weight of evidence (Akaike weight) among the models. The highest-ranked model with a seasonal effect on apparent survival, Φ , was $\{\Phi$ (season) p (species * time) $\}$ with a Δ AIC of 33.16, whereas the highest-ranked model with a seasonal effect on recapture probability, p , was $\{\Phi$ (species + time) p (season) $\}$ with a Δ AIC of 88.06, suggesting little effect of season on Φ or p (Table 4).

We initially calculated estimates of salamander Φ as weekly survival estimates and then converted them to annual Φ (Powell, 2007), resulting in an annual Φ of 0.64 (95% CI = 0.57–0.71) over the duration of the study for the species examined.

Recapture probabilities varied among species, with *P. dunni* having the highest recapture probabilities and *E. eschscholtzii* having the lowest (Table 5). Although

there was variation in recapture probabilities within seasons (spring, fall), we observed a trend throughout the duration of our capture-mark-recapture study with recapture probabilities increasing in late fall into early spring, and tapering off in late spring toward early summer and fall (Table 5). March through May appeared to correspond with peak recapture probabilities for all three species, while June to January corresponded with many of the lowest values.

Movements.—Over the 3.6 years of the mark-recapture study, for our 149 recaptured plethodontids, we found that 61 (41%) animals moved between ACOs at least once, and 22 of 61 (36%) animals moved multiple times, resulting in a total of 91 individual movements. The majority of the movements occurred within the 70-m buffer stand at distances < 15 m from stream edges (Table 6; Fig. 3). Of the individual movements among

TABLE 6. Summary of plethodontid salamander (*Ensatina eschscholtzii*: ENES; *Plethodon dunni*: PLDU; and *P. vehiculum*: PLVE) movements at Green Peak, Oregon, USA for animals that moved one or more times among artificial cover objects in 2006–2009.

| Forest Treatment | Stand | Species | No. Moved Within Arrays | Mean Distance Traveled (m) | Range (m) | No. Moved Between Arrays | Maximum Cumulative Distance (m) |
|-----------------------------|-------|---------|-------------------------|----------------------------|-----------|--------------------------|---------------------------------|
| 6-m buffer, Thinned upland | | ENES | 9 | 4.8 ± 0.70 | 2.5–9.5 | 1 | 31.0 |
| | | PLDU | 0 | 0.0 ± 0.00 | 0 | 0 | 0.0 |
| | | PLVE | 3 | 4.1 ± 0.10 | 4–4.3 | 0 | 4.3 |
| 70-m buffer, Thinned upland | | ENES | 5 | 5.1 ± 0.85 | 3.6–10.1 | 0 | 14.1 |
| | | PLDU | 19 | 4.9 ± 0.45 | 2.3–13.4 | 8 | 21.8 |
| | | PLVE | 3 | 5.5 ± 0.90 | 4.3–8.1 | 1 | 12.4 |
| Unthinned | | ENES | 2 | 5.8 ± 2.90 | 2.9–8.7 | 0 | 8.7 |
| | | PLDU | 4 | 3.05 ± 0.17 | 2.8–4.8 | 0 | 9.6 |
| | | PLVE | 16 | 4.33 ± 0.33 | 2.5–8.7 | 1 | 20.7 |
| Total | | | 61 | | | 11 | |

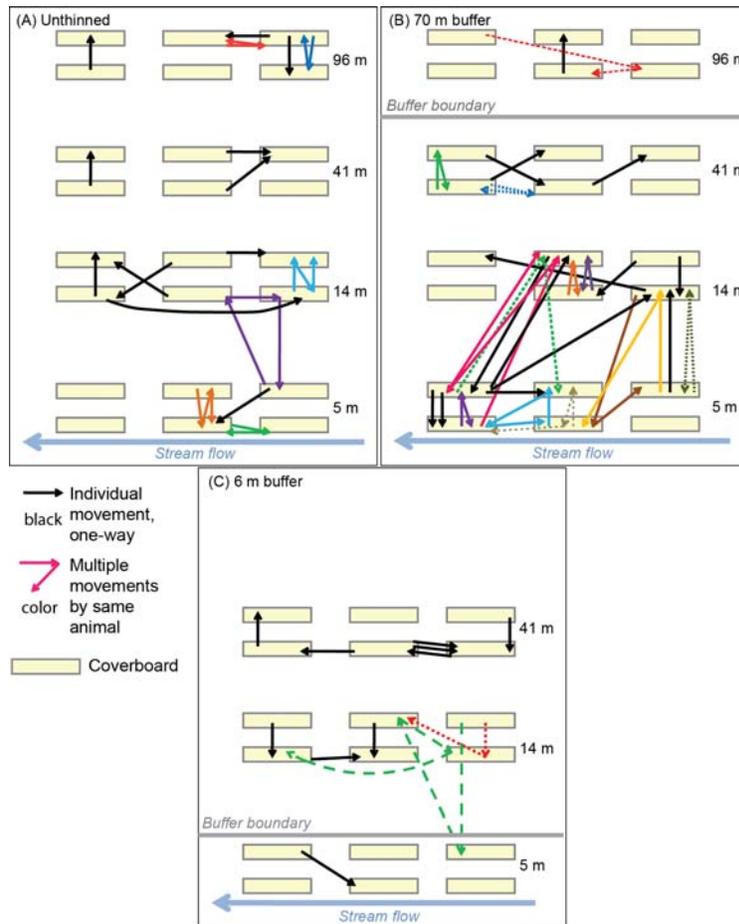


FIGURE 3. Movements of plethodontid salamanders between and within artificial cover object arrays by distance from stream at Green Peak, Oregon, USA, in each of three forest management treatments: (A) unthinned control stand between 26 April 2006 and 20 November 2009; (B) 70-m buffer with upland thinning; and (C) 6-m buffer with upland thinning. Black arrows indicate animals that moved once, colored arrows indicate animals that moved two or more times.

ACOs, 65 (71%) were ≤ 5 m in distance, and 89 (99%) were ≤ 10 m (median = 4.2 m, $\bar{x} \pm SE$: 4.6 ± 0.23 m, range = 2.3–13.4 m, $n = 91$). Overall, the greatest cumulative distance traveled that we observed throughout the duration of the study period was 31 m by an *E. eschscholtzii* in the 6-m buffer stand during a 731 d interval (26 March 2007 to 26 March 2009; Table 6).

However, the farthest distance that we recaptured a marked animal from its original location of capture was 10.1 m (distance ranges: *E. eschscholtzii*, 4.4 to 10.1 m [$n = 4$, mean = 7.1 m, $SE = 1.5$]; *P. dunni*, 2.3 to 9.2 m [$n = 12$, mean = 4.2 m, $SE = 0.6$]; *P. vehiculum*, 2.5 to 8.7 [$n = 6$, mean = 5.3 m, $SE = 1.0$]). Although total number of marked animals differed among plethodontid species, percentages of recaptured animals per species that moved among ACOs were similar (*P. dunni*: 40%; *E. eschscholtzii*: 46%; *P. vehiculum*: 39%).

We examined directions of movements, upslope-or-downslope and upstream-or-downstream, within the two riparian arrays, 5 m and 14 m from the stream, where we had more documented movements. There were no clear patterns in directions moved, examining movements of all species combined for all stands together. Overall, we documented 23 upslope, 26 downslope, 18 upstream, and 16 downstream movements among the riparian ACOs; a few more salamanders moved downslope and upstream, but a significant pattern was not apparent (upslope vs. downslope: $\chi^2 = 0.18$, $df = 1$, $P = 0.66$; upstream vs. downstream: $\chi^2 = 0.12$, $df = 1$, $P = 0.73$). It should be noted that our ACO spacing and layout design may have been a limiting factor in fully monitoring salamander movements, especially in upstream and downstream directions.

DISCUSSION

Riparian areas have been noted as a nexus of biodiversity in the US northwest (Olson et al. 2007). Cool and moist microclimate conditions, aquatic proximity, and habitat heterogeneity contribute to this pattern. In particular, many amphibian species requiring both aquatic and terrestrial habitats are frequently encountered in riparian areas. About a quarter of northwestern US amphibians occur in forested headwaters (Olson et al. 2007), an area that may serve as a ‘funnel,’ concentrating a variety of species with diverse life histories into a small area. Headwater riparian areas appear to be spatially compressed (Sheridan and Olson 2003), occurring as a narrow ribbon along small streams, supporting this funnel analogy.

A funnel spatial pattern is more apparent in managed forests, especially when timber management with riparian buffers creates edges along the riparian-to-upland gradient. This pattern is evident relative to both habitat conditions and species diversity patterns. In terms of habitat conditions, relatively sharp microclimate

gradients from streams into forested uplands in headwater systems have been described in western Oregon, where cool, moist streamside conditions persist in narrow riparian bands along streams (Anderson et al. 2007; Olson et al. 2007; Rykken et al. 2007a). Although a steep gradient of microclimate conditions radiates 10–20 m from streams in intact forest stands, the ‘countervailing’ spatial extent of upland harvest effects on this gradient is not fully described and would vary with site conditions and riparian buffer management (e.g., different no-entry buffer widths or forest management within riparian buffers; Anderson et al. 2007; Olson et al. 2007). In the western United States, managed forests in western Oregon have relatively high amphibian diversity in-stream and within 2-m of streams in managed headwaters (11–13 amphibian species: Olson and Rugger 2007; Olson and Weaver 2007), with some terrestrial salamanders having strong associations with near-stream areas (e.g., Kluber et al. 2008). In British Columbia, more Coastal Tailed Frogs (*Ascaphus truei*; Wahbe et al. 2004) and Coastal Giant Salamanders (*Dicamptodon tenebrosus*; Johnston and Frid 2002) occurred along streams and fewer occurred in uplands in clearcuts compared to intact forests; this pattern was thought to be a result of restricted movements in response to microclimate gradients. Lastly, in support of the riparian funnel concept, in Idaho, landscape genetic analyses showed that Rocky Mountain Tailed Frogs (*Ascaphus montanus*) moved along riparian corridors in landscapes with timber harvest (Spear and Storer 2010). They also found that these frogs had greater overland movements in areas that were not harvested but had been previously burned, suggesting that the signature of fire effects differs from timber harvest and widens the potential ‘funnel’ of activity.

Abundance and movements.— By showing a pattern of increased surface activity of plethodontid salamanders in near-stream areas, our study supports the funnel concept. Our window into plethodontid ecology remains largely obscured, but these new insights suggest that the behavioral ecology of riparian animals may differ from upland animals. The apparent near-stream hub of plethodontid activity supports previous conjecture that cool, moist riparian microclimates may allow for more amphibian movements (Dupuis et al. 1995; Johnston and Frid 2002), a pattern also supported by recent gene flow analyses from timber harvest landscapes (Spear and Storer 2010). Riparian microsite conditions such as more down wood near streams (Kluber et al. 2008; see also Anderson and Meleason 2009) may also facilitate near-stream activity for cover-seeking animals. It remains to be investigated whether near-stream areas might also be areas with greater salamander reproduction and survival.

Our 2006–2009 movement data supports previous reports of plethodontid salamanders generally having small home ranges (e.g., Ovaska 1988; Staub et al. 1995; Davis 2002). However, the design of our ACO arrays constrained our ability to fully monitor animal movements, and maximum distances reported here cannot be cited as reflective of their movement capability. Although we had maximum cumulative distances traveled for animals ranging from 20.7 to 31.0 m, the maximum straight-line distance from an original location of capture was only 10.1 m. We have probably underestimated distances traveled by these animals: we captured animals multiple times under the same cover board, but with months between captures. Animals could well have moved much more often and for longer distances than we were able to detect, and then returned. Some site tenacity was evident, nevertheless.

Although we sampled in three forest management treatments, our ACO sampling design was not sufficient for a well-quantified test of treatments. As a result of this, we were only able to examine general patterns in abundance and movement and saw no distinct differences in these patterns among the treatments. Two previous studies of plethodontid salamander relative abundance in response to thinning in which this study site was examined found treatment effects immediately after thinning (Rundio and Olson 2007) and no treatment effects at 5–6 years after thinning (Kluber et al. 2008). Both of those studies suggested that differences in site microhabitat conditions may have contributed to results. In our current study, the spatial variation we observed in abundances and movements among ACOs lends support for a signature of microsite differences among areas of our study that may be related to site attributes such as subsurface rock deposits or hydrology patterns rather than to forest treatments. For example, the 6-m and 70-m buffer stands and the unthinned control stand differed greatly in species occurrences throughout the study timeframe, pre- to post-treatment, despite their relative proximity (Fig. 1). This emphasizes the importance of including control units in study designs, and replication to account for spatial variation. Plethodontid studies in the northwest are time-intensive, and sufficient sampling to address spatial and temporal variation may be financially prohibitive. Information gleaned from case studies such as ours is important, although it should be recognized that due to the variation inherent in these systems, the narrow spatial inference of case studies needs to be acknowledged.

Several factors may have contributed to the increasing *P. dunni* numbers over the course of the study. Although we do not know why this occurred, it could reflect the fluctuating population dynamics of the species, increased recruitment or recovery from a past disturbance (timber harvest, possibly disease), altered hydrology or moisture regimes at the site, interactions

within the forest community, or observer bias. This species has been described as semi-aquatic, often occurring within a few meters of streams (Storm 2005). Increased surface moisture may explain its increasing occurrences upland in our study. This hypothesis warrants further examination with microclimate data available from the study site (Anderson et al. 2007), stream flow patterns, and with regard to precipitation patterns during our sampling period over the last decade. Increased moisture on the forest floor may be a consequence of thinning, but the *P. dunni* abundance patterns that we observed did not appear to be related to the thinning treatments at our site.

Relative to observer bias, *P. dunni* and *P. vehiculum* can be difficult to distinguish to the untrained surveyor due to color variation, especially at small body sizes. Although our field crew leader was consistent across the study for all years and trained field assistants in a similar manner to control for such bias, it is possible that color morphs changed over time and affected species identification. If you sum *Plethodon* captures and disregard species distinctions (Table 2), during transect surveys, *Plethodon* captures ($N = 325$) were more than twice *Ensatina* captures ($N = 157$; ratio = 2.07), whereas the *Plethodon/Ensatina* ratio during ACO sampling was 3.14. This supports an altered assemblage composition over the course of the 1998–2009 study, rather than observer bias relative to species identification. However, there may be method bias in the detection of species by the different methods. The ‘trap-happy’ *Plethodon* species may have increased capture rates, in particular.

Survival and recapture probability.—Relative to our second study objective, determination of survival and recapture probabilities among species, additional insights into the ecology of plethodontid salamanders emerged. Annual apparent survival for the three dominant plethodontids was 64% over the 3 years of capture-mark-recapture ACO data collection (2006–2009). This supports previous suggestions that these animals can live many years as adults (lifespan: 10–15 years; Jones et al. 2005). Although no significant fall or spring seasonal effect on recapture probability was detected, recapture probability showed a pattern of increasing in late fall to early spring, likely mirroring the animals’ active seasons. Recapture probability was highest for *P. dunni* and lowest for *E. eschscholtzii*. This is interesting because *E. eschscholtzii* is often considered a down wood associate (Bury and Corn 1988; Olson et al. 2006), yet showed no trace of ‘trap-happiness’ or tendency to return to ACOs. As *E. eschscholtzii* is a species known to use a variety of microrefugia including bark piles, wood piles, leaf litter, and rocky substrates (Kuchta and Wake 2005), ACOs may provide insufficient habitat for these animals. Additionally, *E.*

eschscholtzii is also known to have longer movements in forests, to the extent that they are a species that may be encountered during night driving surveys in British Columbia (Ministry of Environment, Lands, and Parks 1999). Furthermore, *E. eschscholtzii* may not be territorial and may have a more vagrant lifestyle. Consequently, ACOs may be less effective for questions addressing *E. eschscholtzii* life history.

ACO utility.—Overall, general use of ACOs as a sampling technique was supported by our study, where the advantage of not disrupting natural down wood and cover during timed or area searches has allowed us to census animals at a long-term experimental site over a 10-year timeframe. We also were able to recapture marked individuals to reveal information on plethodontid salamander movements. Our ACOs were rapidly sampled, and our entire array has often been sampled in a half day by two people, with more time needed as the number of new animals that need marking increased.

Although we did not conduct a survey of upland down wood during our study, it was previously noted that our study site may have relatively ‘limited’ large down wood, having 3 to 4 times less large down wood than another western Oregon site of similar age (Olson et al. 2006). This may have heightened the efficacy of our ACOs for salamander detection, and may have resulted in attracting the ‘ACO-happy’ *P. dunni* and *P. vehiculum* to these potentially limiting refugia over the time of our study.

Several other caveats about our ACOs are important to note. First, the Davis boards we used were effective due to their stacked design; most animals were found between the top and bottom boards in the interstitial spaces created by lathe spacers. The utility of a single board in contact with the ground would seem to be much reduced, and additional layered or bundled ACO designs warrant testing. Second, our boards had a time window of effectiveness of about 8 y. Initially, about one year was needed for board acclimation and animal colonization; eventually, wood decay occurred, reducing their sampling effectiveness by about year-10. Longer-term monitoring requires board replacement, as we have now done in our study. We opted to replace ACOs in the fall to allow about 6 months of acclimation before warmer spring temperatures and concurrent increased salamander surface activities were seen. After replacement, we saw reduced abundances likely reflecting a time period of board acclimation or weathering. Also, new boards appear to dry out quickly, reducing the time windows within a season that they may be used by salamanders. Long-term monitoring by ACOs across decades would be periodically interrupted by acclimation time periods following board replacement.

Third, the ACO arrays we used had clear limitations relative to the types of questions we could address. For example, our design yielded insufficient captures to robustly test some spatial patterns of abundances and movements. In 2008, two 6 × 6 board arrays ($n = 72$) with 2-m spacing between boards were deployed at a second site in the central Oregon Cascade Range province to better address salamander movement patterns. Although that design may be improved in some respects, we have not had much salamander recruitment to those boards in the first 2 years. Although board acclimation may still be occurring, site differences in species composition (e.g., a species thought to have reduced movements occurs there: Oregon Slender Salamander, *Batrachoseps wrighti*; Keel Mountain site; Clayton and Olson 2009) and habitat conditions such as more abundant natural down wood may contribute to the lower efficacy of cover boards to sample salamanders there or the longer acclimation period (vs. one year at our initial site; Green Peak site, Olson et al. 2006). ACOs may be more useful at sites where naturally occurring down wood refugia are scarce. Also, an unsuccessful pilot study of ACO sampling is known from a more southern site in the Oregon Cascade Range (Chris Maguire and Kirsten McDade, pers. commun.). ACOs appeared to be too dry to provide suitable microhabitat for salamanders at that site, which was in a much warmer and drier forested area. Additionally, their dominant capture species was *Ensatina*, which our data suggests may have reduced ACO use. Eight salamander species were subsequently captured using their alternative sampling method of pitfall trapping (Maguire et al. 2005). Pitfall trapping may have species detection biases as well, and is rarely used in the US northwest now as a result of mortality concerns raised by institutional animal use and care committees. In summary, we suggest that ACO efficacy be further tested before wide-scale installation.

Forest ecology and management implications.—Due to the sensitivity of plethodontids to environmental conditions including microclimate (Feder 1983), they have been suggested to be ideal indicators of forest ecosystem integrity (Welsh and Droege 2001). However, Pearce and Venier (2009) questioned the utility of plethodontids as indicators in Ontario, Canada boreal forests where their abundances were very low, and capture rates were spatially and temporally variable. This boreal forest plethodontid characterization is not dissimilar to some northwest forests, where plethodontid abundances are similarly low and variable in comparison to eastern US forests. The paradigm of plethodontids as ideal forest ecosystem indicators may not hold well in portions of their northwest ranges where microsite physical habitat conditions that are not related to vegetation condition play a dominant role in their

occurrences. Our observations of local spatio-temporal dynamics in species occurrences over short distances and over about a decade of time suggests that there are unexplained elements to their ecology that may not simply reflect forest vegetation type. Old-forest conditions are more than the age of standing trees, and understanding other aspects of the system will be important to put the plethodontid role in forests into full perspective.

Nevertheless, information on plethodontid species population ecology including an understanding of habitat associations, population structure and dynamics, and dispersal capabilities is of keen interest to natural resource managers interested in retaining biodiversity in northwest managed forest landscapes. Questions arising in this context include: (1) how large should the size of a protected forest patch be to retain a source population of a plethodontid species; (2) can riparian areas serve as such source areas for upland-associated plethodontid populations; (3) how far can a plethodontid salamander move; and (4) can this information be used in order to manage for forest connectivity among habitat patches? Our study contributes to several of these questions.

Down wood recruitment: directional felling and ‘chains’.—We observed high use of surface cover objects by three plethodontid species, and movements among these cover objects was associated with both riparian areas and cover proximity. Hence, we suggest that retaining proximity of cover objects from riparian areas into upland forest would facilitate plethodontid movements, and consequently population connectivity across forest stands. In managed forests that are depauperate of down wood, down wood recruitment may be considered in spatial patterns that bridge riparian-to-upland areas (Olson and Burnett 2013). Directional felling to align logs across this slope gradient perpendicular to streams (i.e., upslope trees felled toward streams, or riparian trees felled toward ridgelines) may create continuous refugia for salamanders. This design might facilitate upland dispersal and population connectivity (Fig. 4). Logs positioned along the ground, not suspended, would be important for amphibians, and hence bucking newly placed logs to increase their contact with the ground might be needed.

Such designs in headwaters (Fig. 4) may be particularly important due to headwater ‘funnels’

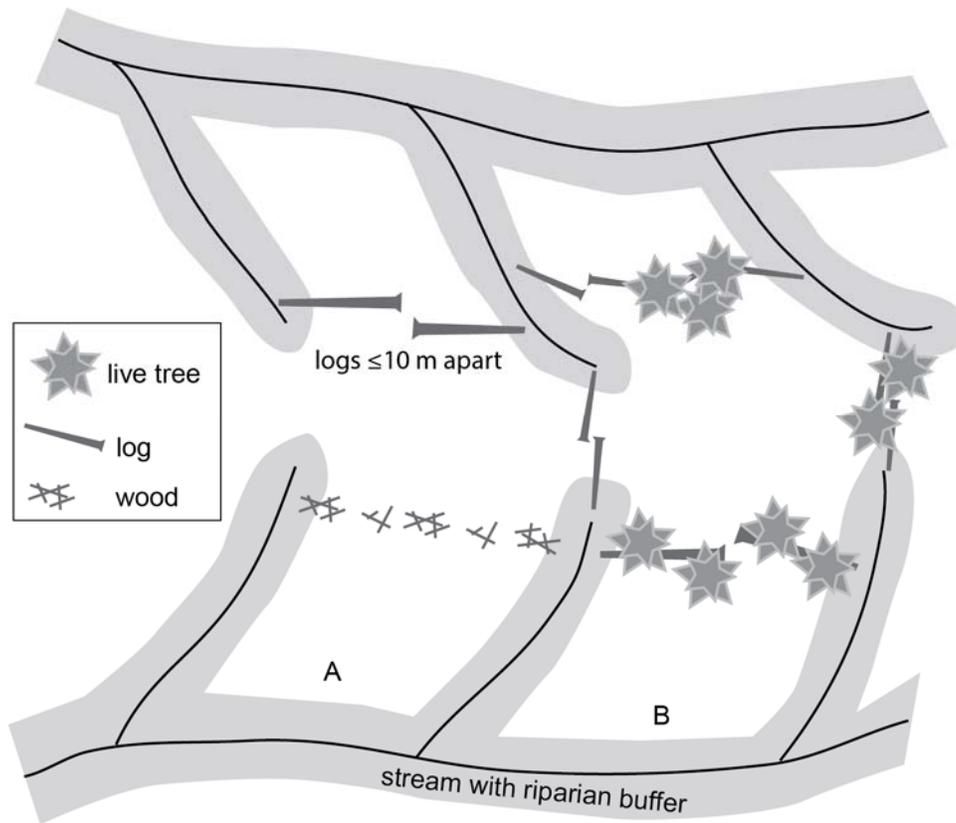


FIGURE 4. Conceptual spatial design of forest structural elements in managed forests, aligned to span among riparian areas of different drainages to provide overland connectivity for riparian-dependent and wood-associated species with limited vagility, such as salamanders. (A) Log placement designs; (B) log placement in conjunction with green-tree retention to aid dispersal of canopy-associated species.

channeling many species into these spatially compressed habitat areas near streams. Although we know relatively little of how plethodontid populations are spatially structured in the northwest, from the movement patterns that we observed, it appears that relatively small areas such as the riparian corridors as wide as ~15 m may be providing important habitat for terrestrial *Plethodon* species. Uplands and ridgelines may be less populated and in some cases represent dispersal challenges; this could result in basin structure having an association with population structure, especially in areas with more xeric upland conditions. However, *E. eschscholtzii* may operate at larger spatial scales and occur more frequently in uplands (e.g., in western Oregon; Rundio and Olson 2007; Kluber et al. 2008). Other studies have stressed the potential importance of riparian areas of small streams for a variety of species (reviews: Richardson et al. 2005; Olson et al. 2007; but see also: Oregon plethodontids: Vesely and McComb 2002; Oregon plants: Sheridan and Spies 2005; eastern US aquatic-breeding plethodontids: Crawford and Semlitsch 2007; Oregon invertebrates: Rykken et al. 2007b). These other taxa may benefit by provision of down wood or connectivity areas extending upland from small streams. However, the efficacy of log placement and orientation to provide habitat for plethodontids and other species warrants testing, especially in designs traversing trans-riparian gradients (Olson and Burnett 2013).

Relative to log placement and orientation, several additional designs can be conceived. First, designated areas managed for species' overland connectivity may reduce the need to provide down wood everywhere in a stand undergoing restoration management. Second, more than a single log might be needed, either to extend log 'chains' over ridgelines or to other habitat patches, or to provide log piles to enhance their ecological functions as species 'stepping stone' refugia (Rose et al. 2001). Because we saw salamander movements up to 10 m among ACOs in our study, a preliminary guideline might be considered for down wood spacing on the forest floor in such designated connectivity areas: logs spaced \leq ~10-m apart (Fig. 4). Overland 'chains' of logs across designated linkage areas may provide dispersal or reproductive habitat for a variety of other taxa reliant on down wood (McComb and Lindemeyer 1999; McComb 2001; Rose et al. 2001). If down wood arrays were aligned with green tree retention (Fig. 4), canopy-associated species (e.g., Red Tree Voles, *Arborimus longicaudus*: Carey 1991; Biswell et al. 2000) also might be aided. Although we are suggesting that logs aligned across hillslope contours, up and down slopes, may facilitate movements of small organisms with relatively low vagility, such alignment may impede movements of larger organisms that tend to move along contours (Bull et al. 1997). Hence, gaps between adjacent logs (i.e., breaks in the chain) might be a consideration to allow

easier cross-passage by animals moving *along* contours, such as deer (*Odocoileus* spp.). Log placement might also consider microclimate refugia at the site scale provided by aspect, hill-shading, or tree shading. Logs in cool, moist areas may be favored by northwestern forest amphibians. Lastly, because large-diameter logs are important for many forest-dwelling species (Rose et al. 2001), recruitment of large logs may be considered for this concept of assisted migration of ground-dwelling species (Olson and Burnett 2013), including forest management to encourage growth of large trees for the purpose of future down wood recruitment.

Larger-scale considerations.—Landscape patterns of forest patches and land-ownership patterns may have bearing on log placement for species habitat and designs of optimal linkage areas. Our study site was nested within a larger square of federal land (1.6 km [1mile] per side) in a checkerboard pattern of federal and private lands. For the most part, neighboring lands were new and regenerating clearcuts, and along diagonals of the checkerboard with federal land ownerships, there was greater tree retention and there were more extensive riparian reserves. Retention of habitat connectivity from riparian areas of small streams toward corners in federal land squares is a consideration (Fig. 5a; Olson and Burnett 2013). Connections from riparian areas to other protected areas would be a more general consideration, and would apply to other land-ownership geometries (Fig. 5b). Retaining connectivity from riparian areas over ridgelines to adjacent watersheds (Fig. 5b) has been suggested as an additional consideration, especially for more aquatic-associated amphibian species (Olson and Burnett 2009, 2013). Such linkage areas among headwaters would have relatively short distances (relative to downstream over-ridge distances), affecting other land management priorities the least. At landscape scales, provision of dispersal pathways in north-south directions, such as over watershed boundaries where ridges extend in an east-west direction (Fig. 4c), could aid species resilience to the effects of climate change in areas such as our northwest temperate zone forests (Olson and Burnett 2013).

Because the three dominant plethodontids in our study seem to fare well after forest thinning (Wessell 2005; Rundio and Olson 2007; Kluber et al. 2008; Hawkes and Gregory 2012), it is likely that thinning or heterogeneous patterns from alternative silvicultural designs will contribute to the persistence of these species. Given time, salamander movements are likely across areas managed for timber with a 'soft touch' such as selective harvest prescriptions. However, the geometry of stream proximity may affect salamander occurrences and the rate of movements. Hence, a recipe of riparian retention and thinning with down wood recruitment may be a

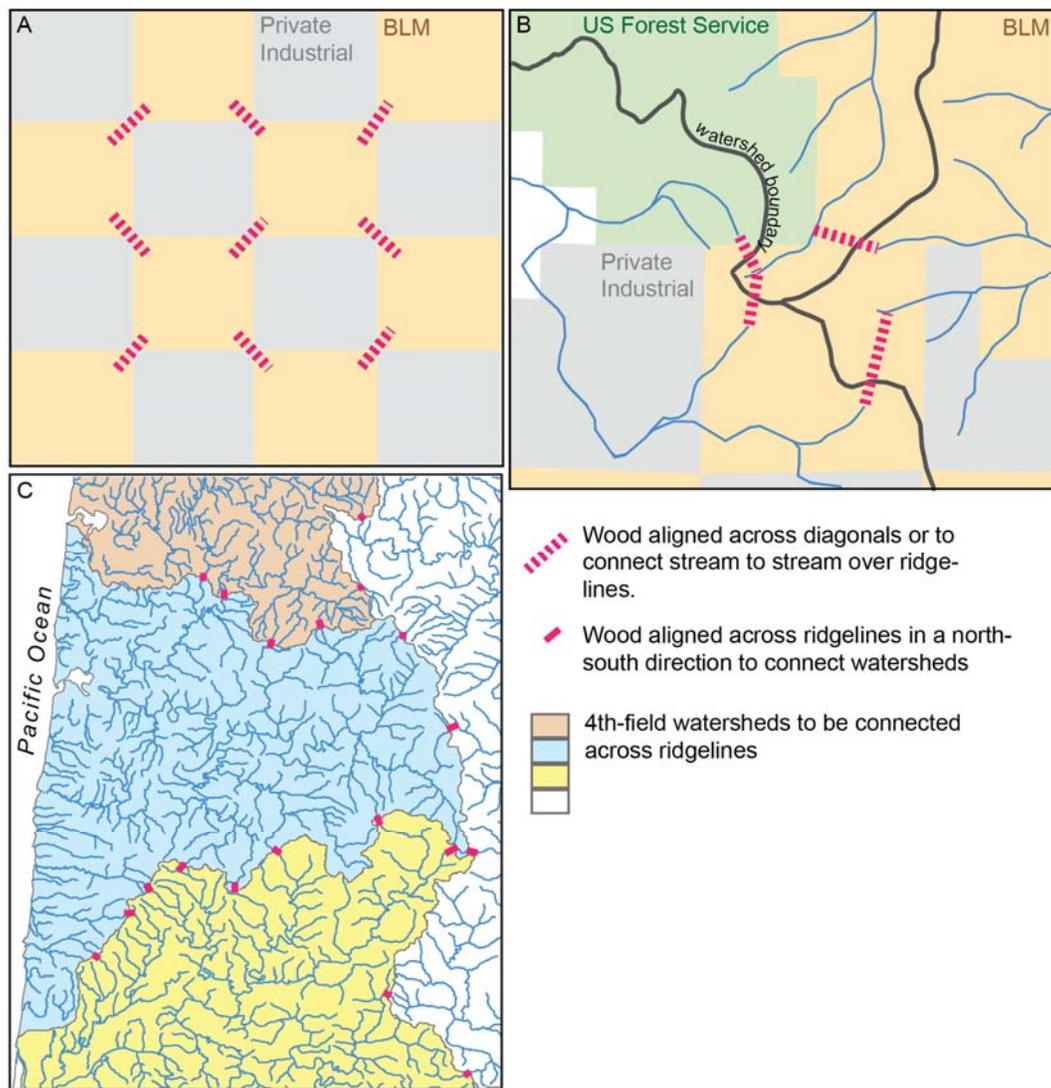


FIGURE 5. Landscape designs for down wood placement and orientation: (A) alignment of wood (red features) across diagonals in a checkerboard ownership pattern (colored squares depict different land ownerships) to retain connectivity among land patches of a single ownership; (B) alignment from stream to stream over ridgelines of distinct watershed boundaries (bold black line) and land ownerships (colored polygons depict different land ownerships), such as this ‘triad’ area where three discrete watersheds join (Olson and Burnett 2009, 2013); (C) alignment in north-south directions over discrete watershed boundaries (ridgelines; colored polygons depict discrete watersheds) to aid dispersal in the face of climate change that may have latitudinal patterns of effects (Olson and Burnett 2013). Figure adapted from Olson and Burnett 2013.

general timber harvest prescription that could aid this biota’s persistence.

Conclusions.—In our case study of using ACOs to assess plethodontid ecology in managed forests of western Oregon, we found that most salamander movements were short (< 10 m), near streams, and between adjacent ACOs. The stream network extending upstream into headwaters may funnel the movements of animals within and along the stream channel corridor. Our observation of short-distance movements of

salamanders between adjacent cover boards suggests that contiguous down wood structures may aid animal dispersal. Positioning of chains of cover objects extending out from riparian areas into uplands in managed forests could link to other habitat patches or watersheds; chains could be managed habitats and are not conceived as no-harvest corridors. We have developed the concepts from our work with ACOs in western Oregon, but the extension of salamander use of ACOs as being analogous to their use of logs is conjecture at this time. The chain concept warrants

further development, especially relative to whether they may aid dispersal functions for a variety of low-vagility taxa that appear to function on fine spatial scales: amphibians, small mammals, mollusks, invertebrates, lichens, bryophytes, and fungi.

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