

Abundance of Plethodontid Salamanders in Relation to Coarse Woody Debris in a Low Elevation Mixed Forest of the Western Cascades

Abstract

Few studies have examined the relationship between populations of plethodontid salamanders and coarse woody debris (CWD) in a low elevation (100 m) Cascade forest that has significant numbers of both coniferous and hardwood trees. Plethodontids feed, breed and respire terrestrially and therefore depend on forest attributes such as CWD. Measurements of rainfall, canopy closure, CWD, and plethodontid abundance were made in an old-growth forest site and an adjacent 50-yr-old site in a low-elevation forest on the north bank of the Sandy River in Multnomah County, Oregon. Rainfall and canopy closure were significantly associated with abundance of plethodontids. Plethodontids were never located in quadrats that lacked coniferous logs in a moderate to advanced state of decay. There were several significant positive correlations between the number of plethodontids and the volume of coniferous CWD in each quadrat. Plethodontids showed significant preferences for coniferous logs over hardwood logs and for coniferous logs of relatively large diameter. These results have implications for the management of forests and plethodontids in the Cascades.

Introduction

The old-growth Douglas-fir-western hemlock (*Pseudotsuga menziesii*-*Tsuga heterophylla*) forests characteristic of Oregon and Washington west of the Cascades provide unique habitat critical to wildlife (Franklin et al. 1981). Forests moderate daily fluctuations in humidity and temperature of air and soil (Chen et al. 1993). Coarse woody debris (CWD), including both snags and logs, provides habitat for invertebrates (Maser and Trappe 1984, Marra and Edmonds 1998) and small vertebrates (Bunnell et al. 1997).

Close associations exist between CWD and vertebrate populations. Bunnell et al. (1997) calculated that 69 vertebrate species in western Oregon are associated with downed wood. Plethodontid salamanders have been of particular interest because they live and breed terrestrially and therefore particularly rely on certain forest attributes (e.g., CWD and canopy closure) to avoid desiccation (Ray 1958, Spotila 1972, Feder 1983). Several species of plethodontid salamanders are positively associated with CWD, including ensatinas (*Ensatina eschscholtzii*) (Bury and Corn 1988, Welsh and Lind 1991, Butts and McComb 2000), clouded salamanders (*Aneides ferreus*) (Welsh and Lind 1991, Butts and McComb 2000), and western red-backed salamanders (*Plethodon vehiculum*) (Dupuis et al. 1995). More specifically, plethodontids favor logs in medium to advanced

states of decay (Aubry et al. 1988, Corn and Bury 1991). Plethodontids may also prefer logs of relatively larger diameter (e.g., Corn and Bury 1991), perhaps because large logs have a smaller surface area-to-volume ratio and so are more resistant to desiccating or gaining heat. Because forest management practices have qualitative and quantitative effects on CWD and canopy closure, many studies have explored the effects of forest management practices on plethodontid populations. A review of these studies shows that clear-cutting generally has a negative effect on amphibian populations and that CWD and canopy cover are often positively correlated with amphibian abundance (deMaynadier and Hunter 1995). Canopy cover helps create the cool and moist conditions required by plethodontids. Compared to clear-cuts, the interior of an old-growth forest experiences slower wind, lower air and soil temperatures, and less daily and seasonal variation in soil and air temperature (Chen et al. 1993).

While degree of canopy closure and amounts of CWD are important habitat attributes, animal communities vary along elevational gradients west of the Cascades in Oregon (Harris and Maser 1984). In the Pacific Northwest (PNW), lower elevation forests have a mixture of conifers and hardwood trees while higher elevation forests are almost exclusively coniferous. Many studies have explored the relationship between habitat variables and plethodontid populations. However, those studies have been conducted primarily in the

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Coast Range of the PNW (Corn and Bury 1991, Dupuis et al. 1995, Gomez and Anthony 1996, Dupuis and Bunnell 1999) or at higher elevations (290–1218 m) in forests of the Cascades that were almost exclusively coniferous (Aubry and Hall 1991, Aubry 2000, Butts and McComb 2000). Few studies of plethodontids have been conducted in low elevation forests of the Cascades in which hardwoods are well represented. Authors of coastal studies of plethodontids (Corn and Bury 1991, Dupuis et al. 1995, Dupuis and Bunnell 1999) have either not included hardwoods when listing dominant forest species or indicated a very low proportion of hardwoods. For example, Corn and Bury (1991) found that 85% of logs were Douglas-fir and only 2% were hardwoods. Comparable studies in the Cascades (Aubry et al. 1988, Aubry 2000) have not included hardwoods in the list of dominant species. Welsh and Lind's 1991 study in coastal northern California and southern Oregon is exceptional in having significant numbers of hardwoods, but their more southern coastal sites experience a different climatic regime than the Cascades. The objective of this study was to examine the relationship between forest structure and plethodontid populations in a forest in the western Cascades that is of low elevation and has significant representation of hardwoods.

Study Area

The study area is a low-elevation (50–150 m) forest on the north bank of the Sandy River in Multnomah County, Oregon (Figure 1). The area is composed of an uncommon plant community called moist temperate river terrace forest occurring at the Humid Transition life zone along

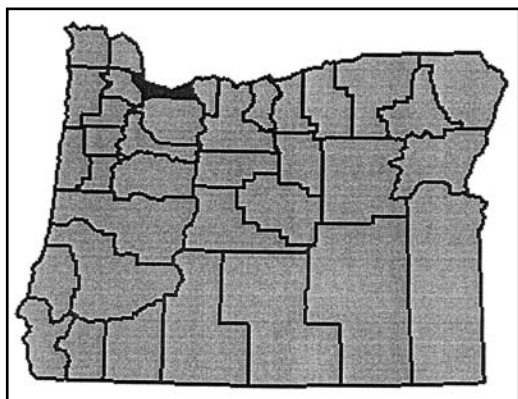


Figure 1. Location of Multnomah County, Oregon.

the Willamette Valley/western Cascades ecotone within westside lowland conifer-hardwood forest (Ratcliffe 1992, Chappell et al. 2001). The mixed composition forest includes big-leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), western hemlock, western red cedar (*Thuja plicata*) and Douglas-fir. The soil is droughty and lateritic (Ratcliffe 1992). The area consists of 52 ha old-growth forest (350–500 yr) and an adjacent forest site (henceforth referred to as the mature site) of similar size that was clearcut ~50 yr ago. The mature site was not replanted or burned after harvesting. The old-growth site is designated as an Outstanding Natural Area by the BLM. The Nature Conservancy administers both sites, which share a north-south border. The area receives ~117 cm rainfall per year. Summers are warm and dry while winters are cool and wet.

Methods

I collected data from early March through early May 2001 coinciding with cool and moist spring conditions that are best for collecting PNW amphibians on the surface (Corn and Bury 1990). I recorded rainfall during each field day (24 hr rainfall) and the rainfall on that day plus the previous day (48 hr rainfall). Rainfall data were obtained from the Integrated Plant Protection Center web site (Oregon State University 2001) that posts weather data from a National Weather Service substation located 8 km from the study area in Troutdale, Oregon.

I placed flagging every 50 m along the border between the two sites and used a random number table to identify the flagged points that would serve as starting points for making transects west (into old-growth) or east (into the mature site). Over the course of the study most of these starting points were used twice, once for each site. All starting points were ≥ 100 m from any forest edges. This distance from the edge is twice as great as that used by Aubry et al. (1988) and is three times greater than the depth at which edge effects had a negative influence on amphibian populations (deMaynadier and Hunter 1998). Each day ($N = 16$) I collected data from either the old-growth or mature site as determined by a coin flip. Using a compass I established 10 m x 10 m quadrats along a transect at 50 m, 100 m, and 150 m from the starting point; on two occasions (one per site) I established a fourth quadrat at

200 m. If I encountered unrepresentative features (e.g. rock piles, seeps, or streams) I added 30 m before establishing the next quadrat. Care was taken to follow compass bearings and to measure these distances as accurately as possible to avoid biasing the placement of quadrats. I established quadrats using stakes and string and stayed outside the quadrat while delineating it to minimize disturbance to woody debris and amphibians. All quadrats were ≥ 40 m away from the potential locations of any other quadrat.

I searched for amphibians using timed area-constrained searches (Butts and McComb 2000). After establishing each quadrat I started a timer and searched for amphibians for 30 min by inspecting the surface and by searching in and under cover objects (rocks, bark, logs). The timer was stopped upon location of a specimen and was restarted upon resumption of searching. I used a soil cultivator to turn and break into woody debris. I raked together the pieces of woody debris from a given log after searching it for salamanders in an effort to recreate the original conditions in the log. Specimens were caught by hand, identified to species, and released at the site of capture. I recorded the microhabitat type (e.g., log, rock) associated with each animal.

I then quantified the amount of woody debris within each quadrat. I measured the length of each piece of down wood that was 5–10 cm in diameter. For each piece of woody debris >10 cm in diameter (henceforth referred to as logs), I measured its length within the quadrat and half of the circumference of both ends of each piece. I defined end as being either a natural end within the quadrat or the place where the log intersected the quadrat boundary. I used the length and average diameter of each log to calculate both the total volume of logs in the quadrat and the area of the quadrat that was covered by the projection of logs. Logs were treated as cylinders for these calculations. I also recorded whether logs were hardwoods or conifers. If they were conifers I assigned each a decay rating of 1 (least decayed) to 5 (most decayed) using the scheme of Franklin et al. (1981). The biomass of coniferous logs was determined using densities provided in Spies et al. (1988) that are specific to each decay class. Biomass of hardwood logs was calculated using a density of 0.38 g/cm^3 (Grier and Logan 1977).

I measured the height (using a clinometer or measuring pole) and circumference of dead trees (snags) at breast height or at their tallest point if they were shorter than breast height. I recorded whether snags were hardwoods or conifers and whether they were logging stumps. If a snag was in a state of decay that allowed me to completely disassemble it, then I measured it before searching for amphibians so that I could measure it accurately. I measured the diameter at breast height of all live trees >10 cm (dbh) within each quadrat and recorded whether they were hardwoods or conifers. Because sword ferns (*Polystichum munitum*) were a common understory plant I recorded the number of sword ferns whose centers fell within the boundary of each quadrat. I then measured the slope, aspect, and degree of canopy coverage of each quadrat using a clinometer, compass, and concave spherical densiometer.

Statistical analyses were performed using Statview Version 5.0.1. I used Z-score histograms to determine whether the data for each variable were normally distributed. I used unpaired t-tests to compare the means of normally distributed variables and Mann Whitney U-tests to compare the means of the remaining variables, χ^2 tests to test for evenness of distribution, and Spearman's rank correlation analysis to test for associations between variables that were not distributed normally. Variables associated with plethodontid abundance were then subjected to partial correlation analysis to determine the relationship of each individual variable with plethodontid abundance when all other variables were held constant. To avoid singularities, only variables that had no association with each other were used in the partial correlation matrix. For example, 24 hr and 48 hr rainfall were associated with each other and so only one of those two variables could be used in the matrix. The significance of partial correlation coefficients was determined using Fisher's r to z test. The level of significance for all statistical tests was set at $P = 0.05$.

Results

I collected data from 25 quadrats in each of the old-growth and mature sites ($N = 50$) representing a total of 0.5 ha. Average daily rainfall for January, February, April, and the first 10 days of May 2001 (the end of the study period) was significantly lower than the 30 year average (all P

≤ 0.018), representing only 31%, 42%, 97% and 19%, respectively, of the 30 year average.

More than one-third of all snags, logs, and live trees in both sites were hardwoods (Table 1). The mature site had significantly more live trees, snags, and logs than the old-growth site, and more coniferous logs in all decay classes (Table 1). In the mature site mean diameter of logs was almost twice that of the old-growth site but mean dbh of snags was smaller, and dbh of live trees was significantly smaller (Table 2). The mean

TABLE 1. Comparison of the number of live trees, snags, and logs ≥10 cm in diameter in old-growth forest and mature forest. Twenty-five 10 m x 10 m (0.01 ha each) quadrats were surveyed in each site. NS = not significantly different.

	Number of specimens		P value
	Old-growth	Mature	
Live trees			
Conifers	34	41	NS
Hardwoods	20	68	<0.001
Total	54	109	<0.001
Snags			
Conifers	15	28	<0.05
Hardwoods	9	26	<0.005
Total ¹	25	64	<0.001
Logs			
Conifers	75	133	<0.001
Hardwoods	60	70	NS
Total	135	203	<0.001

¹ Includes small or heavily decayed individuals that could not be classified as conifers or hardwoods.

TABLE 3. Comparison of coarse woody debris of old-growth Douglas-fir forests in the western Cascades of Oregon and/or Washington. The present study examined a forest with significant representation of hardwoods; hardwoods were rare or absent in the other studies.

Study	Elevation (m)	Age (yrs)	Dry log mass (Mg/ha)	Number logs/ha by diameter (cm)			
				10 - 29	30-59	> 60	Total
Present	50-150	350+	24.1 ¹ (34.9) ²	132 (348)	152 (172)	16 (20)	300 (540)
Spies et al. 1988	847	417	73	191 ³	161	64	417
Grier & Logan 1977	430-670	450	190	100.8 ⁴	44.5	49	194.3
Sollins 1982	340-610	350-550	81	(N/A)			

¹Data for conifers only.

²Numbers in parentheses are totals of conifers and hardwoods.

³Spies et al. (1988) used slightly different categories: 10 - < 30, 30 - 60, and > 60 cm dia.

⁴Grier and Logan (1977) used 15 - 30 cm.

canopy cover of the old-growth site (89.5%) was not significantly different from the mature site (90.8%). The dry mass of coniferous logs in the old growth site was low in comparison to other old-growth forests in the PNW (Table 3).

I captured one or more plethodontids in 18 of 50 quadrats (36%). Species captured included 14 ensatinas, 13 Oregon slender salamanders (*Batrachoseps wrighti*), one Dunn's salamander (*Plethodon dunni*), and one red-backed salamander. The distribution of plethodontids between the two sites was not significantly different from even.

TABLE 2. Comparison of the mean size of live trees, snags, and logs ≥10 cm in diameter and total number of plethodontids encountered in old-growth forest and mature forest. NS = not significantly different.

	Old-growth	Mature	P value
Dbh of live trees (cm)			
Conifers	63.60	30.45	<0.001
Hardwoods	37.26	27.37	0.001
Dbh of snags (cm)¹			
Conifers	54.09	41.14	NS
Hardwoods	22.67	15.24	0.019
Maximum dia. coniferous logs (cm)²			
	18.11	34.97	NS
Number plethodontids	11	18	NS

¹Includes snags shorter than breast height measured at their highest point.

²Does not include regions of greater diameter that may have extended out of quadrat boundaries.

I compared the means of attributes of all quadrats containing one or more plethodontids ($N = 18$) to those of quadrats that lacked plethodontids ($N = 32$). The two groups of quadrats differed significantly in rainfall, canopy cover, number of live trees, and average snag height; no other measure of CWD differed significantly (Table 4). Correlation analysis of those four variables and all other measured variables showed that canopy cover was positively correlated with the number of live trees ($P = 0.02$) and that mean snag height was negatively correlated with the number of logs >10 cm ($P = 0.03$).

TABLE 4. Means from 18 quadrats in which plethodontids were present compared to 32 quadrats in which plethodontids were absent. Only variables that were significantly different are shown.

Variable	Plethodontid Status		P value
	Present	Absent	
24 hr rainfall (cm)	0.208	0.064	0.03
48 hr rainfall (cm)	0.874	0.203	0.001
Canopy coverage (%)	94.96	87.43	<0.001
Number of live trees	4.61	2.63	0.016
Average snag height (m)	1.82	10.75	0.003

In examining correlations of plethodontid abundance with measures of CWD, I analyzed separately three sets of data: all 50 quadrats, the 25 old-growth quadrats, and the 25 mature quadrats. The following variables were significantly [or nearly so; values slightly >0.05 are shown in brackets] positively associated with plethodontid abundance (Spearman's rank correlation) in all three data sets: 48 hour rainfall (all $P \leq 0.019$); canopy cover (all $P \leq 0.007$); number of live trees (all $P \leq 0.041$) and the volume of class 1 coniferous logs (all $P \leq 0.046$). The following correlations were significant in all 50 quadrats and in the 25 old-growth quadrats but not in the mature quadrats: volume of coniferous logs in class 2 ($P = 0.029$ [and 0.054] respectively), class 3 ($P = 0.045$ and 0.019); classes 3 and 4 combined ($P = 0.024$ and 0.017); classes 4 and 5 combined ($P = 0.031$ [and 0.052]), and classes 3, 4 and 5 combined ($P = 0.031$ and 0.006). Twenty-four hr rainfall was correlated with plethodontid abundance in all 50 quadrats and in the 25 mature quadrats ($P = 0.003$ and 0.017).

Some correlations were significant in only one of the three sets of data. In the old-growth site, plethodontid abundance was correlated with the

volume of coniferous logs in class 5 ($P = 0.024$) and the mean circumference of live trees ($P = 0.047$). When considering the data from all 50 quadrats, the abundance of plethodontids was negatively correlated with mean snag height ($P = 0.05$), positively correlated with the number of snags ($P = 0.009$), and marginally correlated with the volume of coniferous logs in class 4 [$P = 0.058$].

Variables found to be associated with plethodontid abundance (listed above) in all 50 quadrats were then subjected to partial correlation analysis. Rainfall ($P = 0.002$) and canopy cover ($P = 0.01$) were the only two variables significantly correlated with the abundance of plethodontids when the effects of the remaining variables were held constant.

Plethodontids captured in association with a log were not distributed evenly with respect to the type, diameter, and decay class of available logs. Nineteen of the 29 plethodontids (65.5%) were located in or under a coniferous log (16 individuals) or snag (3 individuals), with one animal under a hardwood log and the remainder either on the surface or under rocks. Based on the numbers of coniferous and hardwood logs searched (208 and 130) the plethodontids that were found in association with logs showed a significant association with coniferous logs ($P < 0.01$). The average maximum diameter (57.5 cm) of all coniferous logs associated with a plethodontid was significantly greater than that of coniferous logs where plethodontids were not found (33.03 cm, $P = 0.002$). All plethodontids associated with coniferous logs were found in logs of decay classes three, four, or five, and plethodontids were never located in quadrats lacking coniferous logs in those decay classes.

Discussion

The abundance of plethodontids was significantly correlated with rainfall, canopy closure, and several measures of the volume of CWD. Plethodontids were associated with logs of moderate to advanced states of decay and showed significant preferences for logs of relatively large diameter and for coniferous logs over hardwood logs.

The old-growth and mature sites in this study are considerably different from most other forests where associations between CWD and plethodontids have been explored with respect to the

abundance of hardwoods. The volume of coniferous trees in forests of the PNW has been estimated to be 1000 times greater than the volume of hardwoods (Küchler 1946, cited in Franklin and Dyrness 1973). In contrast, 34–66 % of all types of wood (live trees, logs and snags) at both sites were hardwoods (Table 1) and the mass of hardwood logs was 31% that of coniferous logs (Table 3). This old-growth site also differs from other old-growth forests in amount and kind of coniferous CWD. There are fewer large logs, more small ones, and half or less of the total log biomass compared to other sites (Table 3). Indeed, the amount of log biomass in the old-growth site falls well below the range of 85–190 Mg/ha described as typical for old-growth forests of the PNW (Franklin et al. 1981). Clearly this low-elevation old-growth site has atypical characteristics.

Most of the significant correlations between plethodontid abundance and measures of CWD held true for analyses that considered both mature and old-growth sites. The volume of coniferous logs, especially those in classes three, four, and five, was significantly correlated with the number of plethodontids found in each quadrat. This finding agrees with results from several other studies (Aubry et al. 1988, Corn and Bury 1991, Butts and McComb 2000). CWD in general and decayed logs in particular provide microhabitats in which plethodontids can feed, breed, and stay cool and moist.

Mean snag height was significantly smaller in the quadrats in which plethodontids were found and was negatively correlated with abundance of plethodontids. Short snags have decomposed more than tall ones (Maser et al. 1979), thus providing appropriate microhabitats for some plethodontids; however I found few plethodontids in snags. A possible explanation for the negative correlation between snag height and salamander abundance is the negative correlation between the number of logs and snag height. The latter relationship may be attributable to the influence of the mature quadrats, which contained abundant logs (a heavily used habitat element) (Table 1) and logging stumps (short snags), thus creating a negative correlation of salamander abundance with snag height.

Plethodontids are often captured in association with logs (Bury and Corn 1988, Welsh and Lind 1991, Olson et al. 2001). This study found that logs associated with plethodontids showed a significant

tendency to be conifers and of relatively large diameter (mean = 57.5 cm). This finding closely agrees with the findings of Corn and Bury (1991), but not with Aubry et al. (1988) who found that plethodontids were most commonly associated with logs 10–30 cm in diameter. These two log attributes may be important because of their effects on temperature, humidity, ease of penetration, longevity, and invertebrate population.

The sites used in this study are unusual in having a large proportion of hardwoods, which has implications for managers of plethodontid habitat. The presence of hardwoods in low-elevation forests provides primary habitat for more vertebrate species than is found in forests of higher elevations in the PNW (Harris and Maser 1984). However, the present study indicates that when available hardwoods do not necessarily provide important habitat for plethodontid salamanders in the Cascades. In contrast, a study of mixed forests in the Coast Range and at higher elevations (427–1556 m) in the Klamath Mountains of NW California and SW Oregon found that plethodontids were approximately equally likely to use hardwood and coniferous woody debris (Welsh and Lind 1991).

Significant relationships between plethodontid abundance and canopy cover, decayed CWD, and rainfall clearly indicate the importance of moisture to plethodontids. Moisture levels are affected by both rainfall and canopy cover (which in turn is affected by the number and age of live trees), and have an effect on efforts to sample amphibians on the forest floor. Canopy cover helps to create the cool and moist conditions required by plethodontids. Eleven species of plethodontid have been found to be positively associated with canopy closure (deMaynadier and Hunter 1995). The finding that rainfall was significantly correlated with the abundance of plethodontids in all three data sets and was significantly greater on days when plethodontids were encountered agrees with findings from other studies (Dupuis et al. 1995, deMaynadier and Hunter 1998). When conditions are unfavorable (dry or hot), plethodontids may retreat into underground sites (Grizzell 1949) where they will be missed by surface sampling methods. Kramer et al. (1993) estimated that only 3%–10% of a population of Peaks of Otter salamanders (*Plethodon hubrichti*) was active on the surface at any one time. Although sampling results based on area-constrained searches can

be highly correlated between years (Smith and Petranka 2000), the rainfall during the study period was so anomalous that the associations found in the present study may differ from those that would be found during years of typical rainfall. For example, logs of large diameter may be better able to retain moisture during times of drought and therefore may have been a more heavily used habitat element in 2001 than they are in years of typical rainfall.

The distribution of plethodontids between the old-growth and mature sites was not significantly different from even. This distribution is not surprising since two of the strongest correlates with the abundance of plethodontids (rainfall and canopy closure) did not differ significantly between the sites. The similar degree of canopy closure between the old-growth and mature (50 yr old) sites agrees with the findings of Dupuis et al. (1995) and Aubry (2000). The mature site had more CWD in most size and decay classes (Table 1), including relatively large logs (Table 2) probably as a result of the more selective logging

that was characteristic of the period prior to 1960 (Butts and McComb 2000). The even distribution of plethodontids supports the suggestion of Bunnell et al. (1997) that the attributes of a forest (e.g., degree of canopy closure and availability of appropriate CWD) may be more important to plethodontids than is forest age. Forest management strategies that include reforestation with conifers and recruitment of large logs and snags are likely to be beneficial to plethodontids.

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Literature Cited

- Aubry, K. B. 2000. Amphibians in managed, second-growth Douglas-fir forests. *Journal of Wildlife Management* 64:1041-1052.
- Aubry, K. B., and P. A. Hall. 1991. Terrestrial amphibian communities in the southern Washington Cascade Range. Pages 327-338 *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (technical coordinators), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.
- Aubry, K. B., L. L. C. Jones, and P. A. Hall. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir forests in Washington. Pages 32-37 *In* R. C. Szaro, K.E. Severson, and D. R. Patton (technical coordinators), *Proceedings - Management of Amphibians, Reptiles, and Small Mammals in North America*. USDA Forest Service General Technical Report RM-166. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.
- Bunnell, F. L., L. L. Kremsater, and R. W. Wells. 1997. Likely consequences of forest management on terrestrial, forest-dwelling vertebrates in Oregon. Centre for Applied Conservation Biology Report M-7. University of British Columbia, Vancouver, British Columbia
- Bury, R. B., and P. S. Corn. 1988. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. Pages 11-22 *In* R. C. Szaro, K.E. Severson, and D. R. Patton (technical coordinators), *Proceedings - Management of Amphibians, Reptiles, and Small Mammals in North America*. USDA Forest Service General Technical Report RM-166. Rocky Mountain Forests and Range Experiment Station, Fort Collins, Colorado.
- Butts, S. R., and W. C. McComb. 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. *Journal of Wildlife Management* 64:95-104.
- Chappell, C. B., R. C. Crawford, C. Barrett, J. Kagan, D. H. Johnson, M. O'Mealy, G. A. Green, H. L. Ferguson, W. D. Edge, E. L. Greda, and T. A. O'Neil. 2001. *Wildlife habitats: description, status, trends, and system dynamics*. Pages 22-114 *In* D. H. Johnson and T. A. O'Neil (managing directors), *Wildlife-Habitat Relationships in Oregon and Washington*. Oregon State University Press, Corvallis, Oregon.
- Chen, J., J. F. Franklin, and T. A. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology* 63:219-237.
- Corn, P. S., and R. B. Bury. 1990. Sampling methods for terrestrial amphibians and reptiles. USDA Forest Service General Technical Report PNW-GTR-256. Pacific Northwest Research Station, Portland, Oregon.
- Corn, P. S., and R. B. Bury. 1991. Terrestrial amphibian communities of the Oregon Coast Range. Pages 305-317 *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (technical coordinators), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.

- deMaynadier, P. G., and M. L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* 3:230-261.
- deMaynadier, P. G., and M. L. Hunter, Jr. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology* 12:340-352.
- Dupuis, L. A., J. N. M. Smith, and F. L. Bunnell. 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conservation Biology* 9:645-653.
- Dupuis, L. A., and F. L. Bunnell. 1999. Effects of stand age, size and juxtaposition on abundance of Western Redback salamanders (*Plethodon vehiculum*) in coastal British Columbia. *Northwest Science* 73:27-33.
- Feder, M. E. 1983. Integrating the ecology and physiology of plethodontid salamanders. *Herpetologica* 39:291-310.
- Franklin, J. F., and Dyrness, C.T. (editors) 1973. Natural Vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8. Pacific Northwest Research Station, Portland, Oregon.
- Franklin, J. F., K. Cromack Jr., W. Denison, A. McKee, C. Maser, J. Sedell, F. Swanson, and G. Juday. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service General Technical Report PNW-118. Pacific Northwest Forest and Range Experimental Station, Portland, Oregon.
- Gomez, D. M., and R. G. Anthony. 1996. Amphibian and reptile abundance in riparian and upslope areas of five forest types in Western Oregon. *Northwest Science* 70:109-119.
- Grier, C. C., and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecological Monographs* 47:373-400.
- Grizzell, R. A., Jr. 1949. The hibernation site of three snakes and a salamander. *Copeia* 1949:231-2.
- Harris, L. D., and C. Maser. 1984. Animal community characteristics. Pages 44-68 *In* L. D. Harris (editor), *The Fragmented Forest: Island Biogeography and the Preservation of Biotic Diversity*. The University of Chicago Press, Chicago, Illinois.
- Kramer, P., N. Reichenbach, M. Hayslett, and P. Sattler. 1993. Population dynamics and conservation of the Peaks of Otter salamander, *Plethodon hubrichti*. *Journal of Herpetology* 27:431-435.
- Kuchler, A.W. 1964. Manual to accompany the map of potential natural vegetation of the conterminous United States. American Geographical Society Special Publication 36.
- Marra, J. L., and R. L. Edmonds. 1998. Effects of coarse woody debris and soil depth on the density and diversity of soil invertebrates on clearcut and forested sites on the Olympic Peninsula, Washington. *Environmental Entomology* 27:1111-1124.
- Maser, C., and J. M. Trappe. 1984. The seen and unseen world of the fallen tree. USDA Forest Service General Technical Report PNW-GTR-164. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Maser, C., R. G. Anderson, K. Cromack, Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78-95 *In* J. W. Thomas (technical editor), *Wildlife Habitats in Managed Forests—the Blue Mountains of Oregon and Washington*. USDA Forest Service Agriculture Handbook 553.
- Olson, D. H., J. C. Hagar, A. B. Carey, J. H. Cissel, and F. J. Swanson. 2001. Wildlife of westside and high montane forests. Pages 187-212. *In* D. H. Johnson and T. A. O'Neil (managing directors), *Wildlife-Habitat Relationships in Oregon and Washington*. Oregon State University Press, Corvallis, Oregon.
- Oregon State University. 2001. Integrated Plant Protection Center. Available online at www.orst.edu/Dept/IPPC/wea/current/Troutdale01.txt.
- Ratcliffe, R. 1992. Sandy wild and scenic river and state scenic waterway management plan: environmental assessment (edited by M. M. Leger). USDI Bureau of Land Management, Salem District, Salem, Oregon and Oregon State Parks and Recreation Department.
- Ray, C. 1958. Vital limits and rates of desiccation in salamanders. *Ecology* 39:75-83.
- Smith, C. K., and J. W. Petranka. 2000. Monitoring terrestrial salamanders: repeatability and validity of area-constrained cover object searches. *Journal of Herpetology* 34:547-557.
- Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69:1689-1702.
- Spotila, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs* 42:92-125.
- Welsh, H. H., Jr., and A. J. Lind. 1991. The structure of the herpetofaunal assemblage in the Douglas-fir hardwood forests of northern California and southwestern Oregon. Pages 395-414 *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (technical coordinators), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, Oregon.

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