Response of Ground-dwelling Vertebrates to Experimental Levels of Downed Woody Debris - Long-term Ecosystem Productivity Study, Willamette National Forest

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INTRODUCTION

Previous descriptive and associative research approaches have identified associations between the amount of coarse woody debris (CWD) and either the occurrence or abundance of certain species of forest floor mammals and herpetiles (e.g., Aubry et al. 1988, McComb et al. 1993). Managers are using information such as this along with observations regarding nutrient exchange sites around coarse woody debris to develop management guidelines for retention of woody debris following harvest. However, the hypothesis that retention of high levels of woody debris will result in high numbers of certain species of forest floor vertebrates has not been tested experimentally. The long-term Ecosystem Productivity (LTEP) study was designed to examine the effects of various seral-stage developmental pathways and coarse-wood retention levels on a range of ecosystem properties. In addition to nutrient cycling and soil productivity, the LTEP study affords the opportunity to examine the effects of experimental levels of coarse woody debris on ground-dwelling vertebrates.

The goal of this study was to monitor the relative abundance of forest floor small mammals and herpetiles in 80+ yr-old Douglas-fir forests prior to logging and following clear-cut harvests of stands with experimental levels (i.e., low and high) of CWD retention. Results from this study will elucidate the relationships between relative densities of ground-dwelling vertebrates and extremes of CWD levels. This information will allow managers to identify the levels and types of woody debris that should be retained following harvest on similar sites in the Willamette National Forest and central Cascades region.

METHODS

Study Site

This study was conducted at the Willamette National Forest (WNF) LTEP site, located in the Isolation Block of the WNF. The nine stands of the WNF LTEP study receiving the mid-seral, high and low CWD treatments and their respective controls were sampled in this study (Table 1). Low CWD treatments consisted of removal of all trees plus removal of some of the current downed woody debris. For the high CWD treatment, all but 15-20% of the original live stems was removed; retained stems were felled to provide the high coarse-wood component. In both CWD treatments, no live-trees or large snags were left on site. Stands were harvested between 1995-96 in one of the blocks and in all remaining blocks by the fall of 1997 (Table 1). However, the high CWD treatments were not fully implemented (i.e., felling of residual boles) until the summer of 1998.

Table 1. Mid-seral coarse-wood treatments and control plots monitored for treatment effects on relative abundance of ground-dwelling vertebrates, Willamette National Forest Long-term Ecosystem Productivity Study.

Replicate block	Subplot No.	Coarse woody debris treatment	Year of treatment	Stand size (ha)
I	5	Control	-	6.07
I	17	Low	1996	6.07
I	19	High	1996*	6.48
II	1	Control	-	6.07
II	3	Low	1997	6.48
II	2	High	1997*	6.48
III	15	Control	-	6.07
III	14	Low	1997	6.48
III	16	High	1997*	6.48

* stands were harvested, but coarse-woody treatment not implemented until 1998.

Vertebrate Sampling

Sampling of ground-dwelling vertebrates was conducted in the fall (October-November) in 1995-97 and 1999-00. Four 100-m long, permanent transects were established in each of the nine stands in 1995. Trap stations were spaced 10 m apart along a transect. Transects were distributed to adequately sample a stand without traversing the centrally located mensuration plots. Transects were equidistant from the stand perimeter and the perimeter of the mensuration plot. Bearing and distance from the corners of mensuration plots to transects, and between transects were recorded for future reference. Stations were marked with numbered wire flags.

Two types of traps were used to sample small mammals and herpetiles owing to trap selectivity of species (McComb et al. 1993). Pitfall traps were used to sample shrews and herpetiles. One pitfall trap (two #10 cans attached end-for-end) was established within one meter of each trap-station center. The top of traps was flush with ground level. Holes were punched in the bottom of the traps for drainage of rain water. To minimize trap deaths, a small amount of moss and/or polyfiber matting was placed on the bottom of the traps to absorb moisture and for insulation. Additionally, a pint-size juice carton filled with batting and bait was placed in a pitfall trap. Bait consisted of a mixture of peanut butter, rolled oats, and sunflower seeds. When in use, a plastic funnel made from a 2-lb margarine tub was placed in the neck of the pitfall trap to prevent escape of captures. Between trapping periods, pitfall traps were filled in with sticks or rocks to prevent animals from entering. Sherman live-traps (7.62 x 8.89 x 22.86 cm) were primarily used to record rodents. These traps were also baited and filled as much as possible with polyfiber batting, and placed inside empty one-half gallon milk cartons to shelter captures from rain. During a trapping period, two traps were placed within two meters of a trap station, one on each side of the transect. Sherman traps were removed when a stand was not being trapped. All three stands of a replicate block were trapped simultaneously for 6-8 nights in all years.

Each capture was identified to species, sexed, weighed, measured (body and tail lengths), and released at the site of capture. Rodents and larger insectivores were marked with Monel #1 ear tags. Most species of shrews and all herpetiles were toe clipped. Tag or toe number was recorded for each capture as was capture status (i.e., new, recapture). Numbers of disturbed or closed traps were recorded for calculating comparable measures of captures per trap night among stands.

Data were assigned to pre- and post-treatment periods. The pre-treatment period consisted of data from all nine stands in 1995 and the six uncut stands in blocks II and III in 1996 (Table 1). Post-treatment data were from all nine stands sampled in 1999 and in 2000. Data from 1997 were not analyzed because of the confounding effects of the partial high-CWD implementation.

Downed Wood and Vegetation Sampling

Live and dead wood were sampled by other researchers in various years of the LTEP study. Dead wood was sampled before (1995) and after (1997) clear-cut harvest with the planar-transect method (Buford 1999). Downed wood levels were additionally sampled on the high CWD treatments in 1999 after the felling of residual, standing stems. Sampling in 1995 used 10-meter transects, which were later considered too short for reliable estimates. A 25-meter transect was used in all other years. Live vegetation was sampled on all plots in 1993 and in the treated stands in 1999. Data used in this study consisted of only understory cover measures which were measured in 1999. Percent cover of shrub, fern, and herbaceous species was measured in 15-16 9-m^2 plots located in the center of each stand.

Analyses

Treatment effects on ground-dwelling vertebrates species were evaluated by examining changes in four population attributes and overall species diversity between pre- and post-treatment periods. Changes in relative capture rates (no. individuals/ 1000 trap nights) of individual species were examined to determine overall population response to treatments. Recorded observations from both Sherman-live traps and pitfall traps were used to calculate capture rates for shrews, the coast mole, and the creeping vole; pitfall-trap observations were used for Ensatina. Capture rates of all other species were based upon Sherman-live trap captures and associated trap-night effort.

Changes in capture rates alone are not necessarily indicative of changes in habitat quality. Higher capture rates can result from a higher proportion of transients dispersing through an area. Conversely, high quality habitat may support fewer but resident individuals; capture rates of individuals would be lower compared to habitats occupied by transients but individuals would be captured more frequently. Also, higher relative densities of small mammals have been associated with sub-optimal habitat inhabited by numerous young individuals displaced from optimal habitat by older, established individuals (Van Horne 1982). To more fully evaluate treatment effects on habitat suitability, pre- and post-treatment differences in mean body mass (a surrogate for age), mean percentage of recaptures ([number of individuals recaptured/total number of individuals]*100) and mean gender ratios ([no. individual males/total no. individuals]*100) were additionally analyzed.

Because of differences in numbers of stands sampled between treatment periods and violation of parametric ANOVA assumptions, I used a nonparametric analysis to determine treatment differences in all attributes except body mass and species diversity. I averaged data by pre- and post-treatment periods, calculated differences between treatment periods for each stand, and used the ranked differences in an ANOVA. If an ANOVA was significant ($P < 0.05$), I used Friedman rank sums to determine specific treatment differences. Mean body mass of a species was derived for each stand for each treatment period. Treatment effect on body mass was analyzed by a generalized linear model with treatment and treatment period (pre-treatment vs. post-treatment) as fixed effects (Proc GLM, SAS 1990). If the treatment by year interaction in an ANOVA was statistically significant, contrasts of treatment type vs. control were performed to determine treatment effects. Simpson′s Index of diversity was derived for the pre- and post-treatment periods and compared among coarse-wood treatments with the same methods employed for body mass.

All ANOVA analyses examined the combined effects of clear-cutting and coarse wood treatment. To specifically examine coarse-wood treatment effects, I examined correlations between downed-wood levels and relative capture rates of species on stands receiving CWD treatments. I used the Pearson Correlation statistic (Proc CORR, SAS 1990) to determine relationships between average species′ capture rates for the post-treatment period with total downed wood volume (>7.6 cm diameter), and with downed volume by three size classes (<30-cm diameter, ≥30-cm diameter, and >50-cm diameter). Because understory cover is an important determinant of species′ use of harvested stands (e.g., Garman 2000, Gashwiler 1970), I also examined correlations between capture rates and understory cover (i.e., percent shrub, fern, and herbaceous cover).

RESULTS

A total of 12 species of small mammal, a species of weasel, and six species of herpetiles were recorded over the five years of trapping (Table 2). The Townsend's chipmunk was the most frequently recorded species in the pre-treatment period (33% of the total number of recorded individuals) followed by Trowbridge's shrew (16%) and California red-backed vole (14%). In the post-treatment period, the deer mouse was the most frequently recorded species (36%) followed by Trowbridge's shrew (22%). Capture rates of small-mammal species were generally variable among years within and between treatment periods, and among treatment replicates (Fig. 1). Relative to the two pre-treatment years (1995-96), mean capture rates of the deer mouse and Townsend's chipmunk in the control treatment were noticeably lower in 1999. A similar decline in captures of these species was observed in another small-mammal study conducted in the surrounding area (Garman 2000). Relative to other years, an unusually late spring and dry fall occurred in 1999. These weather conditions either influenced the ability to capture these species or resulted in substantially lower population densities of these species. Relative densities of the California red-backed vole noticeable declined on control stands after 1997. A general decline in this species over the past 4-5 years has been observed in similar studies in the west-central Oregon Cascades (Garman 2000). The only small-mammal species eliminated from treated stands was the northern flying squirrel.

Few captures of herpetiles species were recorded. Ensatina accounted for 63% of recorded herpetile individuals; other species had ≤10 observations (Table 2). The paucity of captures of herpetiles likely reflected the inefficiency of using pitfall traps without drift fences. Also, spring-time sampling is more effective for recording these species due to wetter conditions.

Vegetative Attributes - Post-treatment

Levels of downed-wood were variable among treatment replicates (Table 3). In general, post-treatment downed-wood levels were higher on the high-CWD treatments followed by control then low-CWD stands. However, both volume and mass of larger pieces (>50-cm) were relatively similar among the high-CWD and control treatments. Additionally, there was one high-CWD stand that had substantially less total downed-wood volume than the other two replicates and even less or similar volume than the three low-CWD stands (Fig. 2). Understory cover was generally variable among the coarse-wood treatment replicates; however, percent shrub cover was somewhat inversely related to increasing downed-wood volume (Fig. 2A). Treatment averages for fern and herbaceous cover were similar. Mean shrub cover for the low (62%, 1 se = 9.5) and high (55%, 1 se = 4.0) treatment was similar but lower than for the control treatment (82%, 1 se = 9.0). Incidental removal of understory vegetation occurred during timber-harvest operations. The open-canopy conditions of the treated stands promoted rapid development of understory vegetation which led to similar levels of non-woody understory cover among treatments. The time period between harvest and the post-treatment sampling was too short, however, for shrub cover on the treated stands to reach or exceed control-plots levels.

Table 2. Number of individuals and total captures by species of ground-dwelling vertebrates, Willamette National Forest Long-term Ecosystem Productivity Study. Pre-treatment sampling was conducted Fall 1995 in all blocks and in two blocks in 1996 (cf. Table 1); post-treatment sampling was conducted Fall 1999-00. High coarse-wood treatment was not fully implemented in one block in 1996 and in all blocks in 1997; capture results are listed separately for these blocks. Scientific names of species are listed in Appendix A.

	Pre-treatment		Post-treatment	
Species	No. individuals	No. captures	No. individuals	No. captures
		Mammals		
Coast mole	8	10	20	23
Shrew-mole	0	0	1	1
Fog shrew	99	109	71	85
Trowbridge's shrew	152	154	284	302
California red-backed vole	134	255	24	28
Creeping vole	41	94	99	110
Bushy-tailed wood rat	0	0	1	2
Deer mouse	118	342	460	1417
Townsend's chipmunk	316	1038	248	704
Northern flying squirrel	58	87	43	67
Douglas' squirrel	1	1	0	0
Pacific jumping mouse	9	14	3	3
Short-tailed weasel	2	3	1	1
Total Mammals	938	2107	1255	2743
		Herpetiles		
Dunn's salamander	4	4	0	0
Ensatina	15	15	10	10
Pacific giant salamander	7	7	1	1
Northern alligator lizard	0	0	1	1
Rough-skinned newt	0	0	0	0
Western fence lizard	0	0	1	1
Total Herpetiles	26	26	13	13

Table 2. Cont'd.

Species	1996-97 No. individuals	1996-97 No. captures
Mammals		
Coast mole	16	21
Shrew-mole	0	0
Fog shrew	51	57
Trowbridge's shrew	123	124
California red-backed vole	34	48
Creeping vole	3	3
Bushy-tailed wood rat	1	2
Deer mouse	207	517
Townsend's chipmunk	247	725
Northern flying squirrel	55	81
Douglas' squirrel	1	2
Pacific jumping mouse	20	24
Short-tailed weasel	0	0
Total Mammals	758	1604
Herpetiles		
Dunn's salamander	4	4
Ensatina	9	9
Pacific giant salamander	0	0
Northern alligator lizard	0	0
Rough-skinned newt	2	2
Western fence lizard	0	0
Total Herpetiles	15	15

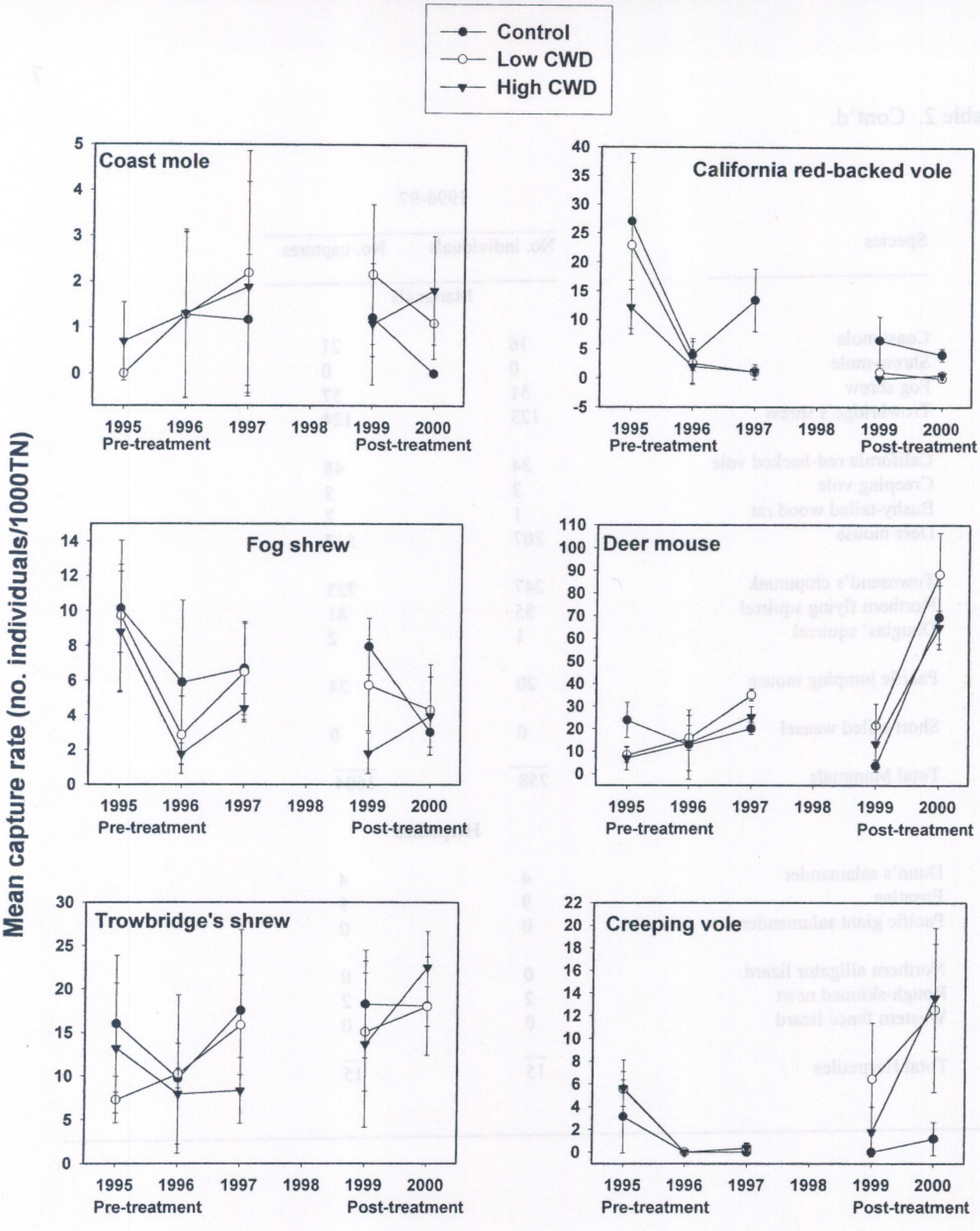


Fig. 1. Mean (1 se) capture rates of ground-dwelling vertebrates, Willamette National Forest Long-term Ecosystem Productivity Study.

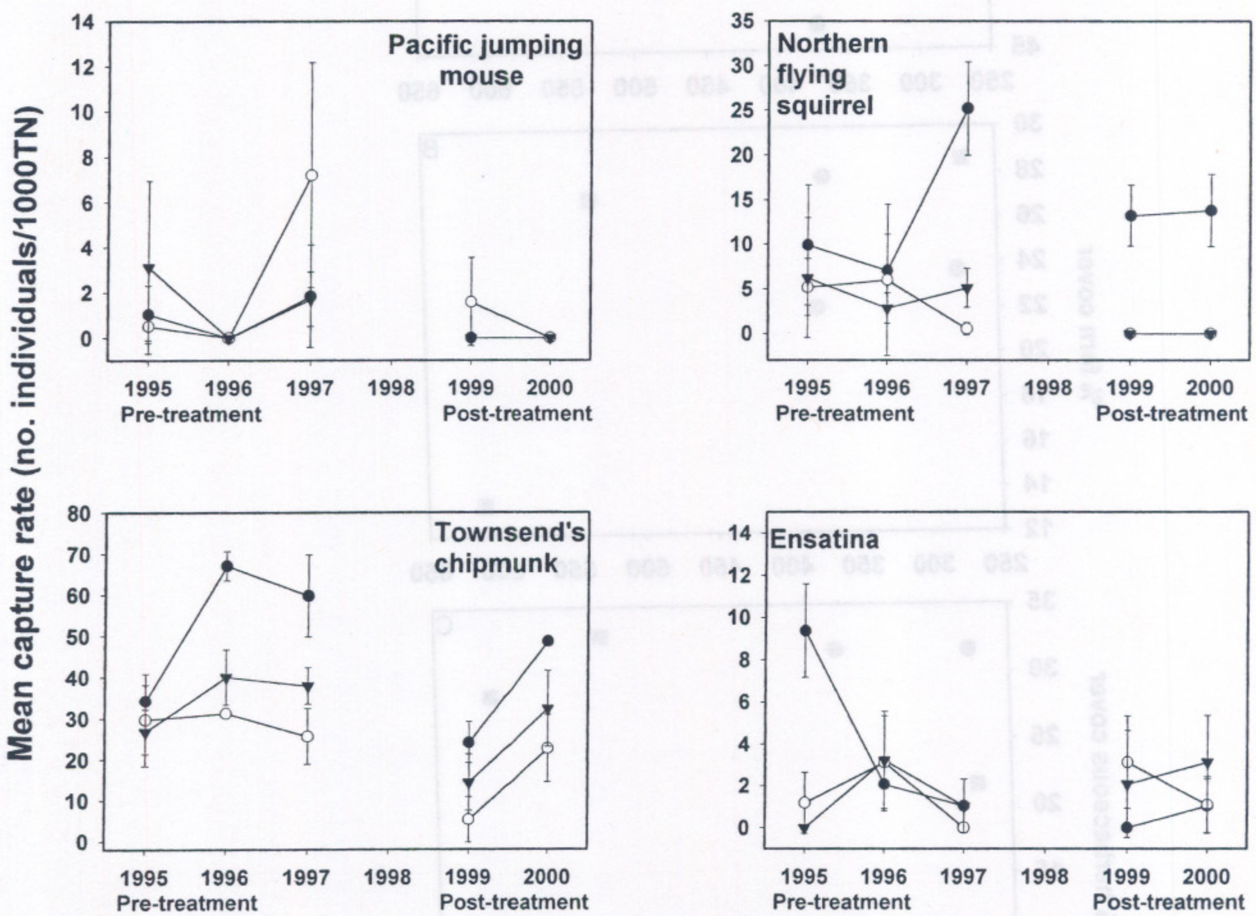

Mean capture rate (no. individuals/1000TN)
Pacific jumping mouse
Northern flying squirrel
Townsend's chipmunk
Ensatina
1995
1996
1997
1998
1999
2000
Pre-treatment
Post-treatment

Fig. 1. Cont'd.

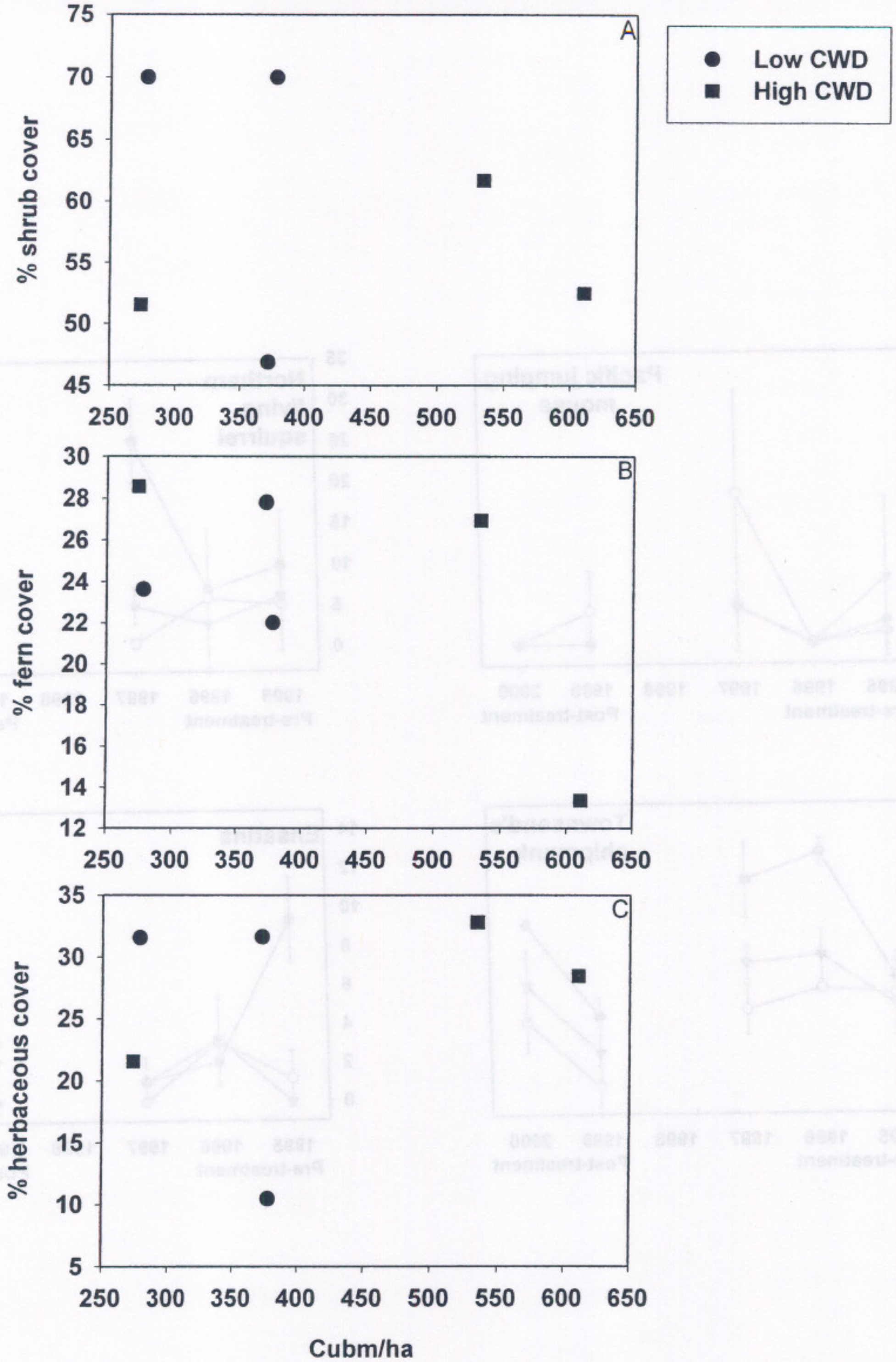


Fig. 2. Relationship between total downed-wood volume (≥7.6-cm diameter) and vegetative attributes after the low and high coarse-wood treatments, Willamette National Forest Long-term Ecosystem Productivity Study.

Table 3. Mean (1 se) volume and mass of downed wood by size class after implementation of woody debris treatments, Willamette National Forest Long-term Ecosystem Productivity Study.

	Size class			
Treatment	Total	<30-cm	≥30-cm	>50-cm
	Volume (m^3/ha)			
Control	362.8 (109.47)	67.6 (22.86)	295.2 (132.32)	223.0 (130.03)
Low CWD	342.4 (39.71)	59.0 (23.39)	283.4 (30.63)	192.9 (18.98)
High CWD	472.8 (125.2)	92.6 (39.34)	380.2 (108.45)	222.1 (64.75)
	Mass (Mg/ha)			
Control	72.8 (16.08)	17.4 (6.98)	55.4 (23.06)	40.0 (25.56)
Low CWD	66.5 (9.95)	16.2 (6.74)	50.2 (3.49)	34.5 (5.41)
High CWD	120.9 (33.29)	27.8 (13.05)	93.1 (28.83)	49.8 (11.64)

Table 4. Results of ANOVA of ranked differences of capture rate of individuals between before and after coarse-woody debris treatments. *P*-values based on $F_{2,6}$. LCWD = low CWD treatment; HCWD = high CWD treatment.

Species	F	*P*-value	Treatment differences
Coast mole	0.76	>0.50	
Fog shrew	0.10	>0.50	
Trowbridge's shrew	0.10	>0.50	
California red-backed vole	0.25	>0.50	
Creeping vole	4.10	<0.10	control < LCWD,HCWD
Deer mouse	2.00	>0.10	
Pacific jumping mouse	0.66	>0.50	
Townsend's chipmunk	1.35	>0.10	
Northern flying squirrel	6.31	<0.05	control > LCWD, HCWD
Ensatina	0.65	>0.50	

Capture Rates

Treatment effects were detected for only two of the 10 species examined (Table 4). The creeping vole exhibited a slightly significant (*P* <0.10) increase in the coarse-wood treatments, although responses were similar between the two treatments. With the removal of all overstory stems, the northern flying squirrel was essentially eliminated from the coarse-wood treatments.

Recapture Rate, Sex Ratio, Body Mass, Species Diversity

Only species with sufficient data were included in analysis of these measures. Recapture rate was analyzed for two species (Table 5), male ratio was examined for three species (Table 6), and body mass was analyzed for five species of small mammals (Table 7). Treatment effect on recapture rate for the deer mouse was slightly significant ($F_{2,6}$; F=3.58; $P<0.10$), with higher but similar recapture rates on the coarse-wood treatments. Also, mean body mass of this species was significantly ($P<0.03$) lower on the low CWD stands after treatment. Treatment effects on percentage of male creeping voles was slightly significant ($F_{2,6}$; F=4.48; $P<0.10$). However, this was due primarily to the lack of captures on the control stands in the post-treatment period (Table 6). Comparing pre- and post-treatment trends using only the low and high CWD stands resulted in no significant treatment effect ($F_{1,4}$; F=2.57; $P>0.10$). Treatment effects on recapture rates, male ratios, and body mass for all other species, and species diversity (Fig. 3) were not significant (*P's* >0.20).

Table 5. Mean (1 se) recapture rate ((no. recaptures/total captures) *100) of two species of small mammals, Willamette National Forest Long-term Ecosystem Productivity Study. Pre-treatment means based on combined data from 1995-96; post-treatment means based on combined data from 1999-00.

	Pre-treatment			Post-treatment		
Species	Control	Low CWD	High CWD	Control	Low CWD	High CWD
Deer mouse	79 (0.9)	40 (29.0)	21 (14.0)	53 (14.7)	68 (5.5)	65 (9.4)
Townsend's chipmunk	47 (17.7)	29 (20.6)	42 (20.9)	52 (9.1)	47 (13.7)	46 (8.1)

Table 6. Mean (1 se) percentage of males ((no. individual males /total no. individuals) *100) of three species of small mammals, Willamette National Forest Long-term Ecosystem Productivity Study. Pre-treatment means based on combined data from 1995-96; post-treatment means based on combined data from 1999-00.

	Pre-treatment			Post-treatment		
Species	Control	Low CWD	High CWD	Control	Low CWD	High CWD
Creeping vole	64 (50.0)	47 (8.6)	38 (11.0)	0 (0)	48 (11.8)	57 (5.2)
Deer mouse	66 (8.4)	31 (10.4)	43 (1.0)	44 (6.2)	48 (1.0)	53 (2.4)
Townsend's chipmunk	61 (4.5)	51 (5.9)	59 (6.9)	60 (6.1)	51 (1.9)	50 (4.6)

Table 7. Average body mass of five species of ground-dwelling vertebrates, by coarse-woody debris treatment, Willamette National Forest Long-term Ecosystem Productivity Study. Pre-treatment means based upon combined data from 1995-96; post-treatment means based upon combined data from 1999-00. x = mean, se = 1 standard error; n = number of individuals.

	Pre-treatment						Post-treatment					
	Control		Low CWD		High CWD		Control		Low CWD		High CWD	
Species	x se	n	x se	n	x se	n	x se	n	x se	n	x se	n
Fog shrew	6.3 (0.19)	29	6.2 (0.21)	27	6.2 (0.22)	27	6.5 (0.16)	27	7.1 (0.26)	26	6.6 (0.21)	16
Trowbridge's shrew	4.4 (0.25)	48	4.4 (0.12)	25	4.4 (.032)	34	4.3 (0.06)	87	4.3 (0.07)	87	4.3 (0.07)	92
Creeping vole	14.1 (0.76)	9	15.2 (0.55)	15	14.4 (0.61)	16	12.0 (4.30)	3	14.8 (0.51)	54	15.1 (0.65)	42
Deer mouse	14.8 (0.32)	57	16.6 (0.70)	33	15.6 (0.69)	26	14.7 (0.31)	102	14.3 (0.27)	209	14.4 (0.28)	151
Townsend's chipmunk	85.1 (0.93)	63	83.7 (1.07)	31	81.5 (1.17)	40	81.3 (0.61)	111	80.2 (0.87)	51	79.6 (0.66)	85

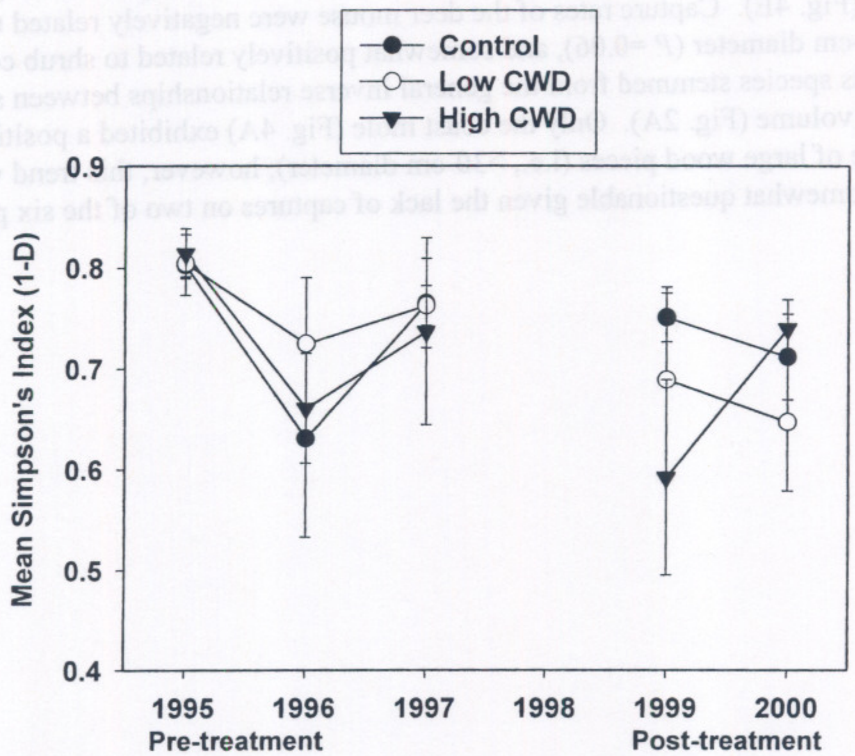


Fig. 3. Mean (1 se) Simpson's Diversity Index for small-mammal species, Willamette National Forest Long-term Ecosystem Productivity Study.

Capture Rate Correlations

Capture rates of most species tended to be more related with understory cover measures than with downed wood volume (Fig. 4). Significant correlations (*P's* <0.10) between capture rates and understory cover were evident for the coast mole (Fig. 4A), Trowbridge's shrew (Fig. 4C), and creeping vole (Fig. 4E). Capture rates of the deer mouse were negatively related to downed wood volume <30-cm diameter (*P* =0.06), and somewhat positively related to shrub cover (Fig. 4F). Trends for this species stemmed from the general inverse relationships between shrub cover and downed-wood volume (Fig. 2A). Only the coast mole (Fig. 4A) exhibited a positive response to volume of large wood pieces (i.e., >30-cm diameter); however, this trend was not significant and is somewhat questionable given the lack of captures on two of the six post-treatment stands.

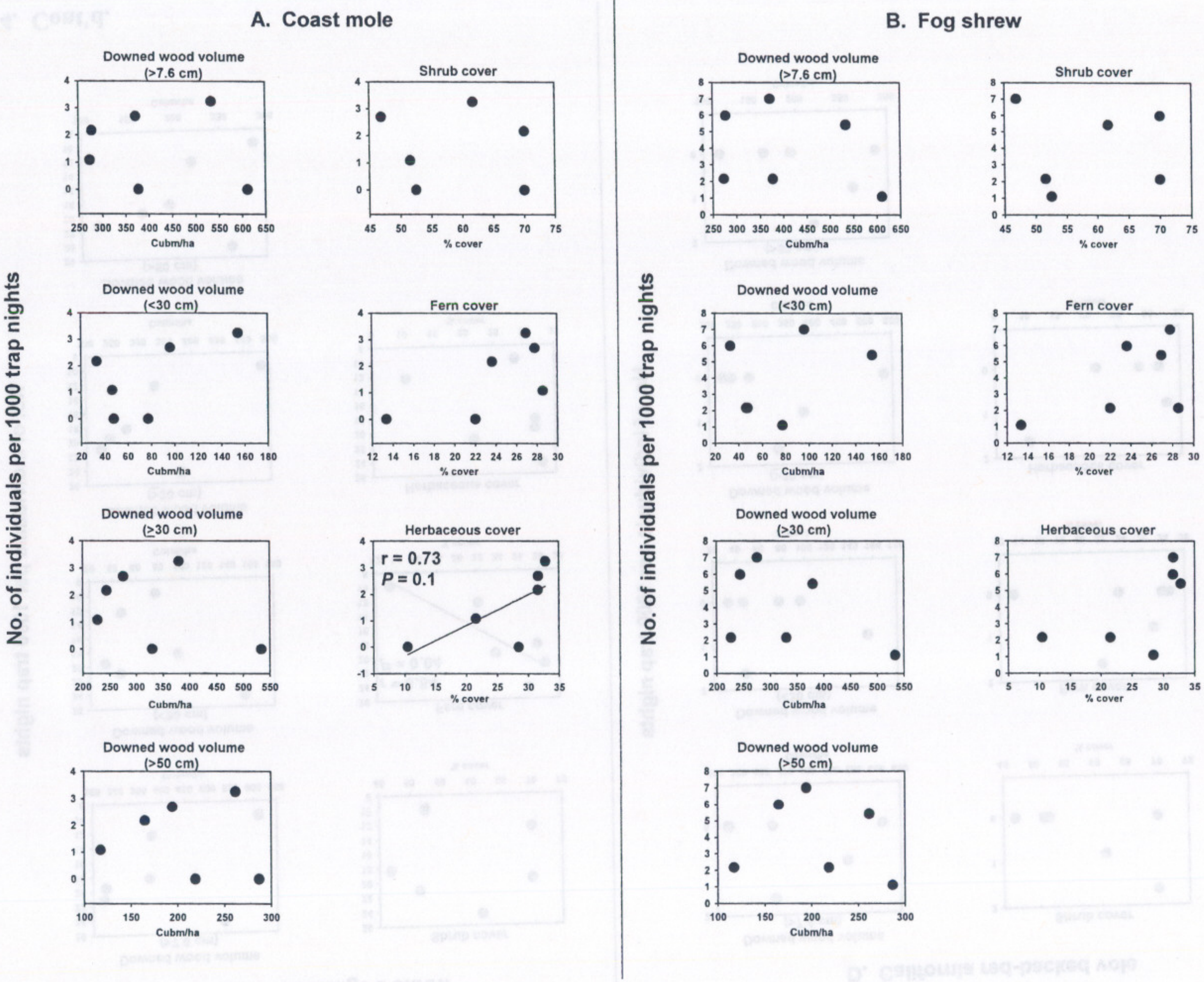


Fig. 4. Correlations between species' capture rates and measures of dead-wood and understory cover on low and high woody-debris stands. Only significant correlations are indicated.

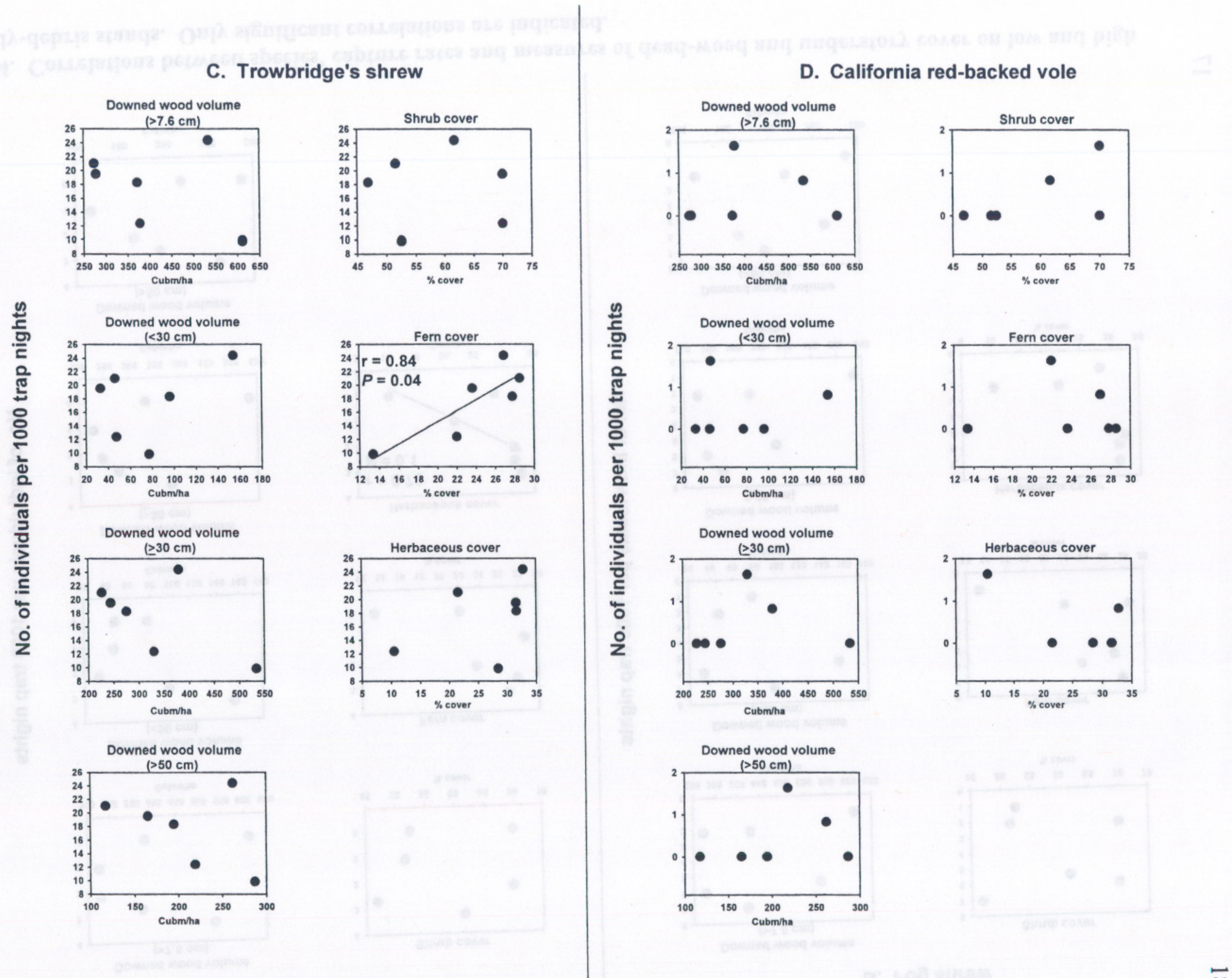

C. Trowbridge's shrew
D. California red-backed vole
No. of individuals per 1000 trap nights
Downed wood volume (>7.6 cm)
Downed wood volume (<30 cm)
Downed wood volume (≥30 cm)
Downed wood volume (>50 cm)
Shrub cover
Fern cover
Herbaceous cover
r = 0.84
P = 0.04
Cubm/ha
% cover

Fig. 4. Cont'd.

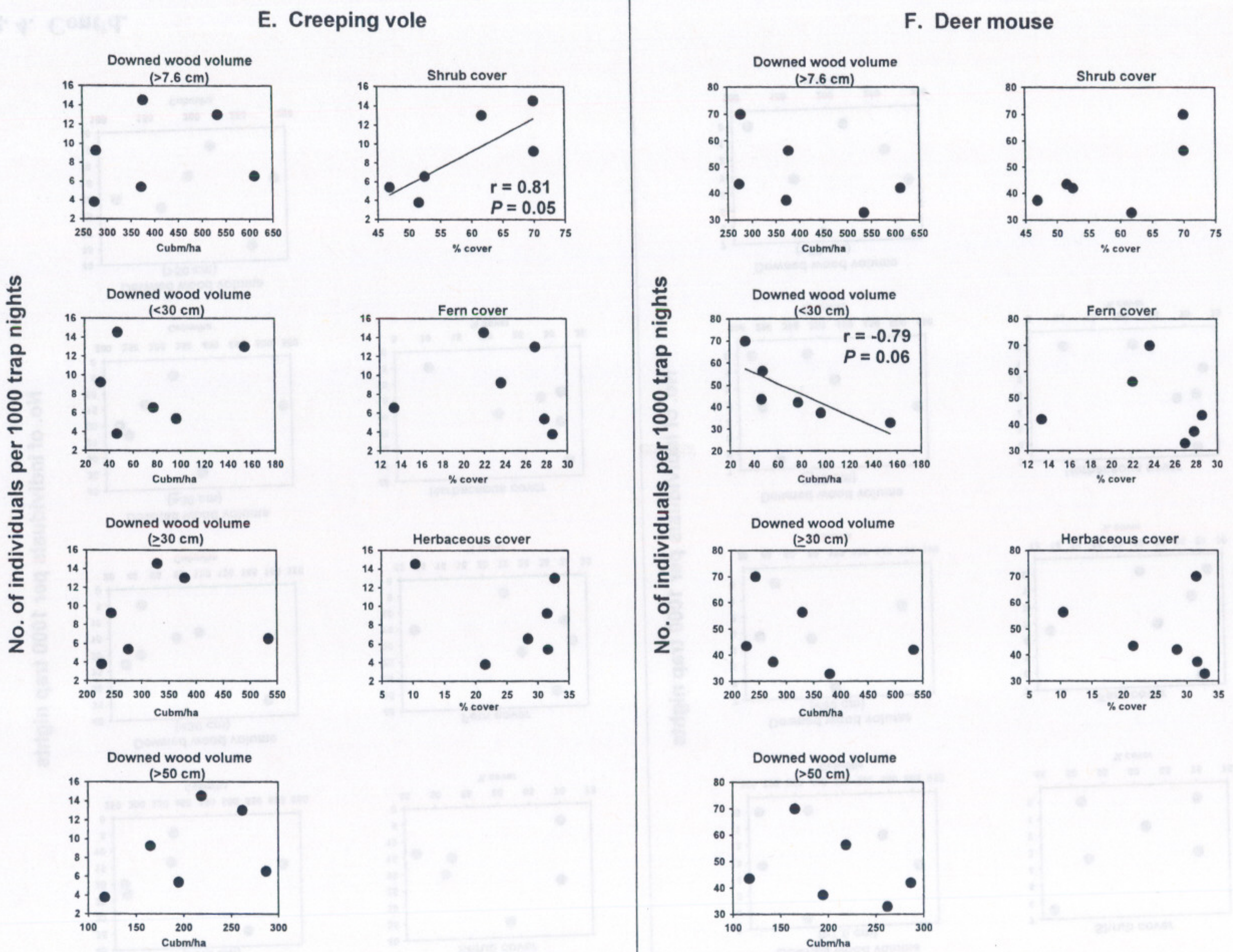
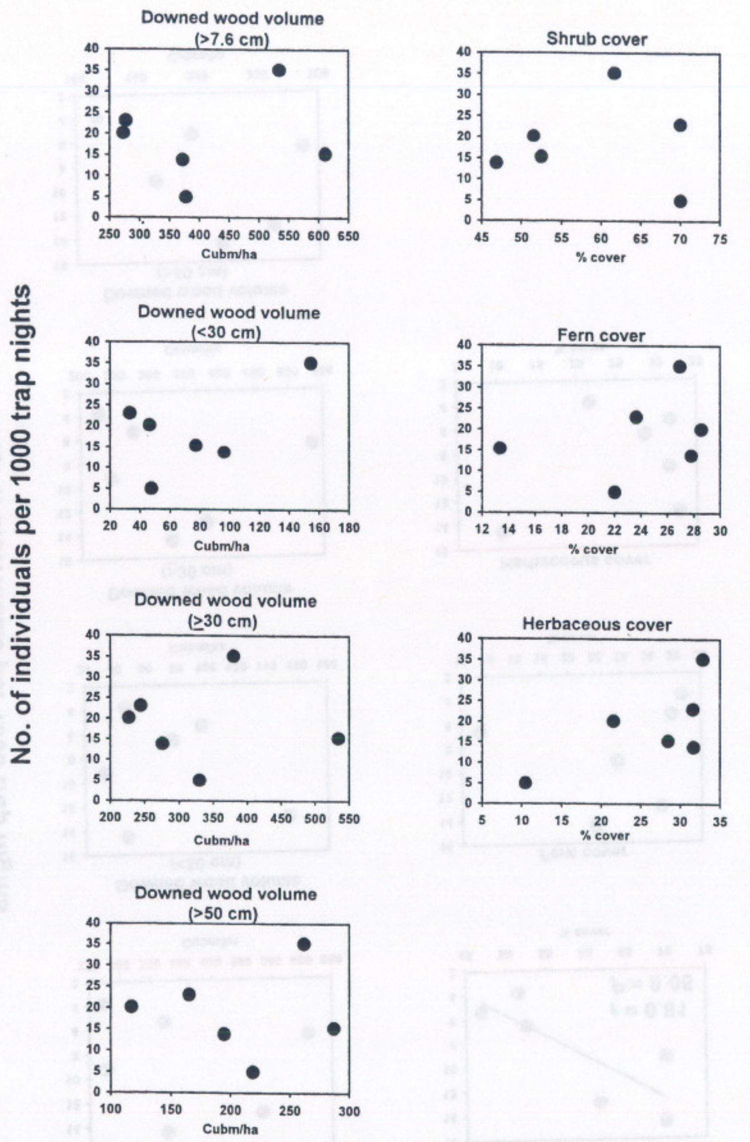

E. Creeping vole
F. Deer mouse
No. of individuals per 1000 trap nights
Downed wood volume (>7.6 cm)
Shrub cover
r = 0.81
P = 0.05
Downed wood volume (<30 cm)
Fern cover
r = -0.79
P = 0.06
Downed wood volume (≥30 cm)
Herbaceous cover
Downed wood volume (>50 cm)
Cubm/ha
% cover

Fig. 4. Cont'd.

G. Townsend's chipmunk



H. Ensatina

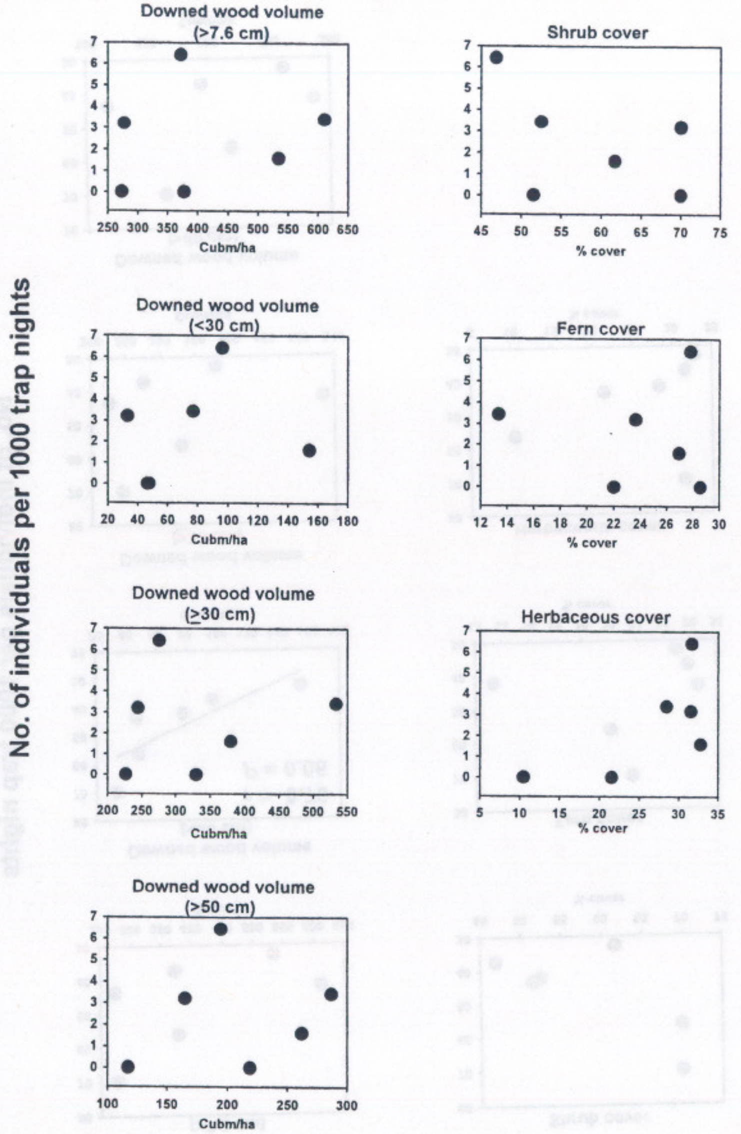


Fig. 4. Cont'd.

DISCUSSION

Clear-cutting with varying woody-debris treatments had little influence on population attributes of ground-dwelling vertebrates. Of the 10 species examined, only the creeping vole and northern flying squirrel exhibited a significant treatment response. The creeping vole prefers grass-forb areas and has been found to be common in clearcuts after the re-establishment of ground cover (Hooven 1973, Corn and Bury 1981, Sullivan and Boateng 1996). This species likely responded to changes in understory cover given that it did not exhibit a clear relationship with downed-wood levels. Removal of overstory stems essentially eliminated critical nesting and resting features of the arboreal northern flying squirrel; the loss of this species from treated sites was unrelated to downed-wood retention levels.

The paucity of treatment effects was surprising given the dramatic floristic changes on treated stands. Most species were expected, at least, to respond to the removal of overstory stems. The shrew species recorded in this study are denizens of mid to late-seral coniferous forests in the Pacific Northwest (Whitaker and Maser 1976; Brown 1985). These species are commonly associated with decaying litter and shrub cover (Hooven and Black 1976) and downed logs (Garman 2000), and negatively associated with low canopy cover (Garman 2000). The Townsend's chipmunk occurs in various habitat types but is generally associated with diverse understory and high levels of residual woody debris (Doyle 1990, Rosenberg and Anthony 1993, Carey 1995). Population densities of these species were expected to decrease on the low woody-debris treatment due to the loss of overstory cover, and possibly to increase on the high woody-debris treatment due to downed-wood enhancement. Although the deer mouse is a habitat generalist, population densities tend to be higher on harvested stands after the development of ground cover (Gashwiler 1970, Hooven 1973, Sullivan 1979, Galindo and Krebs 1985, Garman 2000). Densities of this species were expected to substantially increase on treated stands. Although mean recapture rates and body mass of the deer mouse differed among treatments, the collective assessments of population attributes did not strongly suggest differential habitat quality. Relative to species with comparable capture rates, the deer mouse responded the least to woody-debris treatments.

A relatively broad gradient of downed-woody debris levels was examined, but at most only one species (coast mole) exhibited a numerical increase to increasing levels (Fig. 4A). However, given the limited number of captures of this species, the strength of this relationship is questionable. In this study, understory cover tended to be a stronger determinant of habitat use by ground-dwelling vertebrates. Numerical increases in three species (coast mole, Trowbridge's shrew, and creeping vole) were significantly correlated to shrub, fern, or herbaceous cover. Additionally, deer-mouse densities were weakly correlated with shrub cover. The importance of understory cover to population densities partially explains the general lack of detectable treatment effects. At the time of the post-treatment sampling, understory cover on treated stands was essentially similar to pre-treatment and control conditions. Similar levels of this important habitat attribute effectively lead to similar densities of species between treatment periods. Higher levels of woody-debris presumably would increase ground cover and thus increase habitat quality. However, there was an inverse relationship between total downed-woody debris levels and shrub (and fern) cover (Fig. 2), even though woody-debris levels were not that extensive. This trend essentially limited the ability to separate out the effects of woody debris levels and understory cover.

The lack of relationships between downed-woody debris levels and habitat quality for ground-dwelling vertebrates is unusual. Numerous studies have noted the importance of this feature to many small-mammal and amphibian species inhabiting Douglas-fir stands in western Oregon (Hooven and Black 1976, Garman 2000). However, understory development in some of these studies (e.g., Garman 2000) was not as extensive as in this study. Results of this study suggest that on sites prone to rapid development of shrub and herbaceous ground cover after harvesting, woody-debris levels may only play a limited role in maintaining population densities of smaller vertebrates, at least 2-3 yrs after harvesting. Results should not be interpreted to mean that retention of downed wood is not important, even on sites with rapid understory development. Woody and herbaceous ground cover will decline as the canopy develops. Over time, residual downed-wood levels can become the primary ground cover component until canopy openings form.

MANAGEMENT RECOMMENDATIONS

Goals of this study were to evaluate treatment effects of experimental woody-debris levels on ground-dwelling vertebrates, and to identify the retention levels of woody debris sufficient to maintain pre-harvest population densities of species. The clear-cut harvests in this study negatively impacted only one species, the northern flying squirrel. Based on the sampling and analytical methods employed in this study, the nine other species with sufficient data for analysis lacked a measurable response to the experimental levels of woody-debris. Instead, ground cover (shrub, fern, and herbaceous species) was an important determinant of habitat quality for four of the nine species. These results suggest that on sites prone to rapid development of shrub and herbaceous ground cover after harvesting, woody-debris levels may only play a limited role in maintaining population densities of smaller vertebrates, at least 3-4 yrs after clear-cut harvest. An unanswered question is the role of woody-debris retention over longer time frames. Woody and herbaceous ground cover will decline with canopy development. Thus, residual woody debris will increase in importance as ground cover, at least until canopy openings form or shade-tolerant understory species become establish.

Based on the results of this study, explicit recommendations can not be made regarding retention levels of woody-debris sufficient to maintain pre-harvest densities of ground-dwelling vertebrate populations over the short or long term. Given the potential long-term importance of downed wood to forest-floor species, however, woody debris should be retained at harvest. Studies examining relationships between animal species and attributes of young stands can provide estimates of debris-retention needs for clear-cut harvests. For instance, strong relationships between coarse-wood levels and shrew and chipmunk densities have been found in the Young Stand Thinning and Diversity Study (Garman 2000). Based on results of that study, 218-231 m^3/ha of downed logs >60-cm diameter were associated with densities of shrews and chipmunks comparable to those of the control stands in this study. Similar to slightly greater coarse-wood retention levels in clear-cut stands may be adequate for long-term maintenance of pre-disturbed population levels of forest-floor species dependent on ground cover. Regardless of woody-debris retention levels, monitoring of population levels should be conducted to evaluate long-term effectiveness.

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Appendix A. Common and latin names of ground-dwelling vertebrate species recorded in the Willamette National Forest Long-term Ecosystem Productivity Study.

Bushy-tailed wood rat	*Neotoma cinerea*
California red-backed vole	*Clethrionomys californicus*
Coast mole	*Scapanus orarius*
Creeping vole	*Microtus oregoni*
Deer mouse	*Peromyscus maniculatus*
Douglas' squirrel	*Tamiasciurus douglasii*
Dunn's salamander	*Plethodon dunni*
Ensatina	*Ensatina eschscholtzii*
Ermine (short-tailed weasel)	*Mustela erminea*
Fog shrew	*Sorex sonomae*
Northern alligator lizard	*Elgaria coerulea*
Northern flying squirrel	*Glaucomys sabrinus*
Pacific giant salamander	*Dicamptodon tenebrosus*
Pacific jumping mouse	*Zapus trinotatus*
Rough-skinned newt	*Taricha granulosa*
Shrew-mole	*Neurotrichus gibbsii*
Townsend's chipmunk	*Tamias townsendii*
Trowbridge's shrew	*Sorex trowbridgii*
Western fence lizard	*Sceloporus occidentalis*