2002

Vole use of coarse woody debris and its implications for habitat and fuel management

Dalit Ucitel
The University of Montana

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Vole use of coarse woody debris and its implications for habitat and fuel management

Dalit Ucitel
B.S., Tel-Aviv University, 1999

Presented in partial fulfillment of the requirements for the degree of
Master of Science
The University of Montana 2002

Approved by:

[Signatures]

Chairman, Board of Examiners
Dean, Graduate School

Date 2-19-02
Vole use of coarse woody debris and its implications for habitat and fuel management

Director: Dr. Donald P. Christian

Woody debris is an increasing ecological and management focus in forests, representing multiple and sometimes conflicting values. Fuel management may prioritize removal of coarse woody debris (CWD) within to minimize wild fire occurrence, intensity, or both, whereas management for wildlife habitat or other ecological values often focuses on retention of CWD. Few quantitative guidelines are currently available for accepted coarse woody debris levels. Due to different standard methodologies and metrics, studies involving CWD from different research fields have not been comparable. In this study, we (1) model and quantify CWD use by a habitat specialist, the red-backed vole (*Clethrionomys gapperi*), (2) test if voles are captured and move in portions of forest stands with greater CWD, and (3) correlate stand level measures of CWD as habitat to fuel loads, providing a basis of comparison for CWD quantitative guidelines. Voles used CWD at a greater rate than expected based on CWD availability and moved in portions of stands with greater CWD coverage. This suggests that CWD is an important habitat component that needs to be available on the forest floor, well distributed throughout the stand. The strong correlation between stand-measure CWD coverage and fuel load measure ($r = +0.96$) provides a basis for comparing CWD guidelines. Based on our work, the few guidelines currently available from different research fields are in clear disagreement. None of our stands reached the level of CWD coverage suggested for small mammal habitat requirements and only two of the five stands we sampled fit with guidelines for fuel management and ectomycorrhizae.
ACKNOWLEDGMENTS

This study would not have occurred without the help and support of the Condon community, especially Tom and Melanie Parker, and the Swan Ecosystem center. Special thanks goes to my valuable field assistants: Sue Ibsen, Tova Woyciechowicz, Heather Davis, Erin Bohman, and my ever surprising parents, Hanna & Leon Ucitel who spent long hours in the field with a positive attitude.

I want to thank my main advisor, Don Christian, for his willingness to provide ample support and advise, especially with writing, my committee members, Scott Mills, John Goodburn, Erick Greene and especially Jon Graham for hours of statistical advising and his ability to explain complex statistical concepts; Dean Pearson from the Forest Service RMRS for stimulating discussions; Duncan Lutes from the Forest Service Fire Lab for his infinite patience dealing with my stubbornness, and Claire Emery for the wonderful drawing of the red-backed vole.

Lastly, I want to thank my family and friends back in Israel for great ‘long-distance’ support and care, and friends in Missoula, that made my time here so enjoyable and productive.

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Animal use and care in this study conformed to all applicable standards and guidelines, and was conducted under protocol ACC 033-00 approved by the University of Montana Institutional Animal Care and Use Committee.
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INTRODUCTION

Woody debris is an increasing ecological and management focus in forests, representing multiple and sometimes conflicting values. Fuel management may prioritize removal of coarse woody debris (CWD) within a stand to minimize wild fire occurrence, intensity, or both (Fire and Aviation Management 2000), whereas management for wildlife habitat or other ecological values often focuses on retention of CWD. Growing concern about increased fire danger stems from a build-up of fuel in stands with historically frequent wildfires, but in which fire has been suppressed throughout much of the 20th century (Graham et al. 1994; Fire and Aviation Management 2000).

Fuels are classified by their physical properties, which affect the fire behavior and resultant fire-danger rating (Bradshaw et al. 1983). CWD is only one of several components of forest fuel, and is regularly referred to as the “1000-hour timelag fuel” referring to the mean response time to changes in the surrounding atmospheric moisture (Anderson 1982; Lancaster 1970). Although substantial research has been done on fire behavior and effects, few quantitative guidelines concerning acceptable fuel load and fuel management are available. Acceptable fuel loads are those ranging within the natural historic variation but are difficult to generalize on a large landscape because they are affected by many site-specific factors such as site productivity and disturbance history (D. Lutes, personal communication). Furthermore, fuel management depends primarily on the management objectives of forest stands and their proximity to human structures or dwellings.

Concerns about elevated fuel loads have increased, especially after widespread, high-intensity fires swept through the interior western United States during the summer.
of 2000 (Fire and Aviation Management 2000). These fires followed several consecutive years of drought, and were of special concern due to increased human development and a rapidly growing wildland-urban interface. As a result, there has been increased political pressure and renewed agency initiative to provide a strategic plan to reduce wildland fire risk and restore ecosystem health in these areas (Fire and Aviation Management 2000). One element of the proposed management plan is to lower fuel load from present levels to reduce high-intensity fire damage, and to ensure public and firefighter safety (Fire and Aviation Management 2000).

Beyond representing a fuel that is of concern to fire managers, CWD plays diverse, important roles in forest systems. It provides habitat for many ground-dwelling wildlife species, including small mammals (Butts and McComb 2000; Maser et al. 1979; Maser and Trappe 1984; McCay 2000; Pearson 1999), mammalian predators (Buskirk et al. 1989; Koehler and Aubry 1994; Maser et al. 1979), amphibians (Butts and McComb 2000; Hecnar and McCloskey 1998; Herbeck and Larsen 1999; Maser et al. 1979) and a wide variety of invertebrates (Harmon et al. 1986; Maser and Trappe 1984). CWD contributes important structure that influences not only single species but interactions among species as well (Corn and Raphael 1992; Sherburne and Bissonette 1994). CWD protects the forest floor from erosion and wind, and provides shade (Harmon et al. 1986). It is also known to serve as a potential microsite for establishment of new conifers (Harmon et al. 1986; Freedman et al. 1996; Maser et al. 1979). Decomposing CWD releases nutrients and provides an excellent substrate for nitrogen fixation processes (Jurgensen et al. 1991), with subsequent increases in resources that may limit plant growth (Harmon et al. 1986; Maser 1988). Decomposing CWD is also a primary
substrate for development of ectomycorrhizae known to be essential in forest ecosystems (Harvey et al. 1976; Harvey et al. 1981).

In contrast to current trends in fire management, management for wildlife habitat focuses on retention of CWD. There is concern that management guidelines, even apart from recent pressures to reduce fuel loads, result in inadequate CWD coverage to fulfill such roles (Butts and McComb 2000). Few data are available to address the possible conflicts in CWD management. This study was designed as an integrated analysis of (1) CWD as habitat for an animal species known to be closely associated with CWD across an array of forest types and conditions and (2) CWD as fuel, to provide a basis for biologically relevant approaches to assessing management tradeoffs between fuel and habitat values of CWD.

The southern red-backed vole, *Clethrionomys gapperi*, is widely distributed across much of northern North America, including boreal, sub-boreal, and montane areas in the United States (Wilson and Ruff 1999). Ecologists have been interested in understanding factors that determine habitat suitability for this rodent, in part because of the key roles that it is thought to play in forest ecosystems. These include extensive mycophagy and distribution of mycorrhizal fungal spores (Maser et al. 1978; Maser and Maser 1988; Pastor et al. 1996; Ure and Maser 1982), and the important role of voles in herbivore-based forest trophic interactions (Buskirk and Ruggiero 1994; Hayward 1994; Hayward et al. 1993). In addition, temporal shifts and spatial differences in abundance and distribution of *Clethrionomys* sp. have been interpreted in the context of forest ecology and management, including timber harvest, retention of woody debris, and forest

The red-backed vole inhabits chiefly mesic habitats in coniferous, deciduous, and mixed forests with abundant litter of stumps, rotting logs, and exposed roots and dense vegetative cover (Merritt 1981). This association with coarse woody debris has been widely described in the literature. Most stand-level studies report a positive correlation between red-backed vole presence and the abundance of CWD in mature or old-growth stands (Tevis 1956; Carey and Johnson 1995; Keinath 2000; Pearson 1994; Scrivner and Smith 1984; Martell 1983a, b). Voles in clearcuts or managed stands are found most often in association with residual CWD (Carey and Harrington 2001; Carey and Johnson 1995; Tevis 1956).

Studies at the within-stand (microhabitat) level have more directly demonstrated a relationship of *Clethrionomys* sp. to CWD (Belk et al. 1988; Hayes and Cross 1987; Keinath 2000; Pearson 1994; Tallmon and Mills 1994). Trapping success of red-backed voles is often higher in sites with greater CWD (Belk et al. 1988; Pearson 1994; Keinath 2000). However, trapping provides at best a “snapshot” of an animal’s movement and use of habitat. Because traps are baited, animals might be drawn to a novel location, which could be significant when trying to establish use patterns at a fine microhabitat scale. Second, a capture indicates that the animal is present in the nearby surroundings, but it does not allow inference on intensity or frequency of use of different habitat components. By contrast, the fluorescent powder tracking technique used in this study (Lemen and Freeman 1985; see also Stapp et al. 1994) is useful for assessing and quantifying fine-scale movement pathways and their association with habitat components.
Because red-backed voles are widespread forest dwellers closely linked to CWD, they provide a useful model for studying CWD as a habitat variable and for assessing possible biological tradeoffs between CWD as habitat and as fuel. The purpose of this study was to use trapping and fluorescent powder tracking to (1) test and quantify the association of voles with CWD at a scale of individual movement pathways; (2) test if voles move more extensively and are captured more often in portions of stands where CWD is more abundant; and (3) determine the quantitative relationship between CWD measured as fire fuel (using standard protocols) and as a habitat variable.

Preliminary studies in Minnesota (D. Christian, unpublished) and Montana (D. Ucitel, unpublished) showed that specific vole movement pathways are closely linked to fallen logs. This is probably the finest spatial scale at which we might expect this relationship. Voles are primary prey for a variety of forest predators; movement along CWD likely provides cover and protection from predators. Therefore the association of voles to CWD at this scale should be apparent. We predicted that voles would (1) incorporate CWD at a higher proportion into their movement path than expected on the basis of CWD availability in the area in which they move, and (2) move and be captured in portions of the stands with greater CWD coverage. Quantifying CWD needs for wildlife habitat and translating it into metrics used by fire researchers and managers is critical to managing CWD removal while incorporating broader ecological values.

STUDY AREA

This study was conducted during May-August 2001 in the Seeley-Swan valley, Missoula County, MT, USA. Five mature coniferous forest stands (1100 -1400 m elevation; USDA Forest Service land) were identified to represent the wide range of
stand characteristics and types in the Seeley-Swan valley (Fig. 1). All had been
unmanaged for at least 26 years except for private firewood gathering (T. Parker,
personal communication). We were unable to document the detailed management
histories of these stands, but the presence of large-diameter trees and the general absence
of stumps suggest that the stands were never commercially logged.

The stand at Beaver creek (hereafter BV; T19N R16W sec. 18) was pure
lodgepole pine (*Pinus contorta*). Western larch (*Larix occidentalis*) and lodgepole pine
were the dominant canopy tree species at Swamp stand (SW; T21N R17W sec. 16). At
Holland stand (HO; T20N R16W sec. 35), western larch, Douglas-fir (*Pseudotsuga
menziesii*), and Engelmann spruce (*Picea engelmannii*) were the predominant canopy tree
species. Barber and Teepee stands (BB; T20N R16W sec. 23, and TP; T21N R17W sec.
10 respectively) had a rich variety of canopy tree species including western larch,
Douglas-fir, Engelmann spruce, grand fir (*Abies grandis*), western red cedar (*Thuja
plicata*) and lodgepole pine. Habitat types (Pfister 1977) varied from dry *Abies
lasiocarpa* / *Xerophyllum tenax* habitat type for BV to moist warm habitat types like
*Abies lasiocarpa* / *Clintonia uniflora* for HO, *Abies grandis* / *Clintonia uniflora* for BB,
and *Thuja plicata* / *Clintonia uniflora* for both SW and TP (Habitat type stand layer,
USDA Forest Service Flathead National Forest, Seeley Lake Ranger District,
unpublished). Based on these habitat types, BV is considered a relatively lower timber
productivity stand while all other stands are classified as moderate to very high timber
productivity sites (Pfister 1977).
Fig. 1. Map of the Seeley-Swan valley in Western Montana with the location of the five stands sampled during summer 2001.
METHODS

Field methods

We established a live-trapping grid of 100 trap locations in all stands but TP (80 trap locations). Trap stations (2 folding Sherman traps/station) were placed at 15-m intervals along a systematic random sample of transects, with 20 m between adjacent transects. The number of transects (4-8) and consequently the number of trap locations per transect varied with stand configuration. We trapped for two 2-day sessions, 4-7 days apart, for a total of 4 trapping days/stand. Traps were baited with a mix of sunflower seeds and whole oats, and bedding was provided for insulation. We opened traps in the evening and checked them the following morning. Red-backed voles were sexed, weighed, marked, and held in individual cages away from the site until released. Voles were covered with fluorescent powder (Radiant Color®, Magruder Color Company, Inc.) and released at the point of capture on the evening of the second trapping day. We left the area immediately after release to minimize our disturbance. In each stand we recorded 21-27 trails distributed across the grid, each produced by a different individual vole. On the following night, trails were illuminated using a blacklight and flagged at intervals sufficient to identify changes in movement direction at a fine scale. A distance of 19 - 28 m was flagged on each trail. The first 2 m of trail were excluded from the analysis to minimize incorporating data affected by our presence and handling of the animal.

We included in the analysis all fallen logs >7.5 cm in diameter, consistent with previous research on CWD as fuel and within the broad range of diameters (2.5 - 15.0 cm) used by researchers and managers to define minimum size of CWD (Lofroth 1998). Vole trails were considered to be associated with CWD if they were ≤5 cm away from a
log. A sampling plot (hereafter “movement plot”) was established as the minimum-bounding rectangle for the trail. Length, diameter, and decay class (based on the system of Maser et al. 1979) were measured for all CWD within the plot.

We also measured CWD in a 5m-radius plot centered on a trap location. The plot size was based on the average area of 27 movement plots of red-backed voles sampled during summer 2000 at the same area (Ucitel, unpublished). Data were collected at all trap sites where voles were captured (“capture plot”) and approximately the same number of trap locations where voles were not caught (“non-capture plot”). Non-capture plots were chosen at random to equate the sample sizes of capture and non-capture plots by transects. CWD was measured as described above. We used these data to characterize stand-level area coverage of CWD as well as to compare CWD coverage for capture plots and non-capture plots.

Fuel load was measured at all capture plots and at all non-capture plots where area coverage of CWD was measured. Volume and biomass of CWD were measured using the USDA Forest Service protocol for large-diameter log fuels inventory (Brown 1974; Van Wagner 1968). We positioned two 20-m transects perpendicular to each other, centered at a trap site, with one of the two transects running with the topographical slope. We recorded diameter and decay class for each log intersected by the transects. These data were used to calculate a stand measure for fuel volume and biomass. Because fuel load is typically expressed and managed at a stand-level measure, we did not compare CWD as habitat and as fuel on a point-by-point basis. All calculations were converted to the metric system. Volume (V; m³/m², subsequently converted to m³/ha) was calculated using the following standard equation:
\[ V = \pi^2 \sum_{i=1}^{n} d_i^2 c/8L \]

where \( d \) = diameter of intercepted CWD (m); \( c \) = slope correction factor for the sampling plane \( = \sqrt{1+\left(\frac{\%\text{slope}}{100}\right)^2} \); Brown 1974; \( L \) = length of transect (m). Biomass (kg/m\(^2\)) was estimated as the product of volume (m\(^3\)/m\(^2\)) and wood density (400 kg/m\(^3\) and 300 kg/m\(^3\) for sound and decayed logs respectively [Brown and See 1981]).

**Data analysis**

To address vole microhabitat use of CWD, we established a model (Fig. 2) comparing vole use of CWD to the availability of CWD in movement plots. Using the length of the trail and the sum of all segments of the trail associated with CWD, we defined CWD use as the proportion of the trail associated with CWD. CWD availability was defined as the proportion of the movement plot area covered by CWD using the length and diameter of each log to provide an area measure. For both trails and movement plots, the scale extends from 0 to 1 (0 = no CWD in plot or included on trail; 1.0 = entire area of plot covered by CWD or entire trail associated with CWD). The slope of the regression of use on availability for all trails within a stand provides a stand-specific measure of CWD use as a function of availability (Fig. 2). If use increases at the same rate as availability, the slope of the regression line would be 1.0 (Fig. 2). Any line with a slope < 1.0 would represent avoidance (where the rate of increase in use is less than the rate of increase in availability) and any line with a slope > 1.0 would describe a greater increase in use than the increase in availability (Fig. 2).

All regressions were forced through the origin since CWD use is necessarily zero when CWD availability is zero. We fit the line that best describes the data. This included
Fig. 2. Coarse woody debris (CWD) use as a function of CWD availability. CWD use is defined as the proportion of the total trail length associated with CWD. CWD availability is the proportion of the available area covered by CWD. The dashed line represents the slope of one, describing a constant and equal rate of increase in use and in availability. The line with the slope < 1.0 describes a rate of increase in CWD use that is less than the rate of increase CWD availability, suggesting avoidance of CWD. The line with slope > 1 describes a greater rate of increase in use of CWD than in availability.
least-squares regression for 3 of the five stands (BB, HO, and SW), and least absolute deviations (LAD) regression for BV and TP due to severe influential data points. LAD is robust to outliers by finding the regression line that minimizes the sum of absolute residuals (Bloomfield and Steiger 1983). This is in contrast to least squares regression, which finds the line that minimizes the sum of squared residuals. We decided to remove the two influential points in BV and TP because the linear relationship between CWD use and availability did not extend beyond availabilities of about 20% for these two stands (see Fig. 3). The removal of these influential points allowed us to use least-squares regression for each of the five stands to infer CWD use. Non-homogeneity of variance could not be rectified by data transformation; as a result, we bootstrapped standard errors for all regressions. A t-test was used to test whether the slope of CWD use against CWD availability was significantly $> 1.0$, the expected slope if voles respond to increased CWD availability with direct proportionality in CWD use. A t-test was also used for pairwise comparisons of the differences in slope between all possible pairs of stands, to test whether the CWD use rate by red-backed voles is constant across stands. Weighted least-squares linear regression was used to assess the relationship between CWD area coverage and CWD volume. Data values were weighted by the inverse variance of the stand-measure CWD coverage to take into consideration the variation associated with each stand-measure CWD coverage and different sample sizes. SPSS version 10.0.7 (SPSS, Inc. 1999) was used to perform all least-squares regression analyses. All other analyses were performed using S-plus 2000 (MathSoft, Inc. 1999).

Several analyses were performed using non-parametric analysis of variance (ANOVA) because underlying assumptions of analysis of variance were not met. We
Fig. 3. Coarse woody debris (CWD; > 7.5 cm in diameter) use by red-backed voles in western Montana as a function of CWD availability in movement plots. Dotted lines in Beaver and Teepee represent least absolute deviation regression, which provides best fit with all data points incorporated. Solid lines represent least-squares regressions used to draw inferences. Each point represents an individual trail produced by a vole. CWD use is the proportion of trail length associated with CWD. CWD availability is the proportion of the movement plot area represented by CWD. Slopes are presented in the form of mean ± SE; p designates probability that the slope of the regression is significantly different from 1.0. Dashed lines represent the slope of one describing a constant and equal increase of CWD use with increasing CWD availability.
Fig. 3. (Continued)
Fig. 3. (Continued)
Ucitel used a rank sum test to examine differences in CWD coverage between capture plots and non-capture plots. For these analyses, data were blocked by stand and nested within stand by a priori classification of portions of the stands as wet (swampy) or dry. A signed rank test was used to examine differences in CWD coverage between capture plots and movement plots paired by trapping site. All analyses were performed using SPSS version 10.0.7 (SPSS, Inc. 1999).

RESULTS

Microhabitat use

Trails included in the analysis averaged 22.4 m (SE = 0.2 m) long. Of a cumulative path distance (119 trails) of 2671 m, 761.1 m of travel (29%) were associated with CWD. Of the movement associated with CWD, 40% was on top of logs, 37% on the side, and 23% underneath. Vole use of CWD was positively and linearly associated with CWD availability within the movement plots for all 5 stands (Fig. 3). The slope of the regression of CWD use on CWD availability was significantly > 1.0 (all p < 0.001) for each stand, indicating that voles use CWD at a disproportionally higher rate than expected based on its availability within movement plots. Of the total 119 vole trails analyzed, 113 (95%) had greater use of CWD than the proportion available in the movement plot. For these trails, the difference between the proportion of the trail associated with CWD and the proportion of the movement plot covered with CWD was as large as 71%. In contrast, the difference was ≤ 1% for trails that had a smaller use than availability.
Fig. 4. Comparison of stand-specific rates of coarse woody debris (CWD; >7.5 cm in diameter) use by red-backed voles as a function of CWD availability in movement plots. CWD use is the proportion of trail length associated with CWD, and CWD availability is the proportion of the movement plot area represented by CWD. Rate of increase in CWD use as a function of CWD availability is significantly greater in BV than all other stands (p ≤ 0.03; no Bonferonni correction) when discarding the two outliers (one from BV and one from TP) and fitting all regression lines with least-squares linear regression. Dashed line represents the slope of one describing a constant and equal increase of CWD use with increasing CWD availability.
The slope for BV ($\hat{\beta} = 4.91; \text{SE} = 0.606$) was distinctly higher and significantly greater than those of the other four ($t \geq 1.93$; d.f. range from 42 to 45; $p \leq 0.03$; no Bonferroni correction; Fig. 4), which were not distinguishable from each other. The response of voles to variation in CWD within the BV stand was different than the other stands sampled.

CWD distribution

In all 5 stands, CWD coverage was highest in movement plots ($\bar{X} = 8.6\%$; Fig. 5) and lowest in non-capture plots ($\bar{X} = 5.6\%$; Fig. 5); CWD coverage in capture plots ($\bar{X} = 6.7\%$; Fig. 5) was intermediate to non-capture and movement plots (Fig. 5). The difference in CWD coverage between capture and non-capture plots approached statistical significance ($F(1,307) = 3.285; p = 0.071$). CWD coverage in movement plots was significantly higher than in capture plots ($F(1,120) = 6.024; p = 0.016$). Even though movement plots overlapped slightly with capture plots, they contained more CWD. Voles were more active in portions of the stand with CWD higher than the overall stand average. The 2% difference in CWD coverage between movement plots and capture plots is equivalent to a difference in 250 logs/ha (average log size 4m x 20 cm), or about 2 logs/5m-radius sampling plot used to characterize CWD at trapping locations.

CWD as habitat and as fuel

CWD coverage data for all trapping plots (pooled capture and non-capture plots) were used to calculate a single stand-level measure of mean CWD coverage to compare with the stand-level fuel load value. On a stand level, CWD coverage was closely correlated to fuel load, expressed either as volume or biomass (Fig. 6). For all trapping...
Fig. 5. Stand measure of percent coarse woody debris (> 7.5 cm in diameter) cover calculated separately for capture (trap locations where voles were captured), non-capture (trap locations chosen randomly out of all trap locations where voles were not captured), and movement plots (minimum-bounding rectangle around a vole trail, (N_{Barber}=32, 29, 24; N_{Beaver}=24, 26, 21; N_{Holland}=24, 28, 24; N_{Swamp}=42, 36, 25; N_{TP}=49, 27, 27 respectively).
Fig. 6. Weighted least-squares regressions of stand-level coarse woody debris (CWD; > 7.5 cm in diameter) coverage as a function of fuel loads measured as volume (m$^3$/ha). Each data point with the same shape represents a stand sampled during summer 2001. The data values are weighted by the inverse variance of the stand-measure CWD area coverage to incorporate the variation associated with each stand-measure CWD coverage and different sample sizes.
plots, CWD coverage was strongly correlated with fuel load expressed as volume (m$^3$/ha) and as biomass (kg/m$^2$; $r = +0.95$ for both volume and biomass; $n = 5$). Those same stand-level fuel load values also correlated highly with CWD coverage for capture plots ($r = +0.99$ for both volume and biomass; $n = 5$) and for movement plots ($r = +0.92$ for both fuel volume and fuel biomass; $n = 5$; Table 1).

Regressions of CWD coverage on fuel load were calculated separately for three different plot categories: capture plots, movement plots, and all trapping plots. The slopes of these regressions did not differ from each other ($p = 0.409$ for the difference in slopes between all plots and capture plots; $p = 0.511$ for all plots and movement plots; $n = 5$ for both comparisons). The intercepts of the regression of CWD for all trapping plots and for capture plots on fuel volume were nearly identical ($p = 0.999$; $n = 5$). However, the intercept for the regression of CWD coverage in movement plots on fuel load was higher than for the all-plots measure ($p = 0.059$; $n = 5$; Table 2). There is a predictable relationship between fuel load and CWD coverage for all plot categories in which CWD was measured. For capture plots and stand-level measure, the same regression statistics describe the relationship reasonably well. However, movement plots have consistently greater CWD coverage than other plot categories. A different regression line is needed to describe the relationship between fuel load and CWD coverage in portions of these stands in which voles are known to move (Table 2).

DISCUSSION

Red-backed voles use CWD in their movement paths to a greater extent than expected based on availability. This pattern was consistent across a variety of stands. The
Table 1. Stand level measure of coarse woody debris (CWD; > 7.5 cm in diameter) as habitat and fuel used in weighted linear least-squares regression of CWD coverage on fuel loads. Habitat measures are proportion of the relevant plot (All-plots or movement plots) covered with CWD. All-plots measure was calculated by pooling both capture and non-capture plots. Movement plots are the minimum-bounding rectangles encompassing a vole trail.

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<td>0.096 ± 0.0124</td>
</tr>
<tr>
<td>SW</td>
<td>78</td>
<td>0.065 ± 0.0056</td>
</tr>
<tr>
<td>TP</td>
<td>76</td>
<td>0.076 ± 0.0062</td>
</tr>
</tbody>
</table>
Table 2. Coefficients of weighted least-squares regression of coarse woody debris (CWD; > 7.5 cm in diameter) coverage on fuel loads. Values are terms of equations of the form: CWD coverage = intercept + volume (or biomass) X slope. The units are m³/ha for volume and kg/m² for biomass. The regression is weighted by the inverse variance of CWD coverage to incorporate the variation associated with each stand-measure CWD coverage and different sample sizes. Superscripted letters indicate significantly different values.

<table>
<thead>
<tr>
<th>Stand-level measure</th>
<th>Coefficients</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>CWD coverage</td>
<td>Fuel load</td>
<td>Intercept</td>
<td>Slope</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All-plots</td>
<td>Volume</td>
<td>$0.01005 \pm 0.00671^a$</td>
<td>$0.00032 \pm 0.00006^c$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Movement plots</td>
<td>Volume</td>
<td>$0.03365 \pm 0.01312^b$</td>
<td>$0.00030 \pm 0.00007^c$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All-plots</td>
<td>Biomass</td>
<td>$0.00977 \pm 0.00642^{d}$</td>
<td>$0.00990 \pm 0.00176^{f}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Movement plots</td>
<td>Biomass</td>
<td>$0.03284 \pm 0.01288^e$</td>
<td>$0.00934 \pm 0.00228^f$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
response of voles to increased CWD availability is described well with linear models, although caution must be used in extrapolating beyond the range of CWD availability measured in this study. As CWD availability increases, CWD use increases linearly with it, at a greater rate, as reflected by regression slopes > 1.0 (Fig. 3). It is noteworthy that voles are not limited in their movement to microsites with the highest CWD availability, although as noted above, they tend to move in areas with higher-than-average CWD.

The pattern and extent of vole association with CWD in this study is consistent with the view that voles actively select CWD, perhaps as protection from predators. This view has been widely, if implicitly, held in the literature. An alternative conflicting explanation, however, is that vole association to CWD is a result of CWD representing a physical obstruction to vole movement. In a companion study to the present one (H. Davis, unpublished), red-backed vole movements and use of elevated and grounded logs were similar, suggesting that grounded logs do not constrain or channelize movement. These results strengthen the view that CWD use by red-backed voles in the present study reflects active selection for CWD.

The comparison of CWD use to CWD availability provides a detailed understanding of vole association to CWD and a quantitative expression of CWD use as a function of availability. This stand-level quantitative expression is obtained by compiling data from individual vole trails within a stand, providing a unique, stand-specific description and quantitative expression that reflects actual habitat use. An additional component to this model is the possibility of comparing use rate, reflected by the magnitude of the slope, across a variety of forest stands. In principle, because this measure is unitless, it may be useful for comparing the strength of animal responses to
different microhabitat components (say, CWD and vegetative cover). In this study, we
compared the magnitude of slopes created from CWD use as a function of CWD
availability for all stands. The use pattern in BV was different than for the other four
stands (Fig. 4). BV stand had the smallest stand level CWD coverage, and was the only
stand made up of a single tree species (lodgepole pine). Furthermore, BV is the only dry
and lower productivity habitat type relative to other stands sampled in this study (Pfister
1977). The correspondence between distinctive stand features and the unusually high use
rate (slope) of CWD by voles in BV stand suggests a possible exceptional behavioral
response to low resource (CWD) availability.

Other observations suggest that the regression slopes of CWD use on CWD
availability may be a useful diagnostic measure of animal response to resource
availability. In a previous study (Ucitel, unpublished), we observed a slope of 2.93 (n =
27; SE = 0.46) for CWD use in a nearby Montana stand with similar productivity and
species composition to all stands in the current study except BV (see Fig. 4 for
comparison). The observed slope of 5.54 (n = 47; SE = 0.56) from a multi-year study in
an old growth stand in Minnesota (Christian, unpublished) suggests that a broad range of
voles responses to CWD availability is possible. Our results suggest uniform responses of
voles to CWD availability among stands of similar productivity, within a region, but also
indicate that responses may vary geographically and may depend on stand structure or
productivity.

We expected that CWD coverage in movement and in capture plots would reflect
microhabitat use by red-backed voles, and would be higher than for non-capture plots.
The most striking difference we observed was higher CWD coverage in movement plots,
coupled with slightly higher CWD coverage in capture than in non-capture plots. This result may reflect possible limitations of trapping as a basis for assessing fine-scale microhabitat use and response to structural features such as CWD. Analysis of trails allows us to incorporate precise vole-defined CWD association. Each individual vole trail provides greater information on its association with a habitat component than information gathered by trapping. This approach allows us to quantify the strength of the selection for CWD, in a way not possible with trapping data. These findings suggest that caution is needed in interpreting a lack of difference in habitat structure between capture and non-capture locations. Such approaches may under-represent the actual extent of microhabitat selection by voles. Our results clearly demonstrate greater vole activity in portions of stands with higher CWD coverage. Such selection suggests spatial heterogeneity in CWD distribution within forest stands, discernible at the scale of our movement plots.

In this study, we used red-backed vole association with and movement along CWD as a metric of microhabitat suitability. Although the requirement of voles for CWD is well established, we do not know whether or to what extent patterns of CWD use translate into key demographic processes such as survival and reproductive success. That is, we do not know if the stands we sampled provide the necessary habitat features for sustainable and viable vole populations. This type of information will ultimately be needed to understand quantitative requirements for a variety of habitat factors including CWD.

**MANAGEMENT IMPLICATIONS**

The disconnection of wildlife habitat studies and of research done on fuel loads (which includes CWD) has limited the integration of wildlife habitat requirements and
fire management. We have demonstrated that it is possible to calculate CWD coverage from fuel load measures, and vice versa, while retaining field methods specific to the field of interests (either fuel or habitat research). Thus, it should be possible to establish a common basis for discussion of different, and perhaps competing, values of CWD in forest ecology that would provide land managers with guidelines for ecosystem sustainability. To facilitate that goal, we encourage researchers to standardize the diameter classification of CWD for future studies to the well-defined categorization provided in fuel-related studies (Brown 1974).

Several guidelines regarding CWD levels in forest stands are available. Brown and See (1981) suggested that stands with >3.4-4.5 kg/m² of CWD of diameter > 14cm may present high fire risk. Harvey et al. (1981) suggested that 25-37 tons/ha (2.2-3.4 kg/m²) of CWD > 14 cm diameter would be beneficial for maximizing ectomycorrhizae support, and Carey and Johnson (1995) proposed that stands should have 15%-20% CWD cover well distributed on the forest floor to be adequate for small-mammal communities. Graham et al. (1994) provided recommended amounts of CWD to leave after timber harvesting to maintain forest productivity categorized by habitat types. These ranged from 11-23 tons/acre (2.76-5.77 kg/m²) for Abies lasiocarpa / Xerophyllum tenax habitat type which includes BV and 16-33 tons/acre (4.02-8.28 kg/m²) for Thuja plicata / Clintonia uniflora habitat type which includes SW and TP. Our study provides a conversion tool that enables us to compare these various guidelines, which was not available previously (Table 2). We converted the guidelines of Brown and See (1981), Harvey et al. (1981), and Graham et al. (1994) to habitat metrics. Forest productivity guidelines for post timber harvest (Graham et al. 1994) ranged from 3.7%-6.7% for Abies
lasiocarpa / Xerophyllum tenax habitat type and 4.9%-9.2% for Thuja plicata / Clintonia uniflora habitat type (see Table 2). BV (\( \bar{x} = 2.8\% \)) falls slightly below the range for its habitat type, SW (\( \bar{x} = 6.5\% \)) and TP (\( \bar{x} = 7.6\% \)) are in agreement with the range proposed for post harvest residual CWD to maximize forest productivity. Brown and See's (1981) proposed threshold for high fire risk translates to 4.3%-5.4% CWD cover, and ectomycorrhizae guidelines (Harvey et al. 1981) translate to 3.1%-4.3% (see Table 2). We reanalyzed our data using CWD > 14 cm for comparison with these values. Only two of our stands (BV and BB) have CWD coverage within their recommended ranges. The other three stands in our study would be regarded by Brown and See (1981) as representing high fire-risk stands, yet we do not regard them as containing excessive CWD to meet habitat requirements of voles, based on our observed patterns of CWD use. All of these recommendations are well below that of Carey and Johnson (1995) for CWD retention, although it is unlikely that the latter apply to forest systems in the interior Western U.S. Clearly, none of the stands we sampled approach the CWD coverage recommendations of Carey and Johnson (1995). These comparisons emphasize the lack of communication and the risk of providing CWD guidelines based only on studies of either fuel loads and their effect on fire behavior, or wildlife habitat needs.

The stand-level values of CWD in our study reflect CWD well distributed throughout the stand (see also recommendation in Carey and Johnson 1995). Similar stand-level measures of CWD but with heavily clumped distribution would influence vole distribution within stands, may limit vole numbers, and would not facilitate the same ecological roles of CWD.
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