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## Home Range and Habitat of Western Red-backed Voles in the Oregon Cascades

### Abstract

Western red-backed voles are endemic to western Oregon and northern California and represent a large proportion of the rodent community in mature Douglas-fir forests. Despite their dominance in these forests, little is known about their selection of home ranges. We radiotracked 23 western red-backed voles in 3 mature, coniferous forest stands in the southern Oregon Cascades during 1994 and 1995 and estimated home range size, movements, and habitat associations. Males had larger home ranges than females and males moved farther each evening than females. Females were most active during 2 periods: shortly after dusk and before dawn. Males were active all night. Core areas for home ranges of females were characterized by deep organic soil layers and large volumes of decayed logs. Results underscore the importance of organic matter and coarse woody debris on the forest floor for maintaining populations of western-red-backed voles.

### Introduction

Western red-backed voles (*Myodes californicus* Merriam, nomenclature follows Wilson and Reeder [2005]) are endemic to western Oregon and northern California and restricted to coniferous forests (Alexander and Verts 1992). They are primarily nocturnal (Maser et al. 1981) and make up a large proportion of the rodent community in mature Douglas-fir (*Pseudotsuga menziesii*) forests in the Oregon Cascades (Corn et al. 1988, Gitzen et al. 2007). The diet of western red-backed voles is comprised largely of truffles, the below-ground fruiting bodies of ectomycorrhizal fungi (Cazares et al. 1999, Ure and Maser 1982); thus, these voles serve an important ecological role as primary dispersers of ectomycorrhizal fungal spores (Maser and Maser 1988, Maser et al. 1978). Red-backed voles are also prey for many forest predators including owls, mustelids, bobcats, and coyotes (Alexander and Verts 1992).

Several studies have demonstrated a strong association between western red-backed voles and logs, with highly decayed logs considered an important habitat feature (Doyle 1987, Maser et al. 1981, Tallmon and Mills 1994). Habitat for western red-backed voles has also been characterized by a high percentage of coniferous canopy cover and lichens (Doyle 1987) and deep forest organic layer (Gomez 1992, Rosenberg et al. 1994).

Relative abundance of western red-backed voles was higher in old-growth forests (~250 years old) than in mature forests (~100 years old) (Doyle 1987) and they were believed to occur more frequently in mature and old-growth forests (>80 yrs) than in younger forests in Oregon (Rosenberg et al. 1994). However, other studies did not detect a difference in relative abundance between young (<80 yrs) and old (>80 yrs) forests (Aubry et al. 1991, Gilbert and Allwine 1991). Nonetheless, western red-backed vole populations were reduced or eliminated from sites after clearcutting (Gashwiler 1970, Hooven and Black 1976, Mills 1995) and some green tree retention treatments (Gitzen et al. 2007). This suggests that forest management treatments may reduce levels of certain habitat elements (e.g., coarse woody debris; CWD) important to western red-backed voles.

Although home ranges of western red-backed voles have been studied within old-growth forests (Tallmon and Mills 1994, Hooven 1971), home

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range size, core area use, and composition estimates in mature forests have not been documented. We examined home range use and habitat selection by western red-backed voles in mature forests that had been salvage logged in the 1970s. Core areas are used more frequently than other portions of the home range and likely contain both refuges and dependable food sources. Also, core area size is believed to be determined by both behavior and resource distribution (as defined by Samuel et al. [1985] and Seaman and Powell [1990]). Thus we described habitat use in our study at the level of the home range core area. Our objectives were to estimate summer home range and core area sizes of adult western red-backed voles and describe temporal movement patterns of male and female adult voles related to CWD and other microhabitat features. We predicted that: (1) vole movements are associated with CWD, (2) volume of decayed logs is greater in core areas than outside of core areas, and (3) home range size is negatively associated with volume of logs in the home range.

## Study Area

We conducted our study in 3, 16-ha stands in the southern Oregon Cascade Range on the Umpqua National Forest (47°55'N, 122°34'W), Douglas County, Oregon. Elevation of study stands ranged from 945 to 1,310 m. We selected stands used in the Demonstration of Ecosystem Management Options project (Gitzen et al. 2007) where western red-backed voles had been successfully live-trapped. During our study we never captured voles between stands, so we assumed stands were independent. Stands had log volumes of 96.6 m<sup>3</sup>/ha, 142.6 m<sup>3</sup>/ha, and 188.7 m<sup>3</sup>/ha (Maguire 2002) typical of mature, unmanaged forests in Oregon and Washington (Spies and Franklin 1991), and were located in mixed-conifer forest dominated by Douglas-fir trees 110 - 130 years old. Western hemlock (*Tsuga heterophylla*), ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), and silver fir (*Abies amabilis*) were also present (Franklin and Dyrness 1973). Common understory shrubs included dwarf Oregon-grape (*Berberis nervosa*), creeping snowberry (*Symphoricarpos mollis*), and western serviceberry (*Amelanchier alnifolia*). Stands had been salvage logged to similar basal areas between 1970 and 1978, with basal areas at the time that we conducted our study ranging between 44 and 52 m<sup>2</sup>/ha (Halpern et al. 2005).

## Methods

In August and September 1994 and July and August 1995, we live-trapped western red-backed voles in each stand using Sherman live traps (8 x 9 x 23 cm) set on a 9 x 8 grid with 20-m spacing. Captured animals were weighed and sex was determined. We fastened a collar with an attached 1-g model MD-2(C) radio transmitter (Holohil Systems Ltd., Ontario, Canada) around the necks of adult voles that weighed > 20 g (thus ensuring that radio transmitters were ≤ 5% of total body weight [White and Garrot 1990]). We fitted 29 voles in 1994 (21 females, 8 males) and 18 in 1995 (11 females, 7 males) with radio transmitters. We fastened each collar with a metal crimp and rotated it so that the radio hung on the ventral surface of the neck with the whip antenna lying horizontally along the length of the animal's back. We trimmed the antenna so that it did not protrude past the end of the body. This reduced the detectable range of the transmitter but we did not encounter problems finding voles within their home ranges. Voles were then offered food and water and held for observation for 15 - 60 min prior to release at point of capture (Thompson 1996). All females that we collared were either lactating, pregnant, or in estrus. Reproductive condition of males was difficult to identify and categorized as either active when descended testes were visible, or unknown. Capturing and handling of voles conformed to the guidelines established by the American Society of Mammalogists (1998) under a protocol approved by Oregon State University Institutional Animal Care and Use Committee.

We collected hourly locations for each vole between dusk and dawn every 2 - 3 days. We began tracking a minimum of 24 hrs after collaring and located voles for up to 1 month or until the radio transmitter failed. We located voles initially by obtaining a radio signal from a distance of 40 m or more. We then approached the animal to within approximately 5 m using a hand-held antenna and removed the antenna to locate it with only the coaxial cable. We did not feel that approaching the voles on foot disturbed the animals because no alterations in behaviors were noted. They did not move above ground or flee when we approached, and the radio signal pattern, which can indicate movement, did not change from when we first began tracking the individuals. At each animal's location, we recorded presence of logs and a brief

description of vegetation. The error of location estimates was  $\leq 2$  m of the actual location based on locating inert radiotransmitters placed on the ground in various microsites at the beginning of the study and that had slipped off animals during the study.

We used program CALHOME (Kie et al. 1996) to estimate home ranges. When home range size of each vole was plotted against the number of telemetry locations, on average there was an asymptote at 35 locations (range 25 - 60 locations,  $SE = 1.6$ ). Thus we limited our home range estimates to 18 females and 5 males with 35 or more locations. We were unable to collect 35 or more locations on the 24 additional collared voles primarily due to the radio batteries expiring, the radios falling off, or because of predation. On average we tracked voles for 8 non-consecutive days (range 4 - 14 tracking days) over a 22-day period (range 14 - 38 days). We found evidence of autocorrelation among observations for some animals. However, given our systematic sampling design and the minor effects of autocorrelation on kernel estimates compared to effects of small sample sizes or non-representative sampling (Swihart and Slade 1997, Otis and White 1999), we included all observations.

We used the adaptive kernel (AK) method (Worton 1989) to estimate home range (95% isopleth) and core area size. We modified the methods used by Clutton-Brock et al. (1982) and Samuel et al. (1985) to estimate core areas for each individual. Utilization distributions were plotted against home range size to identify a point of transition representing the split between heavily used portions of the home range (core areas) and areas that were used less frequently. Probability contour estimates used to generate core areas ranged from 45 - 75% and reflected individual habitat use patterns. We used an adaptive kernel estimator with a smoothing parameter of 0.60 (based on least-squares cross-validation) and a grid density of 40 x 40 because it best represented the observed spatial configuration patterns of our voles (Kie et al. 1996, Seaman and Powell 1996, Worton 1989). We also present minimum convex polygon (MCP) home range estimates so that our results can be compared with previous studies that used this metric. Sample sizes were insufficient for detecting differences among years so we pooled home range and core areas by year for each sex to maximize power for detecting overall differences

among sexes. We compared home range and core area sizes between sexes using ANOVA.

We defined movements as the linear distance an individual traveled between consecutive hourly observations. We averaged movement data for each hour sampled from full tracking periods (2 - 5 weeks) for each animal and plotted movement averages for each sex. We calculated mean hourly distances moved per 8-hr telemetry period for individuals of each sex, averaged these values among voles, and pooled the data between the 2 yrs sampled. We compared mean distances moved between the sexes with a *t*-test (Sokal and Rohlf 1995).

We measured 28 habitat variables within the home ranges of voles radiotracked in 1994 (Thompson 1996). Due to time and cost constraints, habitat data were not collected within home ranges of voles tracked in 1995. Variables were grouped into 6 categories: (1) log volume (conifer  $m^3/ha$ ); (2) percent understory cover (conifer and hardwood saplings and shrubs); (3) ground surface conditions (% cover of soil, stone, fine and coarse litter, stumps, and live tree base); (4) percent herbaceous cover (lichens, bryophytes, forbs, shrubs, ferns, and grasses); (5) organic layer (depth of needles, leaves, twigs, and humus); and (6) percent overstory canopy cover. Logs were divided into small (10-19.9 cm), medium (20 - 29.9 cm), and large ( $\geq 30.0$  cm) diameter size classes and categorized into decay class following Sollins (1982). Decay class ranged from 1 to 5, with 1 being in the earliest stages of decay and 5 being in the latest stages of decay. Decay class 1 - 3 (hard) and 4 - 5 (soft) were combined for analysis.

To compare habitat characteristics between core areas and non-core areas, we randomly located and measured 2 plots in non-core areas for each home range core area. Because some animals had more than 1 core area, we sampled 19 core areas and 38 random non-core areas (14 core areas for 10 females and 5 core areas for 2 males). We sampled habitat within 0.06-ha circular plots centrally positioned within the core and non-core areas of each vole (Figure 1). We placed 6-m transects in each cardinal direction within each circular habitat plot (Figure 1) and sampled log volume and understory cover along each transect using a line-intercept method (Daubenmire 1988). Using Daubenmire (1988) microplots (0.2 m x 0.5 m) at 1-m intervals along each transect (24 microplots

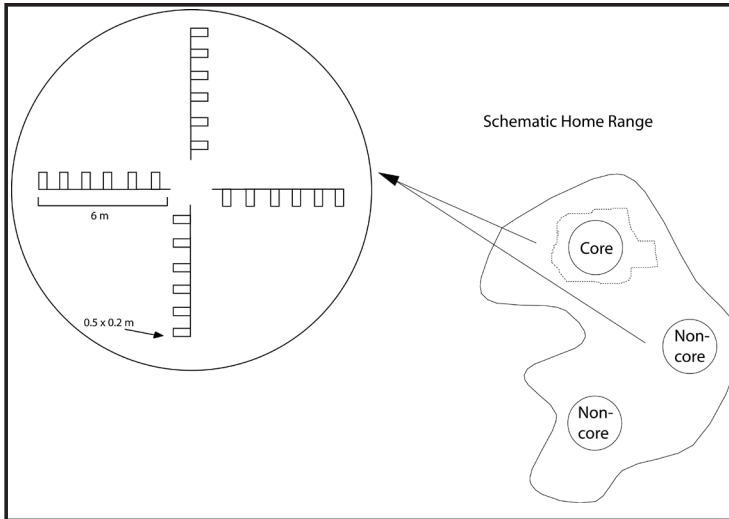


Figure 1. Plot and transect design for sampling habitat of western red-backed voles in the southern Oregon Cascades. Core areas = areas of concentrated use delineated using Adaptive Kernel home range analysis. Non-core = randomly selected non-core areas within the home range.

per plot; Figure 1), a single observer estimated ground and herbaceous cover and organic litter depth at each microplot, and overstory canopy cover at both ends of each transect.

We analyzed habitat associations only for females due to the small sample size of males ( $n = 2$ ) in 1994. We used Friedman's Rank Sum procedure (Hollander and Wolfe 1973) to compare habitat variables between core area and non-core area plots using ANOVA (Sokal and Rohlf 1995). We used conditional stepwise logistic regression for matched case-control studies (Hosmer and Lemeshow 2000) to evaluate the effectiveness of 12 habitat variables (volume of small, medium, and large soft and hard logs, percent cover of the tall shrub and understory tree layer, fine litter, coarse litter, herbaceous layer, and overstory canopy, and depth of organic litter) in separating core areas from non-core areas. The regression procedure in SAS (PHREG) took into account the 2:1 ratio of non-core area to core area plots by averaging the variables of the non-core area plots (SAS Institute 1992). One variable (depth of organic litter) was higher in all core areas than in non-core area plots and was thus completely partitioned. The SAS analysis procedure and the maximum likelihood estimator could not handle such a consistent effect between case and control and thus statistics could not be computed. Because of the nature of this variable, our small sample size, and the

large number of explanatory variables, we could not estimate other parameters in the presence of depth of organic litter. For exploratory purposes, we eliminated depth of organic litter and analyzed our data without this variable.

We used Spearman's rank-order correlation analysis (Sokal and Rohlf 1995) to test for relationships between home range or core area size and average log volume computed for individual home ranges in 1994. We did not conduct these analyses for other habitat variables since our *a priori* hypotheses regarding home range size and other habitat variables were limited to use of logs by voles. We set alpha at 0.05 for all analyses.

In 1995, to quantify our anecdotal observations that western red-backed voles used logs as travel pathways and for cover during their nightly movements, we calculated the percentage of telemetry locations within 2 m of at least one log of any decay stage for males and females individually and combined in 1995. Logs were assigned to one of three decay categories for these analyses: soft (decay class 4 or 5), hard (decay class 1, 2, or 3), and all decay classes (both soft and hard logs  $\leq 2$  m of the telemetry location).

## Results

Home ranges of voles in our study had 1 or more centers of activity. The mean 95% AK home range

TABLE 1. Estimated 95% adaptive kernel and 100% MCP home ranges and core areas (ha) for individual male and female western red-backed voles in the southern Oregon Cascades, summers 1994 - 1995.

Vole ID	No. Loc <sup>a</sup>	95% Adaptive Kernel			100% MCP
		Home Range	No. Core Areas	Core Area <sup>b</sup>	Home Range
<i>Females 1994</i>					
1-94-1	39	0.101	1	0.009	0.085
2-94-1	38	0.322	2	0.036	0.330
3-94-1	49	0.034	1	0.006	0.066
4-94-5	35	0.07	2	0.008	0.091
5-94-5	60	0.196	1	0.014	0.175
6-94-5	60	0.047	1	0.011	0.048
7-94-5	55	0.069	1	0.003	0.057
8-94-6	71	0.142	2	0.025	0.295
9-94-6	49	0.139	2	0.020	0.160
10-94-6	43	0.079	1	0.007	0.079
<i>Females 1995</i>					
1-95-1	71	0.095	2	0.009	0.095
2-95-1	80	0.106	3	0.007	0.116
3-95-1	48	0.201	2	0.022	0.181
4-95-5	91	0.181	3	0.015	0.181
5-95-5	56	0.132	2	0.014	0.120
6-95-5	111	0.169	3	0.025	0.162
7-95-6	60	0.227	1	0.025	0.178
8-95-6	68	0.114	3	0.020	0.128
<i>Mean Females 1994 and 1995 Combined</i>					
	60.2	0.135	1.8	0.015	0.142
<i>Males 1994</i>					
11-94-5	35	0.641	2	0.160	0.613
12-94-5	56	0.521	3	0.088	0.542
<i>Males 1995</i>					
9-95-1	62	0.961	3	0.340	1.222
10-95-1	64	0.779	2	0.086	1.014
11-95-1	64	0.802	3	0.192	0.668
<i>Mean Males 1994 and 1995 Combined</i>					
	56.2	0.741	2.6	0.173	0.812

<sup>a</sup>Number of telemetry locations used in home range estimation.

<sup>b</sup>In cases where voles had 1 or more core areas we present the average of the core areas.

size was 0.74 ha for males (0.11 SE) and 0.14 ha for females (0.02 SE), a difference that was significantly different ( $F = 143.7$ ;  $P < 0.0001$ ) (Table 1). Home ranges contained one to three core areas for females and two to three core areas for males (Table 1). Males had larger mean core areas (0.17 ha, 0.05 SE) than females (0.02 ha, 0.002 SE;  $F = 59.0$ ;  $P < 0.0001$ ) (Table 1). Core area utilization distributions averaged 65% for males (range 55 - 75%) and 57% for females (range 45 - 75%). The mean size of home ranges estimated by the

minimum convex polygon method were similar to those estimated with adaptive kernel (0.81 ha for males; 0.14 ha for females) (Table 1).

Movement patterns varied over an 8-hr crepuscular and nocturnal sampling period (Figure 2). Average distance moved between sequential telemetry locations was greater for males (29.7 m, 5.0 SE,  $n = 5$ ) than for females (11.7 m, 1.2 SE,  $n = 18$ ;  $P = 0.006$ , Figure 2). Both males and females traveled greatest distances within 2 hrs after sunset. The greatest observed travel distance in a 1-hr period was 47 m for females and 105 m for males. Activity of males during an evening sampling period peaked immediately after sunset and then declined through the rest of the night, with occasional periods of low activity or inactivity. Males were least active within 1 hr of sunrise but still more active than females (Figure 2). Females had 2 peaks of activity: one during the 1-hr period after sunset and another within 2 hrs of sunrise (Figure 2), and these periods of activity were short in distance and time. Females were relatively inactive between midnight and 0200 hours and were repeatedly located in the same area.

Nine habitat variables differed significantly between core areas and non-core area plots within female home ranges (Table 2; Friedman's Rank Sum). Volumes of small, medium and large soft logs, all soft logs, all logs, depth of organic litter, and percent cover of bare soil were greater in core areas than in non-core areas whereas percent cover of fine litter and tall forbs was greater in non-core areas than in core areas (Table 2).

We identified one main effect using conditional logistic regression; female voles selected areas with deep organic litter. Because this variable was consistently higher in core areas than non-core areas (as described in the methods section), we are unable to report an odds ratio. When this variable was removed from the analysis, medium-diameter, soft logs were significant for distinguishing core areas from non-core areas ( $\exp(\beta) = 1.032$ , upper and lower 95% CI = 1.002 and 1.062). These results indicate that for every unit volume increase in medium-diameter soft logs, there was a 1.032 increase in probability of a vole using a given site.

Home range size was inversely related to volume of small soft logs ( $r = -0.664$ ,  $P = 0.04$ ; Spearman's rank-order correlation analysis) but positively correlated with volume of medium ( $r$

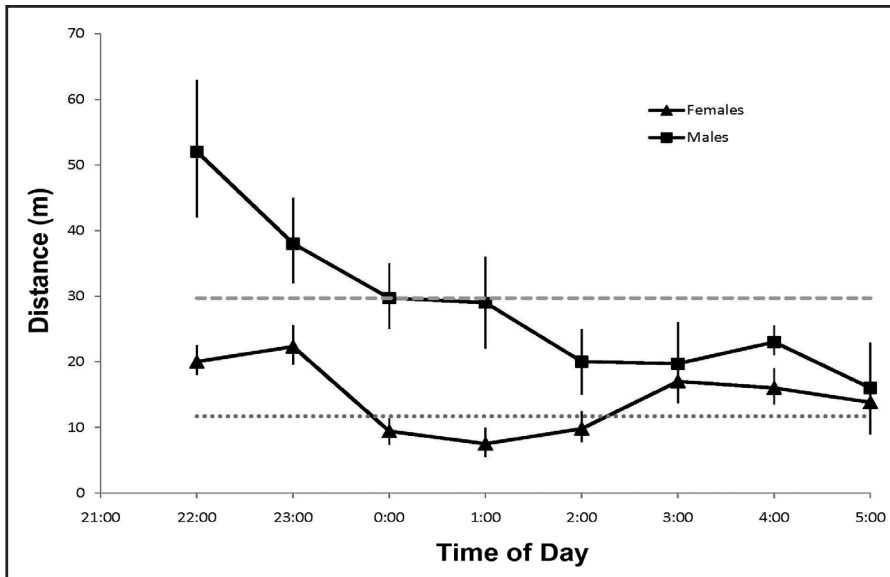


Figure 2. Average hourly movement distance between sequential dusk to dawn locations for western red-backed voles in the southern Oregon Cascades, 1994-1995. Distance moved per hour on time of day axis represents movement within the last hour. Error bars represent 1 standard error. Dashed and dotted horizontal lines represents mean distance moved for males (29.7m) and females (11.7m), respectively, over an 8-hour tracking period.

= 0.65,  $P = 0.04$ ) and large hard logs ( $r = 0.79$ ,  $P = 0.007$ ). Core area size was positively correlated with volume of medium hard logs ( $r = 0.65$ ,  $P = 0.04$ ). There was a marginal positive relationship between core area size and volume of large hard logs ( $r = 0.58$ ,  $P = 0.08$ ).

Of 746 telemetry locations from 1995, 80% were within 2 m of a log. Ninety-six percent of the male locations ( $n = 190$ ) and 75% of the female locations ( $n = 556$ ) were within 2 m of 1 or more logs. Sixty-four percent of the male locations were within 2 m of soft logs, 13% near hard logs, and 18% near both soft and hard logs. For females, 47% of the locations were within 2 m of soft logs, 14% near hard logs, and 14% near both soft and hard logs. When voles were not found within 2 m of logs, they were usually near tree or snag bases or under western serviceberry in association with a thick litter layer.

## Discussion

Tallmon and Mills (1994) found similar, but smaller summer home range areas for female western red-backed voles (0.08 ha MCP,  $n = 2$ ) in an old growth forest remnant, but their male home

ranges were much smaller (0.24 ha MCP,  $n = 2$ ) than those in our study. We had larger sample sizes and number of locations which likely explained some of this difference. However, differences in habitat quality between mature and old-growth forests (e.g., litter depth, CWD volume or decay class) might also affect home range size. Based on trapping data, Hooven (1971) estimated much larger home range sizes for western red-backed voles (4.6 ha for males,  $n = 12$ ; 0.8 ha for females,  $n = 8$ ) in old-growth forests in the western Oregon Cascades compared to ours in mature forest. Usually home range estimates from radio telemetry data are larger (Ribble et al. 2002) than those from trapping data. Hooven's (1971) estimates were derived from a circular bivariate distribution based on the relative frequency of the location of recaptured animals trapped over a several month period. It is possible the difference in methodologies and duration of studies resulted in the larger home ranges. Larger home ranges would be expected for trapping periods over many months and there was potential for baited traps to distort home range boundaries. The home range size estimates of the voles tracked in our study would perhaps have been greater if the battery

TABLE 2. Mean habitat characteristics ( $\bar{x}$ ) and standard errors ( $SE$ ) within female western red-backed vole core and random non-core areas in the Southern Oregon Cascades, 1994. Numbers in bold represent the significantly larger variable.

Variable	Core Area		Non-Core Area		<i>P</i> -Value <i>P</i> >   <i>t</i>
	$\bar{x}$	SE	$\bar{x}$	SE	
<i>Log Volume (m<sup>3</sup>/ha)</i>					
All logs	<b>236.8</b>	40.49	119.7	22.69	0.013
Soft small logs <sup>a</sup>	<b>24.9</b>	4.57	11.9	1.96	0.020
Soft medium logs <sup>a</sup>	<b>38.9</b>	10.32	7.5	2.49	0.020
Soft large logs <sup>a</sup>	<b>83.7</b>	28.99	29.8	10.76	0.032
All soft logs <sup>a</sup>	<b>152.5</b>	33.58	49.2	11.36	0.004
Hard small logs <sup>b</sup>	15.4	3.15	15.0	2.19	0.979
Hard medium logs <sup>b</sup>	13.3	5.67	9.9	2.94	0.350
Hard large logs <sup>b</sup>	55.6	20.50	45.6	18.68	0.620
All hard logs <sup>b</sup>	84.3	25.38	70.5	19.26	1.000 <sup>c</sup>
<i>Ground Cover (%)</i>					
Soil	<b>0.6</b>	0.51	0.5	0.23	0.025
Fine litter (< 5 cm width)	86.1	1.35	<b>90.1</b>	0.83	0.047
Coarse litter (> 5 cm width)	12.3	1.40	9.0	0.83	0.075
Stone	<0.1	0.04	<0.1	0.003	0.956
Stump	0.3	0.20	0.4	0.23	0.364
Tree base	2.0	0.57	1.7	0.36	0.769
<i>Understory Cover (%)</i>					
Tall shrubs >30 cm tall	3.9	1.08	6.3	1.55	0.082
Conifers < 5cm dbh	19.6	4.11	18.4	2.66	1.000 <sup>c</sup>
Hardwoods < 5cm dbh	2.9	1.76	1.7	0.56	0.219
Tall shrubs and trees	24.2	4.11	25.7	2.44	0.514
<i>Organic Layer</i>					
Organic litter depth (mm)	<b>42.3</b>	3.09	21.9	1.00	0.0001
<i>Herbaceous Cover (%)</i>					
Tall forbs (≥ 10 cm)	23.7	2.91	<b>28.6</b>	2.11	0.049
Lichens	2.0	0.26	1.9	0.31	0.815
Bryophytes	28.2	4.97	33.7	3.58	0.335
Low forbs (< 10 cm tall)	23.0	1.76	22.7	1.08	0.723
Low shrubs (< 30 cm tall)	23.9	2.21	24.5	1.31	0.360
Ferns	0.5	0.34	1.0	0.57	0.428
Grass	2.0	0.29	3.1	0.74	0.144
<i>Overstory Cover (%)</i>					
Overstory canopy	75.8	2.10	68.5	2.95	0.111

<sup>a</sup> Decay classes 4 and 5; small logs (10-19.9 cm diameter), medium logs (20-29.9 cm diameter), large logs (≥30.0 cm diameter).

<sup>b</sup> Decay classes 1 – 3.

<sup>c</sup> Because the analysis was run on ranks, it caused some of the P-values to be 1, even though the means differ slightly.

life of the transmitters was longer, enabling us to collect data for a longer period.

In addition to sample period and method of home range analysis, resource availability (logs and truffles) and seasonal variation in food or cover may also account for these differences in home range estimates, as management history and age of stands in these other studies was different than ours. Bondrup-Nielson and Karlsson (1985) found an inverse relationship between food quantity and habitat quality and home range

size for southern red-backed voles (*Myodes gapperi*), and Mills (1995) found that distribution of truffles explained the distribution of western red-backed voles in remnants of old-growth forests in southwest Oregon. Truffles, which are cached by voles, were predominant in the diet of voles at our study area (Cazares et al. 1999) and elsewhere (Ure and Maser 1982, Clarkson and Mills 1994). Therefore, truffle availability and associated log habitat may further explain the small size of home ranges in our study.

The sex-specific difference in size of home ranges observed in our study supports other studies which found larger home ranges of males than females of other species of *Myodes* (Bondrup-Nielson and Karlsson 1985). An evaluation by Bondrup-Nielson (1985) provides rationale for this difference: because males of this genus do not actively defend territories or rear young, they can support larger core areas and home ranges.

Many rodents move young to new nests periodically before weaning (Wolff 1989) which may explain why female western red-backed voles in our study often had multiple core areas. Western red-backed voles undergo post-partum estrus and often start constructing a new nest for a future litter while tending their current litter. So alternatively, females may have changed nest sites between litters. Distribution or depletion of truffle caches may have caused voles to shift to new fungal mats, resulting in use of multiple core areas for both sexes.

Capture rates for western red-backed voles in some studies have been positively associated with logs (Doyle 1987, Hayes and Cross 1987), and telemetry locations for western red-backed voles reported by Tallmon and Mills (1994) were under logs, and more frequently under highly decayed logs (decay classes 3, 4, and 5) than less decayed logs (decay classes 1 and 2). These authors suggested that decayed CWD was a limiting factor for this species. Our study furthers the understanding of importance of decayed logs to red-backed voles by relating home range and core area use to this habitat component. Not only did we also find that 75% of our male and 96% of our female vole telemetry locations were within 2 m of decayed logs, we found that home range size decreased as volume of small decayed logs increased and that volume of decayed logs was important in separating high- from low-use areas. The inverse relationship observed between small decayed logs and home range size suggests that home range sizes may be small if they contain an abundance of resources necessary for survival.

Hayes and Cross (1987) found that western red-backed voles selected large over small logs. In contrast, we found that western red-backed voles selected highly decayed, medium-diameter logs. Large logs may be most useful to small mammals because they provide more cover and persist longer than small logs (Maser et al. 1979, Harmon et al.

1986). However, frequency of large, decayed logs was low in our sites. The positive relationship we found between medium and large hard logs and home range and core area sizes suggests that western red-backed voles used these logs in their daily activities. It is likely that these logs were used as travel corridors and cover (Hayes and Cross 1987, Tallmon and Mills 1994) en route to their core areas, but did not represent substantial food or nesting cover resource areas.

Organic soil depth was positively correlated with western red-backed vole abundance in both the Oregon Coast and Cascade Ranges by Gomez (1992) and Rosenberg et al. (1994) and was the strongest predictor of core area use in our study. Western red-backed voles often foraged in the organic soil layer (Maser et al. 1981), and organic soil depth was associated with truffle abundance in northeastern California mature fir (*Abies* spp.) stands (Waters et al. 1997) and in mesic old-growth Douglas-fir stands in the central Cascade Range in Oregon (Luoma 1988). A tendency for forest floor depth to increase with CWD cover, which provides microsites for truffles, also has been observed in the central Cascades (Luoma 1988).

Hypogeous fungi have been closely associated with decayed logs (Hayes and Cross 1987, Luoma 1988, Amaranthus et al. 1994) and organic soil depth (Maser et al. 1981). Some truffle species have clumped distributions (Waters et al. 1997) and may be more common in areas with high log volumes. We hypothesize that voles in our study used areas with decayed, clumped logs because of higher food availability and that organic soil depth differentiated areas used by voles because of the relationship of soil depth with truffle abundance. Further research that measures truffle abundance in relation to vole and log distribution and litter depth would address this hypothesis.

Several studies found positive associations between relative abundance of western red-backed voles and overstory canopy cover, age class (i.e., 1 or more seral stage), and snag density (Doyle 1987, Hayes 1983, Gomez 1992), and Hayes (1983) found positive associations of abundance estimates of western red-backed voles with overstory and understory tree density. We did not find a significant difference in overstory canopy cover between core areas and non-core areas within vole home ranges, but our sites had little variation in canopy cover compared to other studies. We did not measure

tree or snag density but predict that they would influence the location of vole core areas since they contribute to the forest litter layer through needle loss and decay and to CWD over time.

Males of the genus *Myodes* are not as territorial as females and spend much of their time searching for mating opportunities and resources (Bondrup-Nielson 1985, Gipps 1985). This may explain the movement patterns observed for the male voles in our study (they were active throughout most of the evening). Conversely, the more territorial nature of females combined with the fact that most of the females in our study were lactating, likely explains the shorter and less frequent movements of females. It was inferred from the movement patterns of the females that they were remaining in their nests for the majority of the evening, making only short, occasional sallies away to forage.

Western red-backed vole nest sites have been found in underground burrows or under organic debris (Stephens 1906). We found nests of 6 females that had slipped their radio collars. Five of these nests were located underground within decay class 4 and 5 logs. This further emphasizes the importance of decayed logs for western red-backed voles. Such logs provide thermal protection for young voles and an environment in which hypogeous fungi can fruit and thus provide a food source for nesting females.

Our data represent habitat and space use by western red-backed voles only during summer in specific forest stands in the Oregon Cascades. Extrapolation of these data to other areas within the species' geographic range or to other seasons should be done with caution. During periods when truffle abundance is low (particularly winter and during drought periods), a shift in diet to lichens (Ure and Maser 1982) may cause a shift in habitat and size of home range to accommodate foraging needs.

## Literature Cited

- Alexander, L. F., and B. J. Verts. 1992. *Clethrionomys californicus*. Mammalian Species No. 406:1-6.
- Amaranthus, M. P., J. M. Trappe, L. Bendar, and D. Arthur. 1994. Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Canadian Journal of Forest Research* 24:2157-2165.

The size of home ranges when coupled with habitat associations identify the habitat elements and their spatial arrangements useful when managing forests in a manner that could benefit populations of western red-backed voles. Several studies have shown a sharp decline in capture rates of red-backed voles after clearcutting (Gashwiler 1970, Hooven and Black 1976, Mills 1995), including in the forest stands used in this study (Gitzen et al. 2007). Removal of microhabitat features found important in this study (organic soil layer and CWD), and reduction in associated truffle composition likely contributed to this decline. Mature stands such as ours are typically harvested using clearcutting on private lands and are being thinned on federal lands. If management objectives include maintaining or increasing habitat for western red-backed voles, then resource managers should promote retention of deep organic soil layers and large volumes of logs distributed in 0.1-ha patches in coniferous forest stands. Connecting these patches with corridors of similar conditions may also enhance interpatch movements.

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- Aubry, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors), *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests*. USDA Forest Service, General Technical Report PNW-285, Pacific Northwest Forest and Range Experiment Station, Portland, OR. Pp. 285-294.

- American Society of Mammalogists. 1998. Guidelines for the capture, handling, and care of mammals as approved

- by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416-1431.
- Bondrup-Nielson, S. 1985. An evaluation of the effects of space use and habitat patterns on dispersal in small mammals. *Annales Zoologici Fennici* 22:373-383.
- Bondrup-Nielson, S., and F. Karlsson. 1985. Movements and spatial patterns in populations of *Clethrionomys* species: a review. *Annales Zoologici Fennici* 22:385-392.
- Cazares, E., D. L. Luoma, M.P. Amaranthus, C.L. Chambers, and J.F. Lemkuhl. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade Range. *Northwest Science* 73 (Special Issue):64-76.
- Clarkson, D. A., and L. S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwestern Oregon. *Northwest Science* 68:259-265.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red Deer: Behavior and Ecology of the Two Sexes*. University of Chicago Press, Chicago, IL.
- Corn, P. S., R. B. Bury, and T. A. Spies. 1988. Douglas-fir forests in the Cascade mountains of Oregon and Washington: Is the abundance of small mammals related to stand age and moisture. 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 Forest and Range Experiment Station, Fort Collins, CO. Pp. 340-352.
- Daubenmire, R. 1988. *Plant Communities: A Textbook of Plant Synecology*. Harper and Row, New York.
- Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus*, *Microtus oregoni*, and *M. richardsoni*. *The American Midland Naturalist* 118:258-265.
- Franklin, J. F., and C. T. Dyrness. 1973. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis.
- Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. *Journal of Mammalogy* 40:128-139.
- Gilbert, F. F., and R. Allwine. 1991. Small mammal communities in the Oregon Cascade range. In L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors), *Wildlife and Vegetation of Unmanaged Douglas-Fir Forests*. USDA Forest Service, General Technical Report PNW-285, Pacific Northwest Forest and Range Experiment Station, Portland, OR. Pp. 257-265.
- Gipps, J. H. W. 1985. Spacing behavior and male reproductive ecology in voles of the genus *Clethrionomys*. *Annales Zoologici Fennici* 222:343-351.
- Gitzen, R. A., S. D. West, C. C. Maguire, T. Manning, and C. B. Halpern. 2007. Response of terrestrial small mammals to varying amounts and patterns of green-tree retention in Pacific Northwest forests. *Forest Ecology and Management* 251:142-155.
- Gomez, D. M. 1992. Small mammal and herpetofauna abundance in riparian and upslope areas of five forest conditions. M.S. Thesis, Oregon State University, Corvallis.
- Halpern, C. B., D. McKenzie, S. A. Evans, and D. A. Maguire. 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. *Ecological Applications* 15:175-195.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Hayes, J. P. 1983. Forestry related aspects of the ecology of *Clethrionomys californicus*. M.S. Thesis, Southern Oregon State College, Ashland.
- Hayes, J. P., and S. P. Cross. 1987. Characteristics of logs used by western red-backed voles, *Clethrionomys californicus*, and deer mice, *Peromyscus maniculatus*. *Canadian Field-Naturalist* 101:543-546.
- Hollander, M., and D. A. Wolfe. 1973. *Nonparametric Statistical Methods*. John Wiley, New York.
- Hooven, E. F. 1971. Effects of clearcutting a Douglas-fir stand upon small mammal populations in western Oregon. Ph.D. Dissertation, Oregon State University, Corvallis.
- Hooven, E. F., and H. C. Black. 1976. Effects of some clearcutting practices on small mammal populations in western Oregon. *Northwest Science* 50:189-208.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied Logistic Regression*. Second edition. John Wiley and Sons, New York.
- Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. CALHOME: A program for estimating animal home ranges. *Wildlife Society Bulletin* 24:342-344.
- Luoma, D. L. 1988. Biomass and community structure of sporocarps formed by hypogeous ectomycorrhizal fungi within selected forest habitats of the H. J. Andrews Experimental Forest, Oregon. Ph.D. Dissertation, Oregon State University, Corvallis.
- Maguire, C. C. 2002. Dead wood and the richness of small terrestrial vertebrates in Southwestern Oregon. In W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle (technical coordinators), *Ecology and Management of Dead Wood in Western Forests*. USDA Forest Service, General Technical Report PSW-181, Pacific Southwest Research Station, Albany, CA. Pp. 331-345.
- Maser, C., J. M. Trappe, and D. C. Ure. 1978. Implications of small mammal mycophagy to the management of western coniferous forests. *Transactions of the North American Wildlife and Natural Resources Conference* 43:78-88.
- Maser, C., J. M., R. Anderson, K. Cromack Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody materials. In J. W. Thomas (editor), *Wildlife and Habitats in Managed Forests, the Blue Mountains of Oregon and Washington*. USDA Forest Service Agricultural Handbook No. 553. Washington Office, Washington, D.C. Pp. 78-95.
- Maser, C., B. R. Mate, J. F. Franklin, and C. T. Dryness. 1981. Natural history of Oregon coast mammals. USDA Forest Service, General Technical Report PNW-133:1-496.

- Maser, C., and Z. Maser. 1988. Mycophagy of red-backed-voles, *Clethrionomys californicus*. and *C. gapperi*. The Great Basin Naturalist 48:269-273.
- Mills, L. S. 1995. Edge effects and isolation: Red-backed voles on forest remnants. Conservation Biology 9:395-403.
- Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039-1044.
- Ribble, D. O., A. E. Wurtz, E. K. McConnell, J. J. Buegge, and K. C. Welch, Jr. 2002. A comparison of home ranges of two species of *Peromyscus* using trapping and radiotelemetry data. Journal of Mammalogy 83:260-266.
- Rosenberg, D. K., Swindle, K. A., and R. G. Anthony. 1994. Habitat associations of California Red-backed voles in young and old-growth forests in western Oregon. Northwest Science 68:266-272.
- Samuel, M. D., D. J. Pierce, and E. O. Garton. 1985. Identifying areas for concentrated use within the home range. Journal of Animal Ecology 54:711-719.
- SAS Institute Inc. 1992. SAS Technical Report P-299. SAS/STAT software: changes and enhancements. Release 6.97. SAS Institute Inc., Cary, North Carolina.
- Seaman, D. E., and R. A. Powell. 1990. Identifying patterns and intensity of home range use. International Conference of Bear Research and Management 8:243-249.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman, New York.
- Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research 12:18-28.
- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (editors), Wildlife and vegetation of unmanaged Douglas-fir forests. USDA Forest Service, General Technical Report PNW-285, Pacific Northwest Forest and Range Experiment Station, Portland, OR. Pp. 91-109.
- Stephens, F. 1906. California Mammals. The West Coast Publishing Company, San Diego, CA.
- Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:48-63.
- Tallmon, D., and L. S. Mills. 1994. Use of logs within home ranges of California red-backed voles on a forest remnant. Journal of Mammalogy 75:97-101.
- Thompson, R. L. 1996. Home range and habitat use of western red-backed voles in mature coniferous forests in the Oregon Cascades. M.S. Thesis, Oregon State University, Corvallis.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307-3315.
- Waters, J. R., K. S. McKelvey, D. L. Luoma, and C. J. Zabel. 1997. Truffle production in old-growth and mature fir stands in northeastern California. Forest Ecology Management 96:155-166.
- Wilson, D. E. and D. M. Reeder (editors). 2005. Mammal Species of the World: A Taxonomic and Geographic Reference (3rd ed.). Johns Hopkins University Press, Baltimore, MD.
- White, G. W. and R. A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc., San Diego, CA.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164-168.
- Wolff, J. O. 1989. Social Behavior in Advances in the Study of *Peromyscus* (Rodentia). Texas Tech University Press, Lubbock.

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