

BUSHY-TAILED WOODRAT ABUNDANCE IN DRY FORESTS OF EASTERN WASHINGTON

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We studied bushy-tailed woodrats (*Neotoma cinerea occidentalis*) in the eastern Washington Cascade Range to estimate their density and survival in 3 typical dry forest cover types. We predicted woodrat density to be high, moderate, and low in mature mixed-conifer forests, young mixed-conifer forests, and open ponderosa pine forests, respectively. We livetrapped on 8×8 grids (280 m) over an 8-day period each autumn for 4 years to obtain Huggins mark–recapture estimates of woodrat density. We captured woodrats 617 times and marked 193 individual woodrats in 12 sample stands during 42,165 trap nights. The sex ratio of captures was 62% female and 38% male. Adults made up 79% of captures. Woodrat density averaged 0.49 animals/ha among all cover types and years; woodrat density did not differ among types. Regardless of cover type, stands fell into 4 woodrat-density groups, with densities ranging from 0.13 to 0.93 woodrats/ha. Classification tree analysis revealed that woodrat-density groups could be predicted well (proportional reduction in error = 0.73 to 0.89) by the type and amount of cover provided by large snags, mistletoe brooms, and soft downed logs. Over the 4-year period, woodrat density ranged from 0.28 animals/ha to 0.87 animals/ha, increasing each year at a rate of $\lambda = 1.8$ consistently among cover types. A moderate ($r = 0.55$) density-dependent response in per capita rate of increase was detected. The apparent annual survival rate was a low 0.14. Management to reduce woody fuels and to restore low-intensity high-frequency fire regimes in ponderosa pine and dry Douglas-fir forest likely will reduce bushy-tailed woodrat populations unless prescriptions can mitigate the loss of snag, mistletoe, and downed log cover.

Key words: bushy-tailed woodrat, Cascade Range, density, dry forest, fuel management, *Neotoma cinerea*, survival, Washington

The bushy-tailed woodrat (*Neotoma cinerea*) is an uncommon yet widespread rodent in forests and rangelands of the northwestern United States and southeastern Canada (Smith 1997), where they are an important prey species of avian and mammalian carnivores (Carey 1991). In particular, the distribution and abundance of woodrats (*N. cinerea*, *N. fuscipes*) are thought to strongly influence the foraging behavior, habitat selection, and demography of the northern spotted owl (*Strix occidentalis caurina*) (Carey et al. 1992; Franklin et al. 2000; Zabel et al. 1993). However, density estimates of bushy-tailed woodrats in their various habitats have been unavailable (Verts and Carraway 1998) until recently.

Carey et al. (1999b) described regional patterns of bushy-tailed and dusky-footed woodrat (*N. fuscipes*) distribution, woodrat density, and habitat use in forests of western Oregon

and Washington. In western Washington, bushy-tailed woodrats are found mainly in rocky outcrops along streams in wet Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) forests. Rock outcrops for shelter have long been considered primary habitat for bushy-tailed woodrats throughout the range of the species (Dixon 1919; Finley 1958; Smith 1997; Verts and Carraway 1998). In the drier Douglas-fir and mixed-conifer forests of southwestern Oregon and northern California, bushy-tailed woodrats also are commonly found in young and old forests with diverse herbaceous, shrub, and truffle food sources (Maser et al. 1978) and with snags and logs for den sites and cover (Carey 1991, 1999b; Maser et al. 1984; Zabel et al. 1995).

Information on bushy-tailed woodrat ecology is lacking, however, for interior dry forests east of the crest of the Cascade Range, where prey diversity is thought to influence relatively high recruitment rates of northern spotted owls (Forsman et al. 1996). Bushy-tailed woodrats comprise 18% of the diet biomass of northern spotted owls in the eastern Washington Cascade Range, 2nd only to northern flying squirrels (53%) (Forsman et al. 2001). If prey distribution and biomass are

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TABLE 1.—Environmental attributes of 3 typical forest cover types of the eastern Washington Cascade Range where bushy-tailed woodrats were studied during 1997–2000. Four stands were sampled in each cover type.

	Cover type		Mature mixed conifer
	Open pine	Young mixed conifer	
Elevation (m)	1,115	1,092	1,207
Aspect code ^a	3.8	2.5	1.5
Slope (%)	36	30	39
Canopy closure (%)	40	60	75
Basal area (m/ha)	20	24	32
Age of largest trees ^b	129	112	156
<i>Pinus ponderosa</i> density (trees/ha)	343	164	86
<i>Pseudotsuga menziesii</i> density (trees/ha)	453	319	170
<i>Abies grandis</i> density (trees/ha)	465	1,765	1,565
Large snags (trees/ha) ^b	93	36	105
Coarse woody debris (% cover)	7	13	21
Soft large logs (% cover) ^c	1.2	0.9	3.0
Mistletoe severity index ^d	10.8	11.4	6.3
Understory species richness	38	44	46
Understory species cover (%)	55	60	61
Herb and shrub richness	34	41	43
Herb and shrub cover (%)	24	37	57
Truffle biomass (kg/ha) ^e	1.7	3.6	4.1

^a Aspect code ranges from 1 (cool, moist environment) to 4 (warm, dry environment) as determined by azimuth: 1 = north (315°–45°); 2 = east (45°–135°); 3 = west (225°–315°); 4 = south (135°–225°).

^b Largest trees and snags were >40 cm dbh.

^c Downed logs >23 cm diameter in soft decay classes 3–5.

^d Hawksworth (1977) mistletoe severity rating × frequency of infected trees.

^e Spring biomass from Lehmkuhl et al. (2004).

primary drivers of spotted owl resource selection (Carey 1985; Franklin et al. 2000; Zabel et al. 1995), then we hypothesized that woodrat density among forest cover types is correlated with patterns of resource selection by spotted owls in the eastern Washington Cascade Range. We predicted woodrat density to be high in mature mixed-conifer forests that are selected for by northern spotted owls (Forsman et al. 1990), moderate in young mixed-conifer forests that are used in proportion to availability by the owls, and low in open ponderosa pine forests that are avoided by the owls. Characteristics of those cover types, moreover, support our hypothesis.

Lehmkuhl et al. (2004) found that mature mixed-conifer stands in eastern Cascades dry forest have more large snags and woody debris for den sites, and higher potential food resources (foliage, fruit, seeds, truffles; Maser et al. 1978; Smith 1997; Verts and Carraway 1998) than do young mixed-conifer and open pine forests. Young stands have fewer large snags and large logs, and less woody debris for den sites and cover, although abundant mistletoe brooms (mostly Douglas-fir dwarf mistletoe, *Arceuthobium douglasii*) might compensate for the absence of snags. Young stands also have relatively less food production as a result of more xeric understories under moderate canopy cover. Open pine stands have relatively high numbers of large snags and mistletoe brooms, but little woody debris and few large soft logs. They also have the least food production among the 3 forest types as a result of xeric grass understories.

The primary goals of this research were to quantify the density of bushy-tailed woodrats (*N. c. occidentalis*) in interior Pacific Northwest forests and to determine how woodrat density varies temporally and spatially with forest stand composition and structure. A secondary goal was to provide data on prey density and habitat use to other researchers conducting independent studies of the resource selection and long-term demography of northern spotted owls in the same study area (Forsman et al. 1996).

MATERIALS AND METHODS

Study area.—The study area is in the Swauk Creek drainage of the Cle Elum Ranger District, Wenatchee National Forest, in the east-central Washington Cascade Range (47°15'00"N, 120°37'30"W). Study stands were on low-elevation (900–1,400 m) forest sites characterized by varying dominance of ponderosa pine, Douglas-fir, and grand fir (*Abies grandis*). This was an observational study in which we randomly selected 4 replicate sample stands in each of 3 common forest cover types: open ponderosa pine, young mixed-conifer, and mature mixed-conifer. Selected stands ranged from 13 to 20 ha, typical in the dissected terrain of the area, and were regularly shaped to conform to approximately square trapping grids. Stand overstory and understory live and dead structure and composition were measured from sixteen 0.02-ha plots using methods described by Everett et al. (1997) for the same study area.

Dry open pine stands had canopy closure of 30–45% and were dominated by scattered large (≥40 cm diameter at breast height [dbh]) ponderosa pines (Table 1). A patchy midstory of smaller (<40 cm dbh) Douglas-fir and grand fir was often present in mesic microsites, such as draws. Plant associations were predominantly the dry *Pseudotsuga menziesii*–*Calamagrostis rubescens* plant association (Lillybridge et al. 1995). The more mesic young mixed-conifer stands had moderate canopy closure of 50–70%, with a relatively high tree density (96% <40 cm dbh). Dominant tree species were grand fir and Douglas-fir, with a few ponderosa pines. Plant associations were mostly mesic *Abies grandis*–*Berberis nervosa*–*Calamagrostis rubescens*. The most mesic mature mixed-conifer stands had closed canopies (70–83%) dominated by a mixture of large grand fir and Douglas-fir >40 cm dbh, with some scattered large ponderosa pines, and a well-developed midstory and understory of grand fir and Douglas-fir. These sites had no record of being logged since the late 1930s, and were considered “late-successional forest” for forest management. The dominant plant association was *Abies grandis*–*Achlys triphylla*, the most mesic plant association encountered among the 3 cover types.

Cumulative precipitation (mostly snow) during the study period averaged 98 cm at the Blewett Pass SNOTEL weather station (1300 m elevation) located at the north end of the study area (Natural Resources Conservation Service 2000). Snow depth peaked during March at an average 139 cm (range 114–158 cm). Melt-out of the snow pack occurred during late April or early May. Summers were warm and dry. Mean maximum temperature during the summer was 34°C.

Field methods.—We live-trapped woodrats during the autumn from 1997 through 2000 following approved animal care guidelines (Animal Care and Use Committee 1998). Trapping methods followed design and sampling recommendations by Carey et al. (1991) for arboreal rodents. We put 2 Tomahawk 201 live traps at each grid point on 8 × 8 or 7 × 9 sampling grids with 40-m spacing; the recommended 10 × 10 grids were too big for the small patches found in these landscapes. We positioned a trap on the ground and another trap

1.5 m aboveground on the trunk of the largest tree within 5 m of the grid point. We covered traps with waxed milk cartons and forest-floor debris, included a nest box, and used bait (oats, peanut butter, and molasses) to attract animals and provide food to reduce the risk of hypothermia.

We trapped each stand for 2 weeks during late September or early October, with traps open for 4 days in each week. Traps were closed over the weekend to reduce trapping stress (Carey et al. 1991). Each trapped animal was identified to species, sexed, aged (adult, juvenile), weighed to index condition (Moses et al. 1995), and ear-tagged on both ears. We collected dead animals for examination of reproductive tracts and for voucher specimens retained at the United States Forest Service, Forestry Sciences Laboratory, Wenatchee, Washington.

Data analysis.—Trap nights were estimated with Nelson and Clark's method (1973), which accounts for stuck, sprung, and occupied traps. We estimated woodrat abundance for each stand and year in 2 ways. We calculated total individuals captured (Skalski and Robson 1992), or the minimum number known alive (MNKA—Krebs 1999), as an index of abundance to compare with Carey et al.'s (1999b) review of *Neotoma* abundance in western Oregon and Washington. We estimated true abundance by mark-recapture analysis using Program MARK (White and Burnham 1999). We used Huggins (1991) closed-mixture models (Pledger 2000) to estimate abundance because they allowed use of individual covariates to model capture probabilities and performed well with sparse data (G. White, pers. comm.). We tested the fit of the standard mark-recapture null (M_0), time (M_t), and behavior (M_b) models, and their combinations, to the data. For the capture heterogeneity model (M_h) and its combinations with other models (i.e., M_{th} , M_{bh} , M_{tbh}), we modeled heterogeneity as a 2-mixture model of capture probabilities (p_{low} , p_{high}) with a mixture proportion π for p_{low} . We compared 2-mixture models with weight and sex covariate-based heterogeneity models. We examined the influence of year, stand, and group (i.e., open pine, young, mature) covariates on capture probabilities. We assessed the relative support from the data for these capture models using Akaike's information criterion (AIC_c) model selection methods (Burnham and Anderson 2002). The model best supported by the data was the 2-mixture M_{th} model with constant π . The next best M_h model with $\Delta AIC = 8.1$ had "considerably less support," and the remainder of the tested models had "essentially no support" with $\Delta AIC > 10$ (Burnham and Anderson 2002).

We calculated woodrat density (n per ha) by dividing MNKA and Huggins abundance estimates for each stand and year by the trapped area, which was estimated by adding one-half the mean maximum distance moved to trapping grid dimensions (Otis et al. 1978). Mean maximum distance moved was estimated to be 86 ± 11 m (95% CI, $n = 140$ woodrats) from successive capture locations on all trapping grids within years. Carey et al. (1991) reported a similar mean maximum distance moved (85 ± 16 m, 95% CI) for western Washington and Oregon.

Survival was estimated by pooling stands within cover type, not by individual stands as for density, because too few woodrats were recaptured in some sample stands during consecutive years to estimate survival individually for those stands. We estimated apparent year-to-year survival as the percentage of animals captured in year t that were recaptured in year $t + 1$. Annual recapture data were too sparse to use more sophisticated mark-recapture models: only 13% of the woodrats were captured in >1 year. There seemed to be little apparent bias in estimating annual recapture probability because all annual recaptures were in 2 consecutive years, except for 1 animal that was captured in 3 consecutive years. We used repeated measures analysis of variance (ANOVA) with 3 cover types to test for annual differences in apparent survival.

We estimated the finite rate of population increase (λ) from successive changes in woodrat density (Huggins estimator) as $\lambda_{t+1} = \hat{N}_{t+1}/\hat{N}_t$ (Franklin 2002; Hines and Nichols 2002). Evidence for a density-dependent response in per capita rate of increase $r_t = \ln(\hat{N}_t/\hat{N}_{t-1})$ was examined by regressing r_t against $\ln(\hat{N}_{t-1})$ (Fryxell et al. 1998).

We tested hypotheses of cover type and time effects on mark-recapture estimates of woodrat density for individual stands and years with ANOVA (Coffman et al. 2001) in a 1-way repeated-measures design. We screened data to ensure they reasonably met assumptions of ANOVA; only sex ratios were transformed by the square-root transformation. Differences in dependent variables over time were evaluated in ANOVA as difference contrasts between consecutive years. We used Tukey's honestly significant difference (HSD) test to evaluate multiple comparisons among cover type means to determine if the main effect was significant.

We examined relationships between woodrat density (Huggins estimate) and stand-level habitat covariates that were identified a priori from the literature. We estimated the amount of terrestrial cover for den sites and escape cover by the presence of rock and the percentages of woody debris cover (≥ 13 cm diameter) and large soft logs (≥ 40 cm diameter). Soft logs were downed logs in decay classes 3 to 5 (Maser et al. 1979). Arboreal den site availability was estimated by the density of large snags (≥ 40 cm dbh) and an index of mistletoe infestation calculated as the product of an individual-tree severity index (Hawksworth 1977) and the percentage of infested trees. We estimated food and water resources in a stand from the richness (n species) and the combined percentage cover of herbs (dicots) and shrubs, the truffle biomass of ectomycorrhizal fungi (Lehmkuhl et al. 2004), and the distance from the trapping grid center to perennial or intermittent water sources as measured from United State Geological Survey topographic maps.

We used Pearson correlations to assess the univariate associations between habitat variables and woodrat density among individual stands. We also used algorithms from Breiman et al. (1984) for non-parametric classification tree analysis in SYSTAT (Wilkinson 2004) to explore multivariate relationships between woodrat-density class and habitat covariates of individual stands. The 12 study stands neatly fell into 4 woodrat-density classes in which density nearly doubled between successive groups. To identify habitat variables characterizing those groups, we did classification tree analysis using the Gini loss function and the proportional reduction in error (*PRE*, similar to the R^2 statistic) to assess goodness of model fit (Wilkinson 2004:42).

We accepted $P \leq 0.10$ as the observed probability level for Type I error in hypothesis tests. Although less conservative than $P \leq 0.05$, particularly with the relatively small sample size in this study ($n = 12$ sites), we considered $\alpha = 0.10$ to be an acceptable chance of Type I error for ecological field studies that was well within the bounds of statistical convention and that also allowed for reduced Type II error (Zar 1999). A significant difference is implied where a difference among means is reported, but we report exact P values in the text to allow readers to assess the probability of error relative to their own standard of significance (Zar 1999).

RESULTS

Capture rates.—We captured woodrats 617 times over the 4-year period during 42,165 trap nights, and marked 193 individual woodrats in the 12 sample stands. Capture mortality was 2.5%. Over 12 stands and 4 years, woodrats were captured in 43 (90%) of 48 capture sessions: every year in 8 stands, 3 years

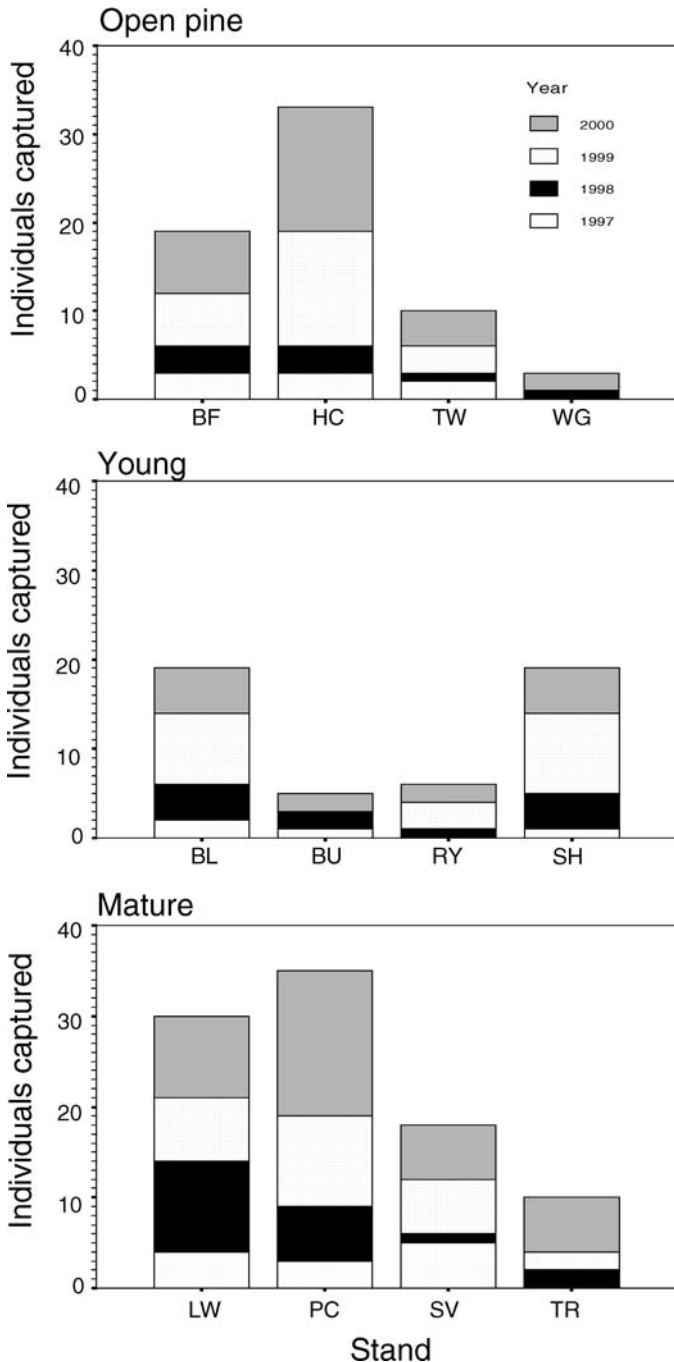


FIG. 1.—Total number of individual bushy-tailed woodrats captured over 4 years (1997–2000) in 12 stands of open ponderosa pine, young mixed-conifer dry forest, and mature mixed-conifer dry forest in the eastern Washington Cascade Range. (Stand labels are abbreviated names of individual sample stands).

in 3 stands, and 2 years in 1 stand (Fig. 1). Mean capture probabilities over the 8-day capture sessions for the 2-mixture M_{th} model were $\bar{p}_{low} = 0.123$ and $\bar{p}_{high} = 0.484$, with a constant proportional mixture of $\pi = 0.36$ for p_{low} . Captures were 38% male and 62% female (1 male:1.6 females); that ratio did not vary among cover types ($P = 0.63$). Adults (≥ 2 years old) composed 79% of overall captures, and that percentage did not vary among cover types ($P = 0.56$); however, age ratio was

TABLE 2.—Density of bushy-tailed woodrats (n/ha) in typical dry forests of the eastern Washington Cascade Range as estimated by the minimum number known alive (MNKA) and Huggins closed-capture modeling of mark–recapture data.

Cover type	Year				\bar{X}
	1997	1998	1999	2000	
MNKA enumeration					
Open ponderosa pine	0.19	0.19	0.53	0.65	0.39A ^a
Young mixed conifer ^b	0.10	0.27	0.48	0.34	0.30A
Mature mixed conifer	0.29	0.46	0.61	0.90	0.56A
\bar{X}	0.19A ^{cd}	0.31A	0.54B	0.63C	0.42
Huggins model estimation					
Open ponderosa pine	0.24	0.27	0.61	0.75	0.47A
Young mixed conifer	0.11	0.34	0.56	0.39	0.35A
Mature mixed conifer	0.34	0.54	0.70	1.04	0.65A
\bar{X}	0.23A ^c	0.38B	0.63C	0.73D	0.49

^a Cover type means followed by the same capital letter are not significantly different ($P \leq 0.10$) by Tukey’s honestly significant difference multiple-comparison test.

^b Mixed conifer: grand fir, Douglas-fir, and ponderosa pine.

^c Consecutive yearly means followed by the same capital letter are not significantly different ($P \leq 0.10$) by difference contrasts in repeated measures ANOVA.

^d MNKA cover type by year interaction not significant ($P = 0.49$).

^e Huggins cover type by year interaction not significant ($P = 0.47$).

less variable among mature stands (i.e., the standard error was 35% lower) than for young and open pine stands.

Woodrat density.—MNKA and Huggins woodrat density estimates in individual stands by year were highly correlated ($r = 0.998$, $P < 0.001$), but Huggins estimates averaged 17% higher than MNKA estimates. Huggins woodrat density (hereafter, simply woodrat density) averaged 0.49 ± 0.20 animals/ha (95% CI) among all cover types and years. The maximum woodrat density encountered in any stand or year was 1.81 woodrats/ha. Although mature mixed-conifer, open pine, and young mixed-conifer cover types appeared to have relatively high, moderate, and low densities of woodrats, respectively, cover type had no consistent effect on woodrat density ($P > 0.43$, Table 2) because of high variability among stands within cover types (Fig. 1). Ignoring cover type, stands fell into 4 readily apparent (Fig. 1) woodrat density groups: low ($\bar{X} = 0.13$, $n = 3$), moderately low ($\bar{X} = 0.28$, $n = 2$), moderately high ($\bar{X} = 0.54$, $n = 4$), and high ($\bar{X} = 0.93$, $n = 3$) densities.

Stand-level habitat covariates were weakly associated with woodrat density among sample stands: not one correlation exceeded the nominal threshold for statistical significance. Woodrat density was most strongly associated with the severity and frequency of mistletoe ($r = 0.48$, $P = 0.11$) and woody debris cover ($r = 0.45$, $P = 0.14$), followed by large snag density ($r = 0.38$, $P = 0.22$) and soft log cover ($r = 0.35$, $P = 0.27$). The presence of rock for den sites had little association with woodrat density ($r = 0.13$, $P = 0.69$). Among food covariates, truffle biomass had the strongest positive association with woodrat density ($r = 0.40$, $P = 0.20$), but truffle biomass was strongly correlated with woody debris cover ($r = 0.85$, $P < 0.001$). Herb and shrub forage richness ($r = 0.17$, $P = 0.61$) and cover ($r = -0.022$, $P = 0.95$) had little relationship to woodrat density, as did distance to perennial or intermittent water sources ($r = -0.23$, $P = 0.47$).

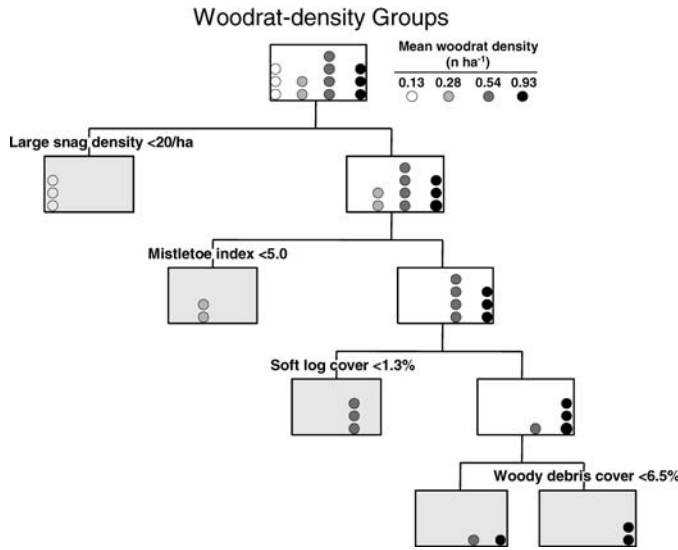


FIG. 2.—Habitat classification tree of sample stands (dots in boxes, $n = 12$) grouped a priori by similar density of bushy-tailed woodrats in dry forest of the eastern Washington Cascade Range. The tree is read like a dichotomous key. Labels at each level indicate the variable and threshold value for splitting cases. Cases in boxes with labels meet the criteria, whereas cases in the adjacent unlabeled box do not. Goodness of model fit to data is expressed as the proportional reduction in error (PRE) = 0.89.

Arboreal and terrestrial cover in the form of large snags, mistletoe, and soft logs together were relatively strong predictors ($PRE = 0.89$) of woodrat-density group in classification tree analyses (Fig. 2). The presence of relatively few large snags (<20 snags/ha, ≤ 30 th percentile of snag density values) best characterized low-density stands. Stands with greater numbers of large snags, but lacking cover supplied by mistletoe brooms (mistletoe index <5, ≤ 30 th percentile of mistletoe index values), supported moderately low densities of woodrats. Where good numbers of large snags and mistletoe brooms were present, but cover from soft logs was lacking (<1.3% cover, ≤ 50 th percentile of soft log values), woodrats were found in moderately high densities in 3 of 4 stands. The highest densities of woodrats were in stands with abundant large snags, mistletoe brooms, and soft log cover. A final split by woody debris cover of the high-density tree node in the classification tree, which included a misclassified moderately high density stand, indicated that relatively high amounts of woody debris ($\geq 6.5\%$, > 80 th percentile) might be negatively correlated with density, but the sample size of the split was small and the effect could be random error.

Over the 4-year period, yearly woodrat density (Huggins estimator) ranged from 0.23 to 0.73 woodrats/ha (Table 2). Mean woodrat density for all stands increased each year ($P < 0.001$) among cover types (i.e., no interaction, $P = 0.47$). The annual mean finite rate of increase (λ) among stands averaged 1.82 and was similar among cover types ($P = 0.59$) and years ($P = 0.22$) (Table 3). A moderate ($r = 0.55$) density-dependent response in per capita rate of increase was detected ($P = 0.002$) (Fig. 3).

TABLE 3.—Annual finite rates of increase ($\lambda_{t+1} = \hat{N}_{t+1}/\hat{N}_t$) of bushy-tailed woodrats in typical dry forest cover types of the eastern Washington Cascade Range.

Cover type	n^a	Year			\bar{X}
		1997–1998	1998–1999	1999–2000	
Open ponderosa pine	3	0.94	2.64	1.19	1.59A ^b
Young mixed conifer ^c	2	3.50	1.90	0.59	2.00A
Mature mixed conifer	3	1.57	2.79	1.30	1.88A
\bar{X}^d		2.03A	2.44A	1.03A	1.82

^a Because of missing data, $n < 4$ possible stands (stand omitted if woodrats were not captured in each year of study, i.e., λ not calculable).

^b Individual means followed by the same capital letter are not significantly different ($P \leq 0.10$) by Tukey’s honestly significant difference multiple-comparison test.

^c Mixed conifer: grand fir, Douglas-fir, and ponderosa pine.

^d No cover type by year interaction ($P = 0.45$).

Survival.—The apparent annual survival rate was a low 0.14 and did not vary over the study period ($P = 0.58$; Table 4). Survival appeared highest in mature stands, followed closely by young stands and much lower in open pine stands. Those differences, however, could not be statistically confirmed because sparse stand data (i.e., few recaptures) were pooled by cover type for survival estimation.

DISCUSSION

Our hypothesis of increasing habitat quality among open pine and young and mature mixed-conifer forests, as reflected in woodrat density and survival, was not supported by the data. Density and survival were too variable within cover types for

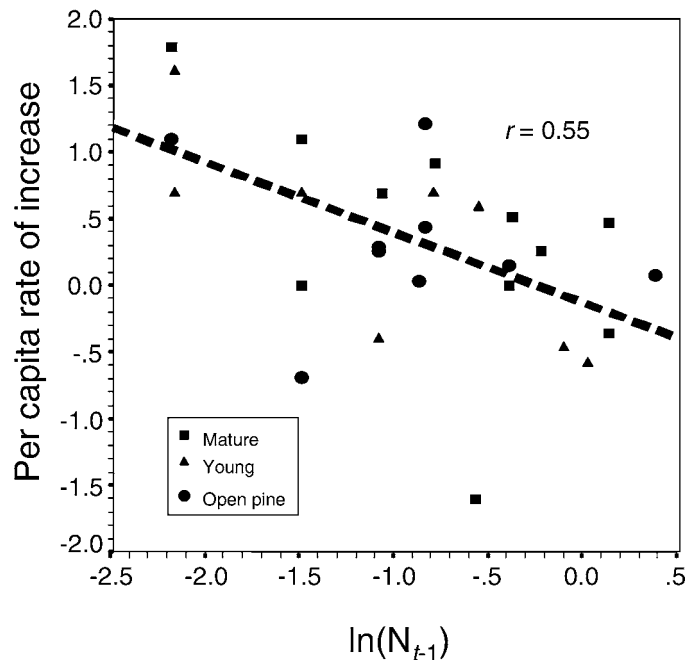


FIG. 3.—Density-dependent response in per capita rate of increase, $r_t = \ln(\hat{N}_t/\hat{N}_{t-1})$, in relation to population size, $\ln(\hat{N}_{t-1})$, of bushy-tailed woodrats in ponderosa pine and mixed-conifer dry forests of eastern Washington, 1997–2000.

TABLE 4.—Apparent annual survival rates of bushy-tailed woodrats in typical dry forest cover types of the eastern Washington Cascade Range, 1997–2000.

Cover type	Year			\bar{X}^a
	1997–1998	1998–1999	1999–2000	
Open ponderosa pine	0.14	0.13	0.05	0.10
Young mixed conifer ^b	0.25	0.17	0.05	0.16
Mature mixed conifer	0.08	0.21	0.20	0.17
\bar{X}^c	0.16A	0.17A	0.10A	0.14

^a Stand data were pooled by cover type for survival estimation, hence no replication to test for cover type effects. Cover types were sample units (i.e., $n = 3$) for repeated measures ANOVA of annual differences.

^b Mixed conifer: grand fir, Douglas-fir, and ponderosa pine.

^c Mean annual survival rate not significantly different ($P = 0.58$), as indicated by similar capital letters following means.

them to be good predictors of bushy-tailed woodrat habitat quality. Those results confirm the importance of cover elements (large snags, mistletoe, large logs) as fine-scale determinants, or primary limiting factors, of woodrat habitat value (Carey 1991, 1999b; Maser et al. 1984; Smith 1997; Verts and Carraway 1998). Although the value of mistletoe brooms for wildlife is well known (Bull et al. 1997; Hawksworth and Wiens 1996), particularly for arboreal rodents like the northern flying squirrel (Bakker and Hastings 2002; Bull et al. 2004; Lehmkuhl et al. 2006; Parks et al. 1999), prior research has not documented such a strong association between mistletoe and woodrat abundance.

Rock shelter has long been considered the primary habitat for bushy-tailed woodrats throughout their range (Carey 1991; Dalquest 1948; Dixon 1919; Smith 1997; Verts and Carraway 1998). Nevertheless, *N. c. fusca* in forests of the Oregon Coast Range has been associated primarily with snags, downed logs, and woody debris in the absence of significant rock fields (Carey 1991, 1999b; Maser et al. 1984). Our results also show that bushy-tailed woodrats can be abundant in dry interior forests where rock is scarce and snags, logs, and mistletoe brooms provide cover. Most study stands had no rocky outcrops or boulder fields, although a few had relatively small (<10 m high) basaltic outcrops along ridges at the periphery of stands. Such outcrops were fractured, but without large or extensive cracks or talus fields that could house woodrat groups. Larger basalt and sandstone slab outcrops occurred sporadically elsewhere in the study area, but not in or adjacent to the study stands.

Bushy-tailed woodrats appear much more abundant and widespread in dry forests of the eastern Cascade Range than in western hemlock, Douglas-fir, mixed-conifer, or mixed-evergreen conifer forests in western Oregon and Washington, where comparable data from Carey et al. (1999b) are available. We captured woodrats during 90% of the capture sessions and in all 12 sample stands, whereas Carey et al. captured woodrats on average in 42% of capture sessions in multiple studies (range 26–100%), often finding no woodrats and periodic local extinctions at upland sites in Douglas-fir forests. Comparing our MNKA estimate of woodrat density with those of Carey et al. overall woodrat density in our study (0.42 woodrats/ha) is

matched only by the mixed-conifer forest in the Umpqua Valley of southwestern Oregon, and our woodrat density is more than 4 times greater than in 6 of the 7 other provinces and locations sampled by Carey et al. in western Oregon. In the western hemlock zone of western Washington, Carey et al. captured no woodrats in upland forest sites ($n = 37$), but rocky forested riparian areas on the eastern Olympic Peninsula supported a high density of woodrats (0.9 woodrats/ha). In comparison, our best high-density woodrat habitats in the eastern Washington Cascades supported an average 0.79 woodrats/ha (MNKA estimate) over 4 years, with a peak woodrat density of 1.26 woodrats/ha (MNKA) during 1 year (2000). The highest MNKA woodrat density we encountered in any stand and year was 1.56 woodrats/ha.

Bear in mind that MNKA values underestimate true abundance (Carey et al. 1991, 1999b): our MNKA estimates were 17% lower than the Huggins estimates, which should be reliable estimates of true abundance because they account for varying capture probabilities (Anderson et al. 2001; Menkins and Anderson 1983; Otis et al. 1978). Our selection of a 2-mixture heterogeneity model for capture probability supports the argument for estimating abundance with methods that model capture probabilities (Otis et al. 1978). A 2-mixture high–low model seems reasonable based on a generally patchy distribution of woodrats in maternal colonies (Escherich 1975; Moses and Millar 1994; Smith 1997) across regular trapping grids. Nevertheless, our MNKA and Huggins estimators were highly correlated ($r = 0.998$) for all stands and years, so, at least in our case, MNKA or other estimators that do not estimate capture probabilities may provide adequate (but low) estimates of true abundance (McKelvey and Pearson 2001; Menkins and Anderson 1983).

Our 4-year mean woodrat density estimate may underestimate long-term average woodrat density and carrying capacity for the study area due to a possible population crash during the hard winter of 1996–1997 that preceded the 1st year of trapping. During that winter, snow pack was about 50% deeper and persisted longer than in the subsequent 3 years when winter conditions were relatively similar and close to long-term averages. A rebound in the population is suggested by the remarkably high estimated rate of increase of $\lambda > 2$ during the first 2 years of the study. In the final year of the study, mean woodrat density (Huggins estimate) averaged 0.73 woodrats/ha across all stands, nearly 50% higher than the 4-year average, and λ appeared to stabilize near 1.0, although a statistically significant trend in λ was not detected.

The mechanism for such a rebound in the population would appear to be high recruitment because the apparent annual survival rate was a consistently low 0.14. Year-to-year survival of 30–50% has been reported for bushy-tailed woodrats in cliff habitats (Smith 1997); however, our low survival rates are consistent with the observation that bushy-tailed woodrats without the protection of rocky dens are subject to intense predation and local extirpation by spotted owls (Carey et al. 1992), and that logs and cavities may not provide adequate thermal protection during the winter in harsh climates (Carey et al. 1999b). There is intense predation on bushy-tailed

woodrats because they are the 2nd most important prey for spotted owls in the study area (Forsman et al. 2001), and rock fields or cliffs for dens largely were not available in our study area (see discussion below).

Our results are consistent with the hypothesis of Carey et al. (1999b) that predation, primarily by the northern spotted owl, is an important determinant of regional patterns of bushy-tailed woodrat abundance. Regionally, they observed declining bushy-tailed woodrat occurrence and abundance in the absence of primary rock habitats (i.e., predation refugia) from southwestern Oregon to western Washington. They attributed that latitudinal pattern of woodrat abundance to increasing predation on woodrats as the diversity and abundance of alternate spotted owl prey declines from south to north, a phenomenon they described as a decreasing “dilution effect” of multiple spotted owl prey. Similarly, the high abundance of bushy-tailed woodrats in eastern Washington forests might be explained in part by a high prey-dilution effect coupled with abundant nonrocky predation refugia (i.e., snag, mistletoe, and downed log microhabitat elements) within stands. Northern flying squirrel density in the study area is high, rivaling that of southwestern Oregon (Lehmkuhl et al., in press): abundance of flying squirrel prey may reduce spotted owl predation pressure on woodrats. A landscape-scale factor that also might contribute to high woodrat abundance in the east Cascades is the predation refugia afforded by open pine forests, which are generally avoided by spotted owls (Forsman et al. 1990).

Management implications.—Current forest management in the dry forest zone represented by the study area is focused on conservation of habitat for the northern spotted owl, restoration of stable fire regimes, and maintenance of healthy dry forest ecosystems that have developed anomalously under nearly a century of fire exclusion (Graham et al. 2004; Okanogan and Wenatchee National Forests 2000). Management in spotted owl habitat, represented by the mature mixed-conifer type in this study, is primarily conservatory with little active manipulation of forest structure at this time. Open ponderosa pine forest and much of the young mixed-conifer types in this study are being actively managed to reduce stand density and fuel loads (i.e., downed wood) by thinning and prescribed fire.

Unmanaged mature stands would remain source habitat for bushy-tailed woodrats, whereas thinned and burned stands likely would be poor woodrat habitat. Cover provided by downed logs and mistletoe trees, whose dense brooms close to the ground torch easily in ground fires (Hessburg et al. 1994), would be mostly consumed by prescribed fire. Existing large snags with defects and old woodpecker cavities that provide woodrat nest sites (Carey 1991) also would be at risk of destruction by prescribed fire. Prescribed fire may kill trees and create replacement snags, but such low-intensity fires likely would not kill the large-diameter fire-resistant ponderosa pine and Douglas-fir trees that are the prime species and size for nest cavity excavation by most woodpeckers (Bevis 1994; Bull et al. 1997; Lehmkuhl et al. 2003). The decay process, moreover, might take up to 20 years to create a snag in which nest cavities could be excavated by most woodpeckers and used by woodrats, unless the tree had defects from bole pathogens

before the fire (Lehmkuhl et al. 2003). Thinning or burning to create patchiness of fire severity effects might mitigate some of these issues. However, long-term structural variability of managed stands might be difficult to sustain with a regular program of postthinning prescribed fire at regular intervals (~10 years) that is patterned after presettlement fire regimes (Everett et al. 2000; Wright and Agee 2004), unless fire management objectives specifically prescribe patchy coverage of fires and include localized fire refugia.

Recent work has suggested that many of these dry forest types typically considered to have widespread low-intensity high-frequency fire regimes (Agee 1991, 1993, 2003) may in fact have mixed-severity fire regimes with elements of low-, moderate-, and high-severity fire effects (Hessburg et al. 2005). Mixed-severity fires create patchy mosaics of varying burn intensity and a consequent complex of open and closed-canopy forest structure with abundant snags, woody debris, and understory development (Agee 1998, 2002; Lehmkuhl 2005). Management prescriptions that emulate such a mixed-severity fire regime might be more flexible than would a single approach that uniformly thins and burns dry forest to recreate open ponderosa pine stands, especially in the relatively mesic Douglas-fir and grand fir plant associations within the dry forest.

An approach similar to that proposed by Carey (1999a, 2000) for variable-density thinning in mesic Douglas-fir and western hemlock forest of western Washington, with retention of woody-debris legacies (large snags and woody debris) on the scale of 0.2–0.5-ha patches, might be a useful starting point for developing new dry forest management prescriptions. Managing for patchiness would also preserve important mistletoe trees while also isolating infected trees (Bull et al. 1997). Habitat patchiness also might better match the patchy within-stand distribution of bushy-tailed woodrats than would uniform stand treatments (Carey et al. 1999b).

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