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Authors: Innes, Robin J., Vuren, Dirk H. Van, Kelt, Douglas A., Johnson, Michael L., Wilson, James A., et al.

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HABITAT ASSOCIATIONS OF DUSKY-FOOTED WOODRATS (*NEOTOMA FUSCIPES*) IN MIXED-CONIFER FOREST OF THE NORTHERN SIERRA NEVADA

ROBIN J. INNES,* DIRK H. VAN VUREN, DOUGLAS A. KELT, MICHAEL L. JOHNSON, JAMES A. WILSON, AND PETER A. STINE

University of California, Department of Wildlife, Fish, and Conservation Biology, One Shields Avenue, Davis, CA 95616, USA (RJI, DHVV, DAK, JAW)
University of California, John Muir Institute of the Environment, Aquatic Ecosystem Analysis Laboratory, One Shields Avenue, Davis, CA 95616, USA (MLJ)
United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, Sierra Nevada Research Center, 2121 Second Street, Suite A-101, Davis, CA 95616, USA (PAS)

Dusky-footed woodrats (*Neotoma fuscipes*) are important components of forest communities, including serving as a primary prey of the California spotted owl (*Strix occidentalis occidentalis*), a species of concern in California. We examined habitat associations of the dusky-footed woodrat at 4 study sites in mixed-conifer forest of the northern Sierra Nevada, California, during 2003–2005. We investigated the importance of California black oak (*Quercus kelloggii*) as a macrohabitat component for woodrats, and we examined microhabitat association at 2 levels, house location and house use, by comparing house-site ($n = 144$) characteristics to random sites ($n = 144$) and characteristics of used and unused houses, respectively. Woodrat density was positively related to density of large (≥33-cm-diameter at breast height) oaks, probably because large oaks are valuable food resources. Location of woodrat houses was strongly influenced by the presence of large (≥30-cm-mean diameter) logs and large (≥30-cm-diameter at root collar) stumps, but also by steeper slopes, and lack of bare ground and mat-forming shrub cover. We found little evidence that adult woodrats distinguished among houses with respect to microhabitat, suggesting that woodrats make decisions about microhabitat suitability when the house is built. In 2005, adults chose larger houses that were characterized by more logs and less poletimber than those of subadults, but we detected no such differences in 2004. Dusky-footed woodrats in the northern Sierra Nevada would benefit from management techniques that promote the growth and retention of large California black oaks and create large logs and stumps within a stand.

Key words: dusky-footed woodrat, habitat association, house-site association, house use, *Neotoma fuscipes*, *Quercus kelloggii*, Sierra Nevada

Arboreal and semiarboreal rodents may be substantially affected by forest management practices (Smith et al. 2003). This is particularly true for species with specialized life-history requirements such as the dusky-footed woodrat (*Neotoma fuscipes*), which builds, maintains, and defends stick houses that are used for nesting, denning, and food storage (Carraway and Verts 1991). Dusky-footed woodrats play an important role in community dynamics. They are prey for many avian and mammalian predators including the California spotted owl (*Strix occidentalis occidentalis*), a species of concern in California due to its dependence upon late-seral forest ecosystems (United States Department of the Interior 2003), which are among the most highly altered ecosystems in the Sierra Nevada (Beardsley et al. 1999; Franklin and Fites-Kaufman 1996). For example, high woodrat biomass may reduce the area requirements of the spotted owl (Carey et al. 1990; Zabel et al. 1995), and measures of fitness of spotted owls may be associated with woodrat abundance (Buchanan 2004; Carey et al. 1992; Carey and Peeler 1995). Additionally, the availability of woodrat houses may influence species richness for small mammals, reptiles, amphibians, and invertebrates by providing shelter for these species, hastening decomposition of plant materials, and increasing soil fertility and moisture (Carey et al. 1999; Cranford 1982; M'Closkey

* *Correspondent: rjinnes@ucdavis.edu*

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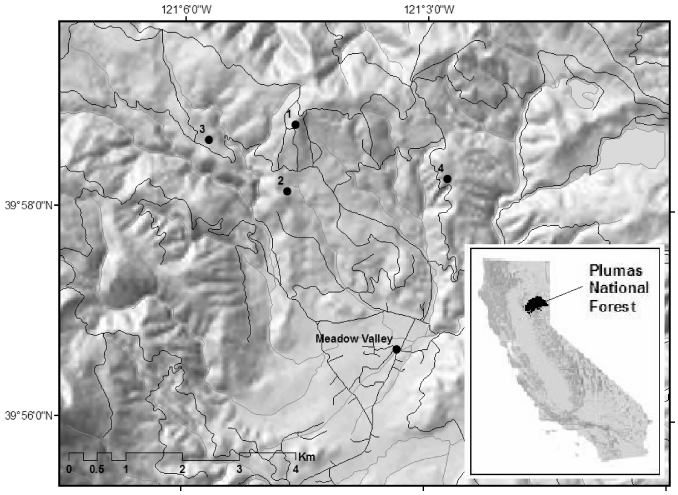


Fig. 1.—Map of study area in Plumas National Forest, California. Numbers indicate study site locations. Inset shows the location of Plumas National Forest in California.

et al. 1990; Merritt 1974; Vestal 1938). Thus, promoting quality habitat for the dusky-footed woodrat may provide a variety of ecological values in managed forests, for example, in the form of increased biological diversity.

The dusky-footed woodrat is a solitary, semiterritorial herbivore that eats the leaves, fruits, and nuts of woody plants and inhabits a wide variety of habitats, including chaparral, juniper woodland, streamside thickets, and deciduous or mixed forests with well-developed undergrowth (Carraway and Verts 1991). We studied the macro- and microhabitat associations of dusky-footed woodrats in mixed-conifer forest of the northern Sierra Nevada. Mixed-conifer forest is one of the most prevalent forest types in this region, and has been a focus of intensive commercial timber harvest for more than 100 years (Franklin and Fites-Kaufman 1996). Macrohabitat (e.g., stand-level) characteristics are important for dusky-footed woodrats in mixed-conifer forests in California and Oregon; woodrat abundance was correlated with vegetative density, and woodrats were most abundant in sapling and early-poletimber stands with a brushy understory component (Carey et al. 1992, 1999; Forsman et al. 1984, 1991; Sakai and Noon 1993). Although vegetative density may be more important in determining woodrat abundance than plant species composition in some areas (Carey et al. 1999; Horton and Wright 1944), certain plants may be important as food sources. California black oaks (*Quercus kelloggii*) are the dominant hardwood species in the mixed-conifer forests of the northern Sierra Nevada (McDonald 1988), and their foliage and acorns are favored food for dusky-footed woodrats (Atsatt and Ingram 1983; Cameron 1971; Meserve 1974), which are considered well adapted to woody plants high in fiber and plant secondary compounds (Atsatt and Ingram 1983; McEachern et al. 2006). Hence, our 1st objective was to quantify the association between woodrat density and density of California black oak at the macrohabitat scale.

The importance of microhabitat (e.g., house-level) variables to dusky-footed woodrats within mixed-conifer forest is not well understood, but such variables influence many species of small mammals (e.g., Coppeto et al. 2006; Manning and Edge 2004; Martin and McComb 2002), and limited information suggests they may influence woodrat distribution and abundance as well (Carey et al. 1991; Vestal 1938). We examined microhabitat association at 2 levels, placement of houses within mixed-conifer habitat and use of houses.

Dusky-footed woodrats typically construct conspicuous, conical houses on the ground using sticks, bark, and plant cuttings, although some houses are built on limbs or in cavities of trees (Fargo and Laudenslayer 1999); our study focused on ground houses. Given the investment involved in building, maintaining, and defending a house, we predicted that houses should be distributed such that they minimize energetic costs of movement, yet maximize individual fitness components (Manley et al. 1993), such as access to food, protection from predators, and a thermally suitable microclimate (Atsatt and Ingram 1983). We evaluated house-site association by dusky-footed woodrats by comparing house sites with nearby random sites. Based upon earlier literature, we developed 4 hypotheses concerning house location. First, we predicted woodrats would favor dense, tall (>1-m) shrub cover for protection from temperature extremes and aerial predators (Fitch 1947; Gander 1929; Lee and Tietje 2005). Second, houses should be placed close to preferred forage (i.e., large California black oaks) to reduce foraging time and exposure to predators (Atsatt and Ingram 1983; Carey et al. 1999; Vestal 1938). Third, house sites should have greater density and basal area of smaller trees (i.e., saplings) than random sites to facilitate access to the tree canopy (Vestal 1938). Finally, woodrats should select house locations with abundant dead wood to provide the framework and foundation for the house (Fargo and Laudenslayer 1999; Linsdale and Tevis 1956) and facilitate rapid and inconspicuous movement (Bakker 2006).

Only a subset of available houses is used by woodrats at any one time (Carey et al. 1991; Cranford 1977; Lynch et al. 1994); some houses are maintained by successive occupants, whereas others are occupied only briefly, or not at all (Vestal 1938; Wallen 1982; Willy 1992), suggesting that some houses are more suitable than others. We evaluated house suitability, or quality, by comparing characteristics of used and unused houses. Because woodrats defend their house against conspecifics, subadults might be forced to settle in lower quality houses (i.e., houses with reduced thermal and protective cover located a greater distance from preferred forage—Vestal 1938); hence, we hypothesized that houses selected by subadults would differ from those selected by adults.

Materials and Methods

Study area.—We conducted our study in the Plumas National Forest near Quincy (121°N, 39°W), Plumas County, California, on managed forest during the snow-free period, 2003–2005 (Fig. 1). Four study sites (1,450–1,750 m elevation) where established in early-seral forest (30–40 years postlogging), representative of the Sierra Nevada westside mixed-conifer forest type characterized by California black oak, sugar

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pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). All study sites had a brushy understory consisting primarily of deer brush (*Ceanothus integerrimus*), buck brush (*C. cuneatus*), and mountain whitethorn (*C. cordulatus*), with lesser coverage by greenleaf manzanita (*Arctostaphylos patula*), whiteleaf manzanita (*A. viscida*), and mountain dogwood (*Cornus nuttallii*). Each study site consisted of a discrete habitat patch (range 3.7–6.7 ha) with woodrat activity extending into 1–3 adjacent habitats. Habitat type and study site extent were defined by geographic information system data layers provided by the United States Department of Agriculture, Forest Service, Davis, California. Habitats varied in composition of overstory and understory dominants, canopy closure, and aspect. Sites 1 and 2 had moderately sloping topography; sites 3 and 4 had mixed terrain or undulating topography. Mean annual precipitation for 2000–2005 was 1,097 mm and mean temperatures ranged from 1.9°C in January to 21.2°C in July (Western Regional Climate Center 2006).

Median historic (i.e., presettlement) fire return intervals throughout the Sierra Nevada mixed-conifer forest are less than 20 years (McKelvey et al. 1996). However, fire suppression and silvicultural practices over the past 100 years have altered the landscape, and created forests that are denser, composed of smaller trees, and have higher proportions of white fir and incense cedar than were present historically (McKelvey et al. 1996). Within our study sites, logging activities and fire suppression practices have contributed to abundant dead wood as well as shrubby gaps interspersed with patches of dense, closed canopy forest. Recent (<5 years) management activities (e.g., prescribed burns and logging) have created open understory and overstory conditions in areas between study sites. Study sites were located 1.2–2.8 km apart, and no woodrats were recorded moving between study sites.

Locating woodrat houses.—We systematically searched for woodrat houses in the spring and fall of 2004 and 2005 by walking overlapping belt transects that covered each study site. In addition, woodrat houses were opportunistically located at all study sites during a concurrent radiotelemetry study of woodrat movements. Each house was marked and its location mapped (≤1 m) using a global positioning system unit (GeoExplorer and GeoXT; Trimble Navigation, Ltd., Sunnyvale, California), and volume was estimated as a cone using measurements of length, width, and height.

Determining house use.—We documented house use by livetrapping in the late summer–early fall (August–September) of 2004 and 2005. Each trap session consisted of 4 consecutive trap-nights. Four Sherman live traps (7.6 × 9.5 × 30.5 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were placed at entrances and along runways located within 1 m of the base of each house, and all houses within each study site were trapped to ensure that all individuals were captured. Traps were baited with raw oats and sunflower seeds coated with peanut butter. Synthetic batting was provided for thermal insulation. Traps were opened before dusk and checked and closed each morning at dawn. Woodrats were readily captured and frequently recaptured; longer trapping efforts (>4 consecutive nights) do not yield higher success (Carey et al. 1991, 1999; Laudenslayer and Fargo 1997; Willy 1992). We assumed that all animals within the population were captured at least once, and we calculated woodrat density as the minimum number known alive divided by size of the study site. A house was considered used if a woodrat was captured at the house at least once during the 4-day trapping session and unused if no woodrats were captured at that house during that time.

Captured woodrats were transferred to a mesh handling bag, marked with numbered Monel ear tags (National Band and Tag Co., Newport, Kentucky), weighed, and sex was determined; they then were released at the point of capture. Age of woodrats was estimated based upon a combination of weight (juvenile: <100 g, subadult: 101–169 g, and adult: ≥170 g), pelage (juvenile: gray, subadult: intermediate, and adult: brown), and reproductive condition (juvenile–subadult: nonreproductive, adult female: pregnant–lactating, and adult male: scrotal). Juveniles typically were captured with adult females, which were presumed to be their parents. All handling procedures were approved by the University of California, Davis Animal Use and Care Administrative Advisory Committee, and met guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

Macrohabitat association.—To quantify the relationship between woodrat density and California black oak density, we estimated California black oak density (no./ha) at each study site by counting trees ≥5 cm diameter at breast height (dbh) during September 2005 in 10 × 100-m belt transects placed in a stratified random fashion, such that approximately 10% of the total area was sampled. We regressed mean density of adult woodrats (2004 and 2005 combined) on oak density with simple linear regression using JMP IN 5.1.2 (SAS Institute Inc. 2004). Because we predicted a positive association, we used a 1-tailed test. We ran residual diagnostics to confirm that the model was appropriate for the data set (Neter et al. 1996). Because California black oaks begin to produce acorns in substantial quantities (>9 kg) at about 80 years of age (≈33 cm dbh—McDonald 1969), we ran separate analyses on small (<33 cm dbh) and large (≥33 cm dbh) oaks.

Microhabitat association.—We measured microhabitat variables within a 4-m-radius circle (50.3 m^2) centered on 144 houses and 144 paired random sites during September–November 2003, May–October 2004, and May–September 2005. Plot size was based upon visual estimates of patch size at woodrat houses (i.e., the microhabitat changed beyond a 4-m radius). We randomly selected 66% and 87% of houses at sites 1 and 2, respectively, where houses were more abundant, and sampled 100% of houses at sites 3 and 4.

At each woodrat house, we visually estimated percent cover of 3 ground cover variables and measured density and cover of shrubs, trees, snags, stumps, and logs (Table 1). We determined density (no./ha) of short and tall shrubs by counting individual stems. To determine if woodrats were selecting for greater density and basal area of smaller trees, we measured density (no./ha) and basal area (m^2/ha) of tree species in 4 dbh classes modified from Bell and Dilworth (1993): sapling, poletimber,

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Table 1.—Description of habitat variables measured in 4-m-radius plots at 144 dusky-footed woodrat (*Neotoma fuscipes*) houses and 144 random sites in Plumas National Forest, California, 2003–2005. dbh = diameter at breast height; drc = diameter at root collar.

Variable	Description
Stems of woody plants	
Short shrub	Woody stems <1 m tall, excluding mat-forming shrubs
Tall shrub	Woody stems ≥1 m tall and <5 cm dbh
Sapling	Woody stems 5.0–9.9 cm dbh
Poletimber	Woody stems 10.0–27.9 cm dbh
Small sawtimber	Woody stems 28.0–53.3 cm dbh
Large sawtimber	Woody stems ≥53.4 cm dbh
Small oak	*Quercus kelloggii* stems 5.0–32.9 cm dbh
Large oak	*Quercus kelloggii* stems ≥33.0 cm dbh
Dead wood	
Log	Downed, dead wood ≥1 m long and ≥5 cm at the narrowest end
Large snag	Standing dead wood ≥30 cm dbh and >1.3 m tall
Large stump	Standing dead wood ≥30 cm drc and 0.1–1.3 m tall
Ground cover (%)	
Bare ground	Exposed soil
Rock	Exposed boulders, cobble and gravel
Mat-forming shrub	Trailing, near ground surface (<0.3 m tall) woody stem cover (e.g., *Symphoricarpos rotundifolius*)
Other	
Canopy closure	Percent closed sky at eye level (1.7 m)
Degree slope	Degree of ground surface decline or incline

small sawtimber, and large sawtimber. California black oaks may be important at the microhabitat level as well as the macrohabitat level; hence, we excluded California black oak trees from tree density and basal area calculations and examined the presence of small (<33-cm-dbh) and large (≥33-cm-dbh) oaks separately. We recorded the presence of large (≥30-cm-dbh) snags because we observed that woodrats frequently accumulate debris in the cavities of large snags. We measured tree and snag diameters using a diameter tape. We measured the diameter at root collar (drc) of stumps using a measuring tape, and recorded the presence of large (≥30 cm drc) stumps because these were big enough to provide a platform for debris. We measured the diameter and length of logs using calipers and a measuring tape, and the volume of each log (m^3/ha) was estimated as a frustrum paraboloid using length of logs and diameters at both ends (Bell and Dilworth 1993). We recorded the presence of large (≥30-cm-mean diameter) logs because we observed that woodrats frequently accumulate debris in the cavities of or on top of large logs. The percent of canopy closure was quantified using a moosehorn with an 8.5 × 8.5-cm grid viewed at eye level (1.7 m) from the center of the plot, and the number of squares obscured by vegetation was recorded (Jennings et al. 1999). Slope was measured using a clinometer. All visual estimates were performed by 1 observer (RJI).

We also sampled, with replacement, the same vegetation and structural characteristics at paired points located a random distance (10–50 m) and a random direction from the center of each house. Random sites were constrained to lie within the same habitat type as the paired house. The distance requirement ensured that the random sites fell outside of the sampled house site, but within the estimated home range of a dusky-footed woodrat (1,942–4,459 m^2—Cranford 1977; Lynch et al. 1994).

Statistical analyses.—We used conditional logistic regression to predict the odds of finding a house at a certain location given the explanatory variables. Conditional logistic regression can fit a model based on conditional probabilities that ''condition away'' or adjust out the grouped effect (Stokes et al. 2001). We considered each house–random pair to be separate strata, adjusted out subject-to-subject (i.e., house-to-house) variability and concentrated on within-subject (i.e., house-to-random) information. In this way, conditional logistic regression conditions out variability due to macrohabitat differences and concentrates on variability due to microhabitat preference. Quantitative comparisons of microhabitats are possible by examining odds ratios, which indicate the increased likelihood of the outcome with each unit increase in the predictor given the covariate pattern (Keating and Cherry 2004).

Before conditional logistic regression analyses, we examined Spearman's rank correlations between variables to identify collinearity. Variables that were highly correlated ($r_s \geq |0.7|$) and those that explained similar biological phenomena were not included together in multivariate models (e.g., sapling density and sapling basal area, $r_s = 0.98$—Hosmer and Lemeshow 1989). In addition, we performed univariate conditional logistic regression using PROC PHREG in SAS 8.02 (SAS Institute Inc. 2001) to reduce the number of candidate variables for model building. We compared microhabitat variables between house and random sites and included habitat type ($n = 10$) as an interaction term in each single-variable model because we hypothesized that some variables might respond differently among habitats. We retained those variables with P-values ≤0.25 from log-likelihood ratio tests or variables that had significant habitat-type interactions (Hosmer and Lemeshow 1989).

We then performed multivariate conditional logistic regression to determine which combination of microhabitat variables best discriminated between house and random sites. We built conditional logistic regression models using forward stepwise selection using the screening criteria recommended by Hosmer and Lemeshow (1989—$P = 0.15$ to enter and $P = 0.20$ to remove), so as not to exclude potentially important variables from the model. At each step, we selected the model with the lowest Akaike's information criterion (AIC) value, and combined this model with all other variables (Table 2); the best model was that with the lowest AIC value, and any model within 2 AIC points of the best model was considered to be a competing model (Burnham and Anderson 1998). The final model(s) were those for which all coefficients were significant. We examined model residual chi-square and residual diagnostics to further assess model goodness-of-fit (Hosmer and Lemeshow 1989; Stokes et al. 2001).

We used likelihood ratio chi-square tests to determine that house use was nonrandom (all tests $P \leq 0.05$). We used a reverse stepwise multiple logistic regression no-intercept model to determine if there were combinations of microhabitat

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TABLE 2.—Frequency, mean values, and standard errors (*SE*s) for microhabitat variables in 4-m-radius plots centered at dusky-footed woodrat (*Neotoma fuscipes*) ground houses ($n = 144$) and paired random sites ($n = 144$) in the northern Sierra Nevada, California, 2003–2005. Parameter estimates, *P*-values for the Wald chi-square statistic, and Akaike's information criteria (AIC) are presented from a univariate conditional logistic regression.

Variable	$\bar{X}$ (*SE*)		Parameter estimate (*SE*)	*P*	AIC
	House site	Random site			
Density (no./ha)					
Short shrub	19,054.2 (1,656.5)	24,552.4 (1,945.9)	−0.00003 (0.00001)	0.003	186.24*
Tall shrub	9,950.0 (641.8)	6,761.1 (561.7)	0.0001 (0.00002)	<0.001	189.39*
Sapling	494.4 (51.0)	418.1 (42.9)	0.0003 (0.0002)	0.241	200.20*
Poletimber	395.8 (41.6)	381.9 (34.2)	0.0001 (0.0003)	0.774	201.54
Small sawtimber	123.6 (15.3)	143.1 (16.7)	−0.0005 (0.0006)	0.385	200.86
Large sawtimber	12.5 (4.0)	16.7 (4.6)	−0.0014 (0.0022)	0.514	201.20
Log	845.7 (77.8)	717.1 (64.2)	0.0002 (0.0002)	0.218	188.95*
Basal area (m^2/ha)					
Sapling	2.0 (0.2)	1.6 (0.2)	0.0778 (0.0549)	0.157	199.47*
Poletimber	8.2 (0.9)	9.0 (0.8)	−0.0087 (0.0126)	0.490	201.15
Small sawtimber	13.3 (1.7)	16.3 (2.0)	−0.0059 (0.0053)	0.266	200.36
Large sawtimber	4.1 (1.4)	4.9 (1.4)	−0.0027 (0.0068)	0.689	201.47
Volume (m^3/ha)					
Log	124.7 (18.2)	38.5 (7.5)	0.0048 (0.0015)	0.001	171.54*
Ground cover (%)					
Bare ground	3.5 (0.5)	5.1 (1.0)	−0.1282 (0.0543)	0.018	192.71*
Rock	1.3 (0.2)	2.8 (0.8)	−0.0216 (0.0148)	0.144	193.65*
Mat-forming shrub	13.9 (1.2)	19.8 (1.7)	−0.0273 (0.0091)	0.003	189.43*
Other					
Canopy closure (%)	67.8 (2.8)	64.2 (2.8)	0.0035 (0.0036)	0.331	199.29
Degree slope	19.3 (0.7)	16.4 (0.6)	0.1257 (0.0311)	<0.001	199.29*
Presence (no. plots)					
Small oak	40%	30%	0.5390 (0.2746)	0.050	197.63*
Large oak	10%	3%	1.7912 (0.7636)	0.019	193.70*
Large snag	4%	4%	0.0000 (0.5774)	1.000	201.63
Large stump	49%	17%	1.4191 (0.2877)	<0.001	169.44*
Large log	39%	12%	1.3471 (0.3113)	<0.001	167.34*

* Variables with *P*-values ≤0.25 from log-likelihood ratio tests were included in multivariate models predicting house sites from random sites.

variables that best distinguished houses used and unused by adult woodrats, and to compare houses used by adults and subadults. All 22 variables were included in multiple logistic regression models; in addition, we included house volume (above versus below the median of 0.3 m^3; "large" versus "small," hereafter) to determine if house size influenced use (Vestal 1938). Chi-square and multiple logistic regression were applied using JMP IN 5.1.2 (SAS Institute Inc. 2004). Only houses used exclusively by an adult or a subadult were included in analyses; houses at which an adult and a subadult were captured at least once during the 4-day trapping session were omitted from analyses comparing adult and subadult house use, resulting in the omission of 6 houses (4.2%) in 2004 and 4 houses (2.8%) in 2005. Juvenile woodrats were excluded from all analyses. Significance level for all tests was set at $\alpha = 0.05$. All means are presented as $\pm SE$.

RESULTS

Macrohabitat association.—Woodrats occurred at higher densities at sites with greater numbers of large oaks ($R^2 = 0.68$, $d.f. = 3$, $P = 0.088$). In contrast, woodrat density was not related to the density of small oaks ($R^2 = 0.30$, $d.f. = 3$, $P = 0.225$).

House-site association.—Across 144 houses and 144 paired random sites, no habitat type interactions were significant at $\alpha = 0.05$. Univariate analyses indicated that house sites were more structurally diverse than paired random sites, with a greater density of tall shrubs, presence of large oaks, and greater cover by downed dead wood, such as logs and stumps (Table 2). Random sites were more likely to have bare ground and short vegetation (i.e., short shrub or mat-forming shrub) cover, and be placed in areas with gentler slopes. Fourteen of 22 habitat variables measured were included in model building (Table 2).

The best multivariate model, based upon AIC scores, indicated that the combination of presence of large logs, presence of large stumps, slope, and cover by mat-forming shrubs and bare ground best distinguished house sites from random sites ($P < 0.001$; Table 3). Odds ratios indicate that a site was more than 4 times more likely to be a house site if it had ≥1 large stump present and almost 3 times more likely

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TABLE 3.—The best habitat model based upon the lowest Akaike information criterion used to explain the difference between dusky-footed woodrat (*Neotoma fuscipes*) house sites ($n = 144$) and paired random sites ($n = 144$) in the Plumas National Forest, California, 2003–2005. Parameter estimates, standard errors (*SE*s), *P*-values for the Wald chi-square statistic, odds ratios, and 95% odds ratio confidence limits are presented from a conditional logistic regression. Odds ratios indicate the increased likelihood of the outcome with each unit increase in the predictor given the covariate pattern.

Variable	Parameter estimate (*SE*)	*P*-value	Odds ratio	95% odds ratio confidence limits	
Large log presence	1.0272 (0.3780)	0.007	2.793	1.331	5.860
Large stump presence	1.4360 (0.3603)	<0.001	4.204	2.075	8.517
Degree slope	0.1392 (0.0428)	0.001	1.149	1.057	1.250
Mat-forming shrub (%)	−0.0362 (0.0136)	0.008	0.964	0.939	0.990
Bare ground (%)	−0.0514 (0.0246)	0.037	0.950	0.905	0.997

to be a house site if it had ≥1 large log present. Slope also was an important component to houses; each degree increase in slope increased the probability of a site containing a house by nearly 15%. No additional models were within 2 AIC points of the best approximating model.

House use.—We captured 40 adult and 30 subadult dusky-footed woodrats in 2004 and 35 adult and 14 subadult dusky-footed woodrats in 2005. Adult woodrats used houses with reduced presence of small oaks in 2004 relative to unused houses (parameter estimate: -0.394 ± 0.197, odds ratio: 0.454, $P = 0.047$). Houses used and not used by adults did not differ in 2005 ($P > 0.05$). Houses used by adults and subadults did not differ in 2004 ($P > 0.05$), but they did in 2005; adults used large houses (parameter estimate: 0.868 ± 0.375, odds ratio: 5.679, $P = 0.020$) in combination with greater density of logs (parameter estimate: 0.002 ± 0.001, odds ratio: 2,942.1, $P = 0.010$) and reduced basal area of poletimber (parameter estimate: -0.085 ± 0.041, odds ratio: 0.013, $P = 0.038$) compared to subadults.

DISCUSSION

Our results suggest that large oaks may be an important macrohabitat component for dusky-footed woodrats in shrubby, mixed-conifer forest. Oaks are an important food plant for woodrats (Atsatt and Ingram 1983; Cameron 1971), and large oaks provide acorns in addition to foliage for food. Acorns can be readily cached in houses and eaten year-round, especially when other food sources are less available (Castleberry et al. 2002; English 1923; Reichman and Fay 1983). In contrast to our results, Willy (1992) found no relationship between oak density and density of woodrat houses in a California coastal hills population. However, other mast-producing trees were common at the California coastal hills site (Willy 1992), but rare in our area; hence, oaks in our study may have been an especially important resource for woodrats.

We predicted that the location of woodrat houses would be influenced by density of tall shrubs, proximity to large oaks, availability of saplings, and abundance of dead wood. However, the final model indicated that abundance of dead wood in combination with slope, bare ground, and mat-forming shrub cover provided the best explanation for house location. Woodrats frequently use dead wood as the framework or foundation of a house (Fargo and Laudenslayer 1999); 92% of houses in our study were close to a stump or a log, and 70% were built close to a large log or a large stump, underscoring the importance of size of individual logs and stumps (Table 2). Our results contrast with other woodland-associated *Neotoma*, which do not appear to select house locations close to dead wood (Gerber et al. 2003). The close association between house location and abundance of dead wood we report may reflect past forest management practices, particularly selective thinning (Carey et al. 1999; Sierra Nevada Ecosystem Project 1996; Thome et al. 1999), which has created abundant logs and stumps in our area. Abundance of *Neotoma* (Carey et al. 1991, 1999; Converse et al. 2006; Lehmkuhl et al. 2006) and many other small mammals (e.g., Carey and Johnson 1995; Manning and Edge 2004; McCay 2000) frequently is correlated with abundance of dead wood. Dead wood is important as denning, nesting, resting, foraging, and cache sites for numerous small mammals (McComb 2003), and small mammals may selectively use dead wood for travel (Bakker 2006; Barnum et al. 1992; McCay 2000; McMillan and Kaufman 1995).

Univariate analyses suggested that density of tall shrubs may be an important microhabitat component at house locations; for example, houses had 33% more stems of tall shrubs on average than random sites (Table 2); however, tall shrub density did not emerge as a significant variable in the final model, despite the importance of tall shrubs as food and cover for woodrats (Carraway and Verts 1991). The model also did not include any variables associated with live trees, including abundance of saplings or proximity of large oaks, suggesting that saplings were not important for access into the canopy. Large California black oaks have spreading branches that drop acorns over a wide radius; hence, proximity of houses to oaks may not have been important for efficient food acquisition. Other studies of microhabitat associations of *Neotoma* that addressed the importance of cover have found mixed results; typically, house sites are associated either with understory or overstory cover (Converse et al. 2006; Gerber et al. 2003; Olson 1973; Turkowski and Watkins 1976).

Our final model indicated that slope was an important microhabitat component at house sites. Woodrats are more likely to excavate burrows in the soil beneath a house if the house is built on a hillside (Gander 1929; Linsdale and Tevis 1956; Parks 1922), perhaps because of better drainage (Vestal 1938); these underground burrows may enhance protection from predators or thermal extremes. In addition, woodrats

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avoided house sites with extensive mat-forming shrubs and bare ground, which may increase their exposure to aerial predators or inhibit efficient movement along the ground. Our final model likely reflects the diversity of habitat elements available within our area that provide protective cover and foraging opportunities in close proximity to woodrat houses, and our results likely reflect a trade-off among microhabitat variables with the importance of having a framework for a house in the form of dead wood outweighing the importance of other variables.

Surprisingly, we found little evidence of adult woodrats distinguishing among houses with respect to microhabitat, especially because numerous houses were available; among our 4 study sites, 57% of houses were unused during the study. Adults selected houses without small oaks nearby in 2004, but we have no interpretation for this pattern, and it was not consistent between years. Large houses may have the advantage of a more benign microclimate (Lee 1963), but we found no evidence that adult woodrats selected larger houses from among available houses. If woodrats make their decision about microhabitat suitability when the house is built, then we would not expect to find differences among used versus unused houses. Woodrat houses may maintain their initial suitability over time because woodrats are selecting for relatively persistent habitat features, such as dead wood.

Differential habitat association between age groups of woodrats has important implications for foraging predators, because younger animals may be forced into more exposed microhabitats and thus made more vulnerable to predation (Sakai and Noon 1997). Adult and subadult woodrats used houses with different microhabitat characteristics, but this pattern was not consistent between years. Adult woodrats used larger houses in combination with more logs and less poletimber during 2005. These results are consistent with the importance of log availability in determining house location, and they provide support for the suggestion that larger, more competitive adults occupy larger houses (Vestal 1938). However, this pattern did not hold for 2004, a year of higher woodrat abundance, which presumably would increase competition for the best houses, thereby accentuating differences between age classes (Rodenhouse et al. 1997). In other *Neotoma*, individual body mass may influence house use (Gerber et al. 2003; Post et al. 1993), with larger animals outcompeting others for the ''best'' houses (Gerber et al. 2003). Our results provided some support for this expectation, although it was not consistent between years.

Our results suggest that dusky-footed woodrats would benefit from management activities that promote the growth and retention of large California black oaks within shrubby, mixed-conifer forest and enhance the availability or development of large logs and stumps. In addition, our findings indicate that once a house is built, it has equal probability of being used by a woodrat; hence, management approaches that retain woodrat houses within a stand may maintain the presence of woodrats within an area. Selective thinning of trees and prescribed fire are common management techniques employed in the northern Sierra Nevada (Sierra Nevada Ecosystem Project 1996). Selective thinning can enhance woodrat habitat by creating dead wood from residual slash and promoting oak and dense shrub growth (Carey et al. 1999); however, large logs, which are an important structural component to houses, are removed in selective thinning. Prescribed fire is commonly used for reducing wildfire fuel loads. Although dusky-footed woodrats have evolved in the presence of fire and other natural disturbance, woodrats appear to reach their highest densities in relatively stable environments (Carey et al. 1999). Light to moderate fire may reduce suitability for dusky-footed woodrats in the short term by destroying houses and reducing dead wood abundance, but benefit dusky-footed woodrats in the long term by reducing the possibility of catastrophic wildfire and enhancing the recruitment of California black oak (Lee and Tietje 2005; Pavlik et al. 1991; Wirtz et al. 1988).

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