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Distribution and Abundance of *Neotoma* in Western Oregon and Washington

Abstract

Bushy-tailed woodrats (*Neotoma cinerea*) and dusky-footed woodrats (*N. fuscipes*) add substantially to the prey base of many avian and mammalian predators. High biomass of woodrats can reduce markedly area requirements of predators; thus, management for woodrats has potential in conservation. But patterns of abundance of woodrats in the Pacific Northwest are poorly understood. Our objective was to determine local abundances and regional distributions of *N. cinerea* and *N. fuscipes* in forests west of the Crest of the Cascade Range in Oregon and Washington.

We sampled a variety of forests from 1985 to 1997 in seven physiographic provinces. In Washington, we found that N. *cinerea* was rare in upland forests, but abundant along rocky streams on the eastern Olympic Peninsula and in rock bluffs on the west slope of the Cascade Range; *N. fuscipes* does not occur in Washington. In Oregon, *N. fuscipes* is at the northern limits of its range and we found that it was rare in Douglas-fir (*Pseudotsuga menziesii*)-western hemlock (*Tsuga heterophylla*) forests; *N. cinerea* was common in old forests and along streams. In mixed-conifer forests both species occasionally were abundant, but their abundances were negatively correlated. *Neotoma cinerea* was rare in mixed-conifer-mixed-evergreen forests but *N. fuscipes* occasionally was abundant in early, and present in late stages of forest development. The distribution of *N. fuscipes* can be explained by its preference for dense shrub cover and it ability to consume plants potentially toxic to other mammals; the only compelling explanation for the irregular distribution of *N. cinerea* is exceptional vulnerability to predation because of its size and social behavior.

Because of zoogeographic restrictions, limited opportunities exist in western Oregon and Washington to manage habitat for woodrats as a means of assisting in the recovery and maintenance of viable populations of predators sensitive to loss or management of forests.

Introduction

Pacific Northwest forests are inhabited by a variety of small mammals (Ruggiero et al. 1991, Carey 1995, Carey and Johnson 1995). They occupy diverse niches in forest communities and intermediate positions in trophic pathways, providing the nutritional foundation for many of the vertebrate predators in forest ecosystems (Carey et al. 1992, 1996). Of particular interest in forest ecosystem management are the larger small mammals (28-280 g), which tend to be arboreal or semiarboreal (Carey 1991, 1996). These rodents are preferred prey for predators including coyotes (*Canis latrans*), foxes (*Vulpes vulpes* and *V. velox*), bobcats (*Lynx rufus*), weasels and skunks (Carnivora: Mustelidae), hawks and other birds of prey (Falconiformes), and owls (Strigiformes) (*see* Ingles 1965, Maser et al. 1981, and Carey 1991 for overviews or Carey et al. 1992, Carey and Kershner 1996, Wilson and Carey 1996, and Watson et al. 1998 for specific examples). The largest of these small mammals, the dusky-footed woodrat

(*Neotoma fuscipes*) and and the bushy-tailed woodrat (*N. cinereus*), are especially attractive to predators (Linsdale and Tevis 1951, Escherich 1981, Carraway and Verts 1991, Carey and Peeler 1995, Sakai and Noon 1997) and measures of spotted owl (*Strix occidentalis*) fitness can be related to abundance of woodrats (Carey et al. 1992, Carey and Peeler 1995). The bushy-tailed woodrat has a broad geographic distribution, encompassing the entire Pacific Northwest, whereas the dusky-footed woodrat inhabits northern California, southwestern Oregon, and the Willamette Valley (Hall 1981). Woodrats are more limited in local distribution and abundance in the forests of western Washington and western Oregon than other small mammals, despite their large size and ability to use low quality foods (Escherich 1981, Carey et al. 1992).

Here we provide empirical data on body mass, sex ratios, abundance, habitats, and distribution of *Neotoma* that we gained from cross-sectional live-trapping surveys of habitat types throughout the Pacific Northwest and develop

hypotheses about mechanisms underlying patterns of woodrat abundance based on a synthesis of our results and the scientific literature.

Study Areas

Vegetation Zones

Our study spanned three vegetation zones, the Western Hemlock Zone, the Mixed-Conifer Zone, and the Mixed-Conifer/Mixed-Evergreen Zone (Franklin and Dyrness 1973). The Western Hemlock Zone encompasses much of low to mid-elevation western Washington and western Oregon. As we use the term, the Mixed-Conifer Zone includes the coniferous forest vegetation at the margins of interior valleys in southwestern Oregon (Figure 1). These valleys <152 m in elevation were described by Bailey (1936) as Upper Sonoran Life Zone-warm, dry areas that are phytologically an extension of northern California flora and markedly different from most of western Oregon and Washington, for example, in having grass, shrubs, and oaks (*Quercus* spp.) as dominant natural vegetation. Mixed-Conifer Zone forests and Upper Sonoran grasslands and oak woodlands occur along the Umpqua and Rogue river valleys north and South of Roseburg, Oregon, respectively
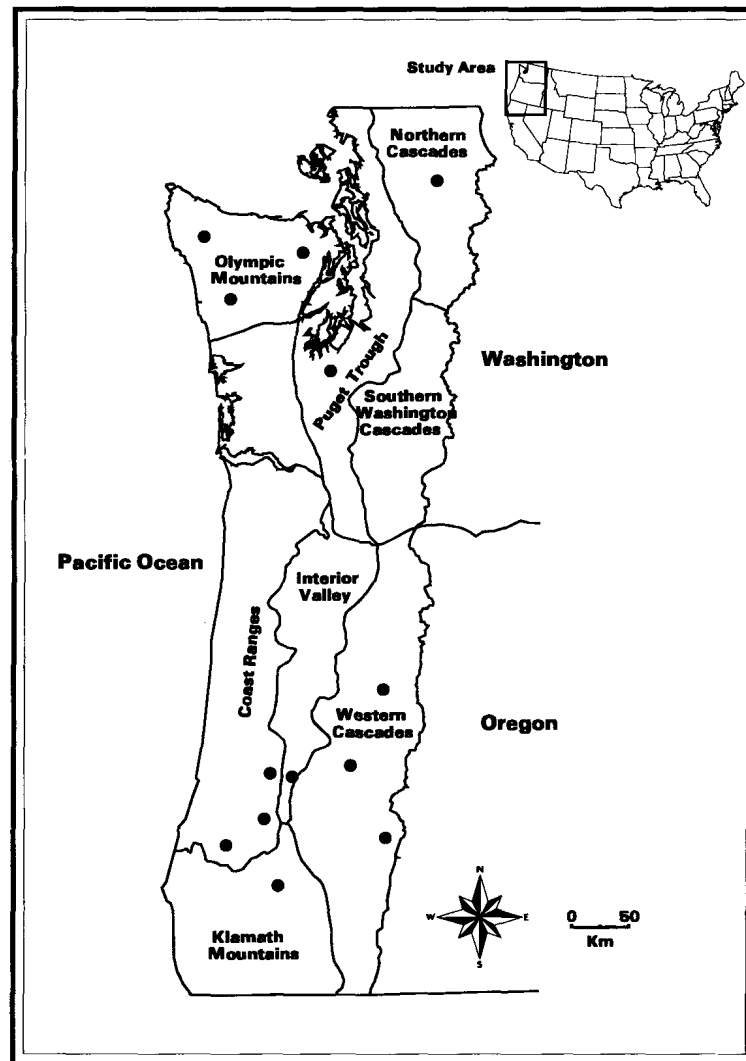

Figure 1. Woodrat (*Neotoma*) study area locations in Washington and Oregon west of the Cascade crest, 1985-1997; physiographic provinces adapted from Franklin and Dyrness (1973); black dots approximate study area locations within provinces; the Southern Washington Cascades were not sampled.

(Bailey 1936, Franklin and Dyrness 1973). The upland forests of southwestern Oregon provide the transition between the Western Hemlock Zone (north of latitude 43ºN, e.g., Roseburg) and the Mixed-Conifer-Mixed-Evergreen Zone (south of 43º N).

Boundaries between vegetation zones were not distinct and forest vegetation did not necessarily correspond strictly to mapped zone boundaries. In areas of moderate relief, the transition was a continuum; in areas of sharp changes in aspect or elevation, changes in plant communities were marked. Vegetation zones did not coincide with zoogeographic regions or physiographic provinces. For example, the Columbia River is a zoogeographic barrier separating the Western Cascades of Oregon and the Southern Washington Cascades, but is spanned by the Western Hemlock Zone (Franklin and Dyrness 1973, Ruggiero et al. 1991). Yet, each province within Washington comprised parts of more than one vegetation zone. No zoo-geographic barriers separated the vegetation zones of southwestern Oregon. Rather, there were bio-geographic ecotones between zones. Composi-tion of wildlife communities varies with both vegetation association and physiographic prov-ince and differences in species of wildlife asso-ciated with various forest communities in vari-ous physiographic provinces were specified by Bailey (1936), Ingles (1965), Maser et al. (1981), Brown (1985), and Ruggiero et al. (1991).

Physiographic Regions

Study areas were in seven physiographic prov-inces (Table 1, Figure 1) west of the Crest of the Cascade Range in Washington and Oregon (Franklin and Dyrness 1973): Northern Cascades, Olympic Peninsula, and Puget Trough in Wash-ington and southern Western Cascades, southern Coast Ranges, Klamath Mountains, and Interior Valleys (hereafter referred to more specifically as the Umpqua Valley) in Oregon. These areas differed markedly in climate, landform, and veg-etation, some of which formed zoogeographic barriers for small mammals (e.g., major features such as mountains, rivers, grasslands) and all of which interacted to shape the fauna and flora of each province (Ruggiero et al. 1991).

In each province, both old-growth and second-growth forests were sampled. Riparian areas were sampled on the Olympic Peninsula and in southwestern Oregon. Special landscape features (ridge tops, talus slopes, rock outcrops, and stream-side deciduous forests) were sampled in southwestern Oregon. We located large study areas in each physiographic province. Within study areas we selected stands (areas of homogeneous forest vegetation >10 ha; e.g. Tables 1 and 2) or sites (special landscape features that often were linear in shape-ridges and streams or small in size <7 ha; e.g. Table 3). We chose stands representative of the most abundant seral stages in the study area and classified them on the basis of vegetation zone, seral stage, and management history (i.e., arising from natural disturbance (natural) or those aris-ing from clearcutting (managed)). Management history was important because stands originating after clearcutting usually have substantially fewer biological legacies (such as large snags and large fallen trees) than stands originating after cata-strophic wildfires or windstorms and may follow a different trajectory of ecosystem development than natural stands. Natural stands often differ in structure, composition, and function from man-aged stands (Ruggiero et al. 1991; Carey 1995, 1998; Carey and Johnson 1995; Carey et al. 1999).

Seral Stages

Seral stages of forest ecosystem development and stages of timber stand development (e.g., clear-cut, sapling, pole, sawlog) are not equivalent and stand age is only moderately correlated with each type of development (Carey and Curtis 1996, Carey 1998). For this study, natural stands were old forest (>80 yr) with some stands >200-yr old (old growth). Managed stands were <80-yr old. We used six of the eight stages of forest development from the ecosystem classifi-cation of Carey and Curtis (1996) to categorize our study stands and sites; the strength of that classification is that it incorporates effects of management history and natural disturbance. The stages we used were (1) old growth, >200-yr old with very large trees, diverse species composition, understory development, and high coarse woody debris loads; (2) niche diversi-fication, 80-200-yr old with developed under-

TABLE 1. Study areas, seral stages, number of stands, years, trappings sessions, nights trapped, and captures and mean densities (number/ha) of bushy-tailed woodrats (*Neotoma cinerea*) in upland and stream-side forests in the Northern Cascades, Olympic Peninsula, and Puget Trough of Washington and Western Cascades, Coast Ranges, Umpqua Valley, and Klamath Mountains of Oregon, 1985-1997.

Province & locations	Seral stage[a]	Stands (n)	Years & periods (n)	Trap nights (n)	Captures (n)	Density(n/ha)
Northern Cascades			1991-1996			
Baker Lake	O	3	2	8,480	0	
Darrington	C	2	2	6,400	0	
Olympic Peninsula			1987-1989			
Eastern	N/U	2	2	6,400	0	
Southcentral	O/U/C	6	1-3	25,600	0	
Western	O/N/C	6	2-3	22,400	0	
			1989			
Eastern riparian	O/N	6	1	6,400	44	0.9
Eastern upland	N	6	1	6,400	6	0.1
Puget Trough			1991-1997			
Ft. Lewis	U/C	16	11	180,224	0	
Lewis and Clark	0	1	3	3,072	0	
Capitol Forest	N	1	4	4,096	0	
Western Cascades			1993-1996			
Diamond Lake 1	N	6	4	20,664	1	<0.1
North Umpqua	O	6	2	5,576	28	0.2
Cottage Grove	U	6	2	11,120	3	<0.1
Diamond Lake 2	U	6	1	2,520	1	<0.1
Coast Ranges			1985-1989			
Roseburg-Coos	O/N	6	3-8	48,576	18	<0.1
Bay-Drain	U/C	5	2-6	16,992	6	<0.1
Umpqua Valley			1985-1989			
North of Roseburg	O/N	3	2-7	26,560	71	0.4
	C	4	4-5	21,632	0	
Klamath Mountains			1988-1989			
South of Roseburg	O	2	2	8,000	1	<0.1

[a] Seral stage codes: old growth (O), niche diversification (N), understory reinitiation (U), competitive exclusion (C).

TABLE 2. Frequency of capture (*F*) of bushy-tailed woodrats (*Neotoma cinerea*, NECI) by number of sampling sessions (*S*) and in relation to the number of dusky-footed woodrats (*N. fuscipes*, NEFU) in old and young stands trapped intensively with grids of traps by physiographic province and vegetation zone (Western Hemlock, WHZ; Mixed-Evergreen--Mixed-Conifer, MEZ; the transition zone between the two; and the Mixed-Conifer Zone, MCZ).

Province-vegetation type	Natural old stands (>80 yr)			Managed stands (35-80 yr)		
	Stands (n)	S_{NECI} (S_{TOTAL})	F_{NECI} (F_{NEFU})	Stands (n)	S_{NECI} (S_{TOTAL})	F_{NECI} (F_{NEFU})
North Cascades-WHZ	3	0 (6)	0 (0)	2	0 (4)	0 (0)
Olympic Peninsula-WHZ	7	0 (20)	0 (0)	7	0 (13)	0 (0)
Puget Trough-WHZ	2	0 (7)	0 (0)	16	0 (176)	0 (0)
Coast Ranges-transition	6	8 (29)	16 (1)	4	4 (20)	5 (0)
Western Cascades-transition	12	10 (34)	29 (1)	4	2 (10)	3 (0)
Umpqua Valley-MCZ	3	15 (15)	101 (26)	4	0 (18)	0 (0)
Klamath Mountains-MEZ	2	1 (3)	1 (27)			

TABLE 3. Density (numbers/ha) of bushy-tailed woodrats (*Neotoma cinerea*, NECI) and dusky-footed woodrats (*N. fuscipes*, NEFU) and number of stick nests recorded in a survey of special landscape elements in southwestern Oregon, 1987-1988.

Stand name	S[a]	Zone- prov.[b]	NECI (n)	NEFU (n)	Nests (n)	Landscape element-habitat features
Rader	O	WH-CR	0.7 (4)	0	0	Stream side, boulders, log jams
Folley	O	WH-CR	0	0	0	Ridge top, talus
Look	O	WH-CR	0	0	0	Ridge top
Wood	O	MC-IV	0	0.5 (2)	2	10% rock cover; intermittent stream
Canyon	O	MC-IV	0	0.8 (3)	2	intermittent stream
Turkey	O	MC-KM	0.2 (1)	0.2 (1)	4	talus
Darby	O	MC-KM	0	2.0 (8)	0	
Wolf2	N	WH-CR	0.7 (4)	0	0	stream side Douglas-fir, bigleaf maple
Wolf3	N	WH-CR	0.3 (2)	0	0	stream side, red alder, bigleaf maple
Cougar	N	WH-CR	0.2 (1)	0	0	stream side, bigleaf maple, red alder
Hubb	N	MC-IV	0.7 (4)	0	0	90% rock outcrops
Doe	N	MC-IV	0	0	0	ridge top
Yello1	N	MC-IV	0.7 (4)	0	0	stream side, boulders, red alder
Yello2	N	MC-IV	1.3 (8)	0	4	stream side, red alder, bigleaf maple
Case	D	WH-CR	0	0	1	stream side, red alder
Camas	D	WH-CR	0	0.2 (1)	6	stream side Douglas-fir, red alder
Bottle	D	MC-IV	0.2 (1)	4.2 (17)	6	stream side Douglas-fir, red alder
O'Shea	D	MC-KM	0	2.0 (8)	9	15% influenced by stream
Tyee	C	MC-IV	0.8 (5)	0	0	2 intermittent streams
Camp	C	MC-IV	0	1.8 (7)	7	small Douglas-fir
Wood	C	MC-IV	0.5 (3)	1.0 (4)	5	small Douglas-fir
Gravel	C	MC-KM	0.2 (1)	0.2 (1)	6	25% stream influence
Cany1	I	MC-IV	0	3.2 (13)	9	intermittent stream, boulder, debris
Cany2	I	MC-IV	0.3 (2)	1.2 (5)	5	Douglas-fir
Cany3	I	MC-IV	0	0	4	25% influenced by stream, boulders
Lost	I	MC-IV	0.2 (1)	0	2	intermittent stream, red alder, grass
Garden	I	MC-IV	0	0	2	int. stream, Douglas-fir, boulders

[a] Seral stages: old growth (O), niche diversification (N), developed understory (D), understory reinitiation (U), competitive exclusion (C), ecosystem initiation (I).

[b] Zones: Western Hemlock Zone (WH), Mixed-Conifer-Mixed-Evergreen (MC); physiographic provinces: Coast Ranges (CR), Interior Valley (IV), Klamath Mountains (KM).

story and abundant coarse woody debris but structures (trees, snags, logs, canopy height) of smaller stature than old growth; (3) developed understory, >40-yr old, with high foliage height diversity including shade-tolerant trees, but with little coarse woody debris; (4) understory reinitiation, 30-200-yr old with developed low shrub layers and a shade-tolerant understory absent or just starting to form; (5) competitive exclusion, 30-200-yr old, densely stocked with trees, closed canopy, little understory; and (6) ecosystem initiation, 0-30-yr old, which includes grass, forb, shrub, and open sapling stages.

Specific Study Areas

Northern Cascades of Washington: Stands were between 365 and 610 m elevation with average annual precipitation of 250 cm and mean minimum January temperatures of -2.5^0 C. The old-growth vegetation type was western hemlock, swordfern (*Polystichum munitum*), and three-leaved foamflower (*Tiarella trifoliata*). Competitiveexclusion stands were dominated by Douglas-fir and *salal* (*Gaultheria shallon*).

Olympic Peninsula of Washington: For upland stands, elevations ranged from 85 to 610 m, average annual precipitation ranged from 130 to 200 cm on the eastern sites to >300 cm on the south-central and western sites, and minimum January temperatures averaged 0^0 C. Old-growth and niche-diversification stands were wet to mesic, dominated by western hemlock

with associates of silver fir (*Abies amabilis*), Sitka spruce (*Picea sitchensis*), or Douglas-fir. Competitive-exclusion and understory-reinitiation stands were in the same rainfall zones as the old stands, but were mesic to dry vegetation types-western hemlock, western hemlock and Douglas-fir, or Douglas-fir with understories dominated by moss, Oregon oxalis (*Oxalis oregona*), or salal. Paired riparian and upland sites on the eastern Olympic Peninsula were dominated by Douglas-fir averaging 38-118 cm dbh, with associates of western redcedar (*Thuja plicata*), western hemlock, and silver fir with understories of Pacific yew (*Taxus brevifolia*), and bigleaf maple (*Acer macrophyllum*).

Puget Trough of Washington: Stands were at 100-160 m elevation with 80-cm annual precipitation and January lows of 0 to 2.5^0 C. Competitive-exclusion stands were dominated by 55-yrold Douglas-fir with sparse understories of salal and Cascade Oregongrape (*Berberis nervosa*). Understory-reinitiation stands were dominated by 65-yr-old Douglas-fir with abundant salal, California hazel (*Corylus cornuta*), and swordfern. The niche-diversification stand was a mixture of mature (>90 yr) bigleaf maple with Douglas-fir, western redcedar, western hemlock and red alder (*Alnus rubra*). The old-growth stand had superdominant Douglas-fir, dominant western redcedar, midstory bigleaf maple and vine maple (*Acer circinatum*), and an understory of deciduous shrubs.

Southwestern Oregon: In the southern Coast Ranges, stands were 79-488 m in elevation, received 100-160 cm precipitation, and had low temperatures of 0° C. Umpqua Valley margins were 290-457 m in elevation, received 60-80 cm precipitation, and had lows of 0 to 2.5^0. Stands in the Klamath Mountains were 390-610 m in elevation, received 80 cm precipitation, and had lows of 0° C. Old-growth stands ranged from Douglas-fir/western hemlock/western redcedar (300-400 yr) to Douglas-fir/grand fir (*Abies grandis*)/incense-cedar (*Libocedrus decurrens*), 275-350-yr old. Umpqua-Valley-margin stands variously had true oaks (*Quercus* spp.), poison-oak (*Rhus diversiloba*), and other vegetation typical of the Mixed-Conifer Zone. Tanoak (*Lithocarpus densiflorus*) and pines (*Pinus ponderosa* and *P. lambertiana*) were common in stands in the Klamath Mountains. Both old-growth stands in the Klamath Mountains were estimated to have dominant trees 210-yr old; Iron had an 80-yr old midstory, whereas O'Shea had two age classes (60 yr and 90 yr) in its midstory. Younger forests were dominated by Douglas-fir and salal with some having evergreen hardwoods (e.g., *Castanopsis chrysophylla* and *Arbutus menziesii*).

In the southern Western Cascades, the Diamond Lake study areas were at the juncture of the Western Hemlock Zone and White Fir (*Abies concolor*) Zone, 945-1,707 m in elevation, with 80-120 cm precipitation, and minimum temperatures of -2.5 to -5.0^0 C. Niche-diversification stands were Douglas-fir, white fir, western hemlock, and Shasta red fir (*Abies magnifica*), 110-130-yr old. Some salvage logging had been done in the 1970s. Commercially thinned understory-reinitiation stands were composed of Douglas-fir, white fir, and incense-cedar, 165-yr old, with light understories of white fir and little coarse woody debris. North Umpqua old-growth stands were at the juncture of the Western Hemlock Zone and Mixed-Conifer/Mixed-Evergreen Zone, wet with seeps and streams, 1,219-1,402 m in elevation, with overstories of Douglas-fir, white fir, western hemlock, and western white pine (*Pinus monticola*) 200-520-yr old, and understories of vine maple and Cascade Oregongrape. Cottage Grove understory-reinitiation stands were at the juncture of the Western Cascades and the Interior Valley (Willamette River Valley) Provinces, in the Mixed-Conifer Zone. These stands were 488-792 m in elevation and had seeps and streams, overstories of Douglas-fir 60-80-yr old, 2-5 old-growth trees/ha, and understories of Pacific rhododendron (*Rhododendron macrophyllum*), salal, vine maple, and Cascade Oregongrape.

Finally, we studied 27 sites in the Coast Ranges Umpqua Valley margins-Klamath Mountains that represented particular elements of landform (ridge tops, riparian areas, areas of exposed rock, boulders, or talus) and early (<40 yr) seral stages. These landscape elements were linear in arrangement, small in area, or patches disjunct from like environments.

Methods

Experimental Design

Our study was exploratory and covered wide areas, but sample sites were not selected randomly from all sites within the range of each species. In some areas, all accessible sites were sampled. In others, samples of common seral stages of forest development were selected preferentially and considered representative of those seral stages in that area. There could be unknown biases in our site selection (for example, preconceived notions of what constitutes "representative" old growth or "typical" managed forests) and there certainly are confounding factors (both biotic and abiotic) that make isolation of causal factors impossible. Practically any category of forest condition we developed was heterogeneous—it could be broken down into finer categories. These limitations are common to almost all field studies; yet, despite violations of assumptions, most field studies use inferential statistics (Cook and Campbell 1979, Hoaglin et al. 1991). Nevertheless, we conducted no statistical tests and present only descriptive statistics and rank correlations. We thereby make it clear that our conclusions are inferences and deductions based on non-statistical assumptions, empirical data, and published reports. Thus, our conclusions should be viewed as hypotheses.

Sampling

We followed the methods developed by Carey et al. (1991a) for sampling populations of arboreal and semi-arboreal rodents, including woodrats. We used Tomahawk 201 single-door, collapsible box traps constructed of 16-gauge galvanized wire mesh (1.3 by 2.5-cm mesh size), 13-cm wide, 13cm tall, and 41-cm long and baited with peanut butter and oats. We placed traps either in grids with 40 m between grid points or just on the ground in paired lines of traps 20-m apart (Carey et al. 1991a). We sampled woodrat populations in forest stands with grids of traps, with equal numbers of traps in trees and on the ground. Traps were placed 1.4-m high on the largest tree within 5 m of a trap station; traps on the ground were placed at locations <5 m from the trap station where captures would be most likely (e.g., near dens, travel ways, under shrubs,

or along fallen trees). Grid size varied from 7 by 9 (10 ha) with 1 trap/ station (Western Cascades) to 8 by 8 (10 ha) with 2 traps/station (Puget Trough), to 10 by 10 (16 ha, with some exceptions) with 2 traps/station (Northern Cascades, Olympic Peninsula, Coast Ranges, Umpqua Valley margins, and Klamath Mountains); traps were opened for 8 nights. We studied woodrats at the sites of special landscape features (including stream-sides on the Olympic Peninsula) with parallel trap lines of 25 stations (2 traps/ station on the ground) each (a total of 100 traps); traps were opened for 3-4 nights. We assumed the areas sampled by trap lines were 4 ha for dusky-footed woodrats and 6 ha for bushy-tailed woodrats as suggested by Carey et al. (1991a, 1992), who based their estimates on mean maximum distances moved between subsequent recaptures during grid trapping. We used numbers of individuals caught per trapping session (minimum number known alive, MNKA) as a measure of the size of the local population or social group. We converted individuals to density by dividing by the effective area sampled. For both arboreal and semi-arboreal sciurids, individuals caught per unit effort and MNKA are highly correlated with each other and with mark and recapture population estimates across a wide range of population densities and linear regression coefficients are similar among physiographic provinces in the Pacific Northwest; total captures per unit effort are poorer predictors of population size than captures of individual animals (Carey et al. 1991 a, 1999; Carey *in press* a, b). We assumed MNKA estimates of population size of semi-arboreal woodrats were as valid as those for sciurids. These estimates slightly underestimate population size. We also assumed density is a measure of carrying capacity and provides an index to habitat quality (Carey *in press* a, b). We recorded numbers of stick nests in the areas sampled only in the Coast Ranges-Umpqua Valley margins-Klamath Mountains studies. Sex and body mass of woodrats were recorded in the Olympic riparian and Coast Ranges-Umpqua Valley margins-Klamath Mountains studies.

Although sampling effort varied among stands and between stands and sites, large efforts were expended at each stand. Even at our small sites (<7 ha) of special landscape fea-

tures we trapped for 300-400 trap nights; trap success was higher at the sites than at stands, suggesting a poor correlation between trapping effort and captures at the levels at which we trapped. Carey et al. (1991 a) and others report the ease of capture for woodrats. For example, Escherich (1981) reported that 85% of bushy-tailed woodrats were caught in the first night of trapping and recommended that the number of individuals caught be used as a measure of abundance and not catch per unit effort of trapping. Catch per unit effort could produce misleading results with animals patchily distributed in small social groups of three to four individuals (like bushy-tailed woodrats) because the longer, more intensively, and larger an area was trapped the lower the population estimate would be. Our experience was similar to that of Carey et al. (1991a) and Escherich (1981)—when we caught woodrats we caught them quickly; when we didn't catch them quickly additional trap nights did not result in greater success. We caution the reader, however, that one can not demonstrate absence with this sort of sampling, only low probability of occurrence; abundance is more easily demonstrated. Laudenslayer and Fargo (1997), moreover, reported difficulty trapping dusky-footed woodrats at 2.2-ha sites in California oak woodlands (2 captures/100 trap nights) except at woodrat houses (10-13 captures/100 trap nights), suggesting probability of capture of woodrats with traps in grids may be low in some vegetation types. With densities and conditions comparable to those studied by Laudenslayer and Fargo (1997), however, using our methods, we would still statistically expect to catch a minimum of 6-8 woodrats per site.

Results

We caught 196 individual bushy-tailed woodrats and 124 dusky-footed woodrats in 199 sam-

pling sessions at 119 sampling locations (Table 4; 93 surveys of stands, Table 1, and 27 surveys of special habitat types, Table 3, with overlap on 1 site; ca. 500,000 trap nights).

Bushy-tailed Woodrats

Bushy-tailed woodrats were not captured in upland forests in the Northern Cascades, Puget Trough, or Olympic Peninsula except in unmanaged, upland forests immediately adjacent to stream-side forest on the eastern Olympic Peninsula. These stream-side forests, however, had the highest average densities of bushy-tailed woodrats of any sites we sampled in Oregon or Washington (Tables 1 and 3)—0.9 woodrats/ha (averaged over six sites). Here, bushy-tailed woodrats had a sex ratio (males: females) of 1:1.3 (10 sessions with 40 woodrats captured). Density in two occupied riparian areas averaged 1.8 woodrats/ha (9-12 woodrats/location) with 0.2-0.3 woodrats/ha (1-2 woodrats/location) in the adjacent uplands; however, another riparian area had 0.3 woodrats/ha (2 woodrats) and three riparian areas had none.

In the southern terminus of the Western Hemlock Zone in Oregon, bushy-tailed woodrats commonly were found in stream-side, natural Douglas-fir/western hemlock forests (niche diversification and old growth, four of four stands) and in upland, mid-slope forests (three of six old-growth stands and three of four second-growth stands), but were absent from two ridge-top, old-growth stands and two managed, stream-side stands with developed understories. As in Washington, the adjacency of streams was not sufficient to ensure occupancy of forests by bushy-tailed woodrats. Average densities were low (Table 1). Over time, occupancy of individual stands was variable, averaging 27% of trapping sessions in

TABLE 4. Percent frequency of occurrence of bushy-tailed woodrats (*Neotoma cinerea*, NECI) and dusky-footed woodrats (*N. fuscipes*, NEFU) in old, natural stands and young, managed stands with and without permanent streams in western Washington and western Oregon; only mixed-conifer and mixed-conifer/mixed-evergreen stands (*n* in parentheses) were counted for occurrence of NEFU.

	Stream present			Stream not present			Total		
Age	Stands (*n*)	NECI (%)	NEFU (%)	Stands (*n*)	NECI (%)	NEFU (%)	Stands (*n*)	NECI (%)	NEFU (%)
Old	27 (1)	78	100	34 (8)	21	63	61 (9)	46	67
Young	12 (4)	33	75	46 (11)	17	45	58 (15)	20	53
Total	39 (5)	64	80	80 (19)	19	53	119 (24)	34	58

old, natural stands and 20% in managed stands (Table 2), suggesting frequent, local (stand-level) extinctions. Overall, bushy-tailed woodrats exhibited a similar pattern of abundance and variable occupancy in the Western Cascades (Table 2).

In contrast to the Washington samples, Oregon Coast Ranges-Umpqua Valley margins-Klamath Mountains samples had skewed sex ratios of 1:2.3 (135 woodrats caught in 43 sessions, averaging 3.1 woodrats/location), significantly different from a 1:1 ratio ($P < 0.05$). Average densities were low and ranged from <0.1/ha to 0.4/ha, depending on habitat type (Table 1). The highest density recorded was 1.3/ha (3 male and 5 female bushytailed woodrats) in a stream-side red alder/bigleaf maple stand. Male bushy-tailed woodrats had a body mass ($O \pm SE$) of 276 ± 10 g ($n = 27$); females weighed 255 ± 6 g ($n = 47$). We found 55% of female bushy-tailed woodrats to be lactating or just post-lactating from 1 May to 15 November.

Dusky-footed Woodrats

Dusky-footed woodrats were not caught in Washington. Only two dusky-footed woodrats were caught in Douglas-fir-western hemlock forests in Oregon despite intensive trapping (Tables 2 and 3); one in a niche-diversification stand at 366 m elevation and one in a stream-side developed understory stand at 488 m elevation; both in the Coast Ranges. Densities of dusky-footed woodrats in occupied mixed-conifer and mixed-conifer-mixed-evergreen stands ranged from 0.1/ha to 4.3/ ha ($O = 1.2 \pm 0.3$/ha). Dusky-footed woodrats were caught in two of six managed, low-elevation, mixed-conifer, understory-reinitiation stands in the Western Cascades (Cottage Grove). Male dusky-footed woodrats had a mean mass of 288 ± 9 g ($n = 29$); females weighed 225 ± 10 g ($n = 25$), on average; sex ratio was 1:1.2 (123 woodrats caught in 22 sessions, $O = 5.6$ woodrats/location). Seventy-four percent of female dusky-footed woodrats were lactating or post-lactating during 16 May-31 October.

Sympatric Woodrats

Both bushy-tailed woodrats and dusky-footed woodrats were more common in the mixed-conifer forests of the Umpqua Valley margins (Tables 1, 2, 3) than in the southern Douglas-fir-western hemlock forests of the Coast Ranges or Western Cascades. Bushy-tailed woodrats were abundant (0.2-1.3/ha) in, but occasionally absent from, late-seral and stream-side stands. In intensively trapped stands, occupancy in old, natural stands and absence from managed stands 35-80-yr old were constant (Table 2). Dusky-footed woodrats were abundant (0.2-0.8/ha) in all but one old-growth stand, in one of three niche-diversification stands (0.1/ha), and especially in one stream-side developed-understory stand (4.3/ha) that also had bushy-tailed woodrats (0.2/ha). Dusky-footed woodrats were found in all but one of the stands sampled in the Klamath Mountains; compared to dusky-footed woodrats, bushy-tailed woodrats were rare in the Klamath Mountains (Tables 2 and 3). The two species were found together in five of eight mixed-conifer old-growth stands, three of six mixed-conifer competitive-exclusion stands, and in one mixed-conifer stream-side stand. Within these sites, abundances of the two species were negatively correlated (Spearman rank correlation = -0.52, $P < 0.05$).

Overall, relative frequencies (percent of sites with woodrat captures, Table 4) suggest that optimum habitat for bushy-tailed woodrats was old, natural forests (>two-fold margin) with streams (almost a four-fold margin). Dusky-footed woodrats were 1.5 times more frequent near streams, but only slightly (1.3 times) more likely to occupy old, natural forest than young, managed forests (mostly 40-90-yr old).

When we caught woodrats in southern Oregon, we caught more dusky-footed woodrats, on average, than bushy-tailed woodrats. The sex ratio of bushy-tailed woodrats was skewed towards females; dusky-footed males and females were equally common. More female dusky-footed woodrats had borne young than had female bushytailed woodrats. The two species did not differ significantly in weight. Biomass of dusky-footed woodrats (1,548 g/ha) was greater, on average, than that of bushy-tailed woodrats (876 g/ha). Abundances of the two species were negatively correlated (Spearman rank correlation = -0.52, $P < 0.05$).

Stick nests, or woodrat houses, were readily apparent in all but one stand (mixed-conifer old growth) where dusky-footed woodrats were captured. Dusky-footed woodrats took shelter in these nests when released. However, the numbers of stick nests and the numbers of dusky-footed woodrats captured were not correlated (Spearman rank correlation = 0.47, $n = 15$, $P = 0.08$). Total numbers of woodrats (both species) were correlated with number of nests (Spearman rank correlation = 0.39, $n = 27$, $P = 0.049$). Bushy-tailed woodrats, however, sought shelter in cavities in trees, under logs, or in rock crevices when released from traps. Few nests were present where only bushy-tailed woodrats were caught and many nests were present when both species were caught.

Discussion

Woodrats in Western Washington

Dusky-footed woodrats were absent, as expected (Ingles 1965, Hall 1981), and bushy-tailed woodrats were unexpectedly rare (given range descriptions by Ingles 1965, Hall 1981, and Brown 1985) in upland Douglas-fir-western hemlock forests in Washington. We found bushy-tailed woodrats only on the relatively dry, eastern Olympic Peninsula, near some streams. The streams with woodrats were narrow, deeply cut, and associated with forested boulder fields. The streams without woodrats did not have nearby boulder fields, talus, or rock outcrops. Some of our upland stands elsewhere on the Peninsula had small streams nearby or within them, too small to have changed the upland nature of the forest or the landform, but no woodrats. Thus, the mere presence of water within a forest was not sufficient for habitation by bushy-tailed woodrats. Additional trapping (4,162 trap nights with Tomahawk 201 traps) in oak (*Quercus garryana*) woodlands and Douglas-fir forest-prairie ecotones in the Puget Trough found no woodrats (Ryan and Carey 1995). The restricted distribution we observed was far more narrow than the broad distribution across stages of forest development and vegetation zones suggested by Ingles (1965) or Brown (1985).

Dalquest (1948) described bushy-tailed woodrats in Washington as inhabiting buildings in the mountains with natural habitat of broken rock or talus from sea level to 3,048 m (on Mt. Rainier in the Southern Washington Cascades). He stated only one or two woodrats would be found at a given locality. His distribution map shows bushy-tailed woodrats at Forks, Quinault, and Quilcene, the vicinities in which we trapped on the Olympic Peninsula. Locations we trapped had little or no broken rock or talus, except for some stream-side areas on the eastern Olympic Peninsula, where we did catch woodrats. There, in stream-side boulder fields, we caught 9-12 woodrats per site (1.5-2.0/ha) and single woodrats in the uplands. These were greater concentrations than the small, scattered groups of one to four and sex ratios were not skewed towards females as is usually reported (Dixon 1919, Dalquest 1948, Escherich 1981). Our stream-side sites, however, were larger (>4 ha) and more continuous than the discrete rock outcrops studied by others. Spotted owls actively foraged in our occupied study areas and their diets included woodrats (E. D. Forsman, pers. comm. 1989; Forsman et al. 1991). Thus, even when bushy-tailed woodrats were not broadly distributed, they were sought out and preyed upon by spotted owls.

Holmes (1995) set traps for bushy-tailed woodrats in a rock bluff (150 m high and 900 m wide) at 500-650 m elevation above Rattlesnake Lake in the Southern Washington Cascades physiographic province near North Bend, Washington and caught 22, 20, and 16 woodrats in 1992, 1993, and 1994, respectively, about 1.5/ha, on average. Woodrats denned in the rock cliffs and foraged in nearby forest. Adult sex ratios (1:4, 1:2.3, 1:0.9, respectively) were skewed towards females in two of three years. Charles R. Knox (pers. comm., 1997) removed, sequentially over four years, three woodrats from his cabin at the juncture of a stream and the Greenwater River (elevation 550 m) in the Southern Washington Cascades in an area of wet forests and rock bluffs. Lawrence L. C. Jones (pers. comm., 1989), while trapping *Martes americana,* occasionally caught woodrats in rock outcrops, talus slopes, and log piles at high elevations near tree line in the Southern Washington Cascades just north of Mt. Rainier. Thus, we can confirm Dalquest's (1948) description of the distribution

and habitat of the bushy-tailed woodrat in Washington, but not his conclusions that only one or two woodrats would be found in a single locality. The number of woodrats present seems more to reflect the area of contiguous denning habitat (rock or talus) than the social behavior of the species.

The association of bushy-tailed woodrats with rock outcrops was also reported in the Canadian Rocky Mountains where it was found that competition for scarce den sites (crevices in rock) resulted in agonistic behavior toward non-kin and stable, cohesive relationships within family groups (Moses and Millar 1992). Far to the south, Dixon (1919) found bushy-tailed woodrats were confined to high elevations in northern and eastern California and almost exclusively associated with cliffs, boulder piles, rock slides, and logs. He thought that use of rock crevices was beneficial in protection from snow storms and predators. Local distribution, however, was irregular. Not all rock slides were occupied. There was rarely more than a family of five or six individuals in a rock slide of 1-2 ha; average density was <0.1/ha. Similarly, Escherich (1981) found woodrats living in groups of one adult male and one to three adult females. Escherich (1981) also reported that the most important resource for the bushy-tailed woodrat was adequate rock shelter for protection from snow and cold; he thought shelter was more limiting than food. Escherich (1981) suggested that much bushy-tailed woodrat biology is adapted to exploiting limited rock outcrops as secure denning sites. In particular, he cited small social groups, polygyny, and sexual dimorphism in body mass as adaptations to exploiting limiting, patchy resources (rock outcrops). In our few occupied areas in Washington, we observed larger groups without sex ratios indicative of polygyny. Our data from Oregon supports small social groups and polygyny, with sex ratios skewed towards females, but the 95% confidence intervals for male and female body mass overlapped completely.

Woodrats in Western Oregon

Bailey (1936) reported that bushy-tailed woodrats were found throughout the forests of western Oregon, primarily in cliffs and masses of broken rock. Maser et al. (1981) also reported the affinity for rock, but stated bushy-tailed woodrats were found throughout coniferous and deciduous forests and denned in hollow trees where rock was scarce. Doyle (1985, 1990) found bushy-tailed woodrats, but no dusky-footed woodrats, in old-growth forests along streams (0.2 ± 0.1/ha) and in adjacent uplands (0.2 ± 0.1 ha) in the Western Hemlock Zone in the central Western Cascades near Blue River, Oregon (north of our Western Cascade study areas). However, in the same general vicinity, Anthony et al. (1987), in a similar comparison of stream-sides and uplands, and Rosenberg (1990), in an intensive comparison of managed and old-growth stands, did not report capturing any woodrats. Cudmore (1986) found bushy-tailed woodrats in talus, rock outcrops, and under bridges near Blue River. Neither he nor Gilbert and Allwine (1991) reported finding bushy-tailed woodrats in their extensive small mammal studies in young, mature, and old-growth upland forests near Hood River in the northern Western Cascades or in the central Western Cascades.

We caught bushy-tailed woodrats in abundance (1) in one old-growth area in the southern Western Cascades (North Umpqua, a flat area of pumice soil with six sites averaging 0.2 woodrats/ha; three sites had 0.3-0.7 woodrats/ha, three sites had 0.1-0.2 woodrats/ha), (2) in old forests in the Umpqua River Valley margins (0.4 woodrats/ha; level to moderate slopes, small streams, one site with rock outcrops), (3) along streams in the valley margins and Coast Ranges, and (4) in one area of rock outcrop in a valley margin. Two streams had boulders associated with them. In general, however, it was difficult to find areas of talus, rock outcrops, or boulders in our southwestern Oregon study areas.

We sampled our old-forest, valley-margin, mixed-conifer sites 2-7 times 4-6 months apart and caught bushy-tailed woodrats each trapping session. Abundances were lower in Douglas-fir transition forests and repeated sampling showed habitat occupancy was variable over time (8 of 29 sampling sessions). It appeared that bushy-tailed woodrats were absent from many upland sites and underwent periodic local extinctions in their habitats in the Douglas-fir transition forests but not in the valley-margin mixed-conifer for

ests. Local extirpations due to predation also were observed by Escherich (1981) in the California Sierra Nevada. He attributed this phenomenon to the harem social structure of the bushy-tailed woodrat, which results in clumping of the small population and concomitant attraction of predators. Both species of woodrats were important prey of the spotted owl in our Oregon study areas and owls actively foraged in most of the old forest sites and many of the stream-side sites occupied by woodrats in the Coast Ranges, Interior Valleys, and Klamath Mountains (Carey et al. 1992, Carey and Peeler 1995).

Several factors may have been important in determining patterns of occurrence of bushy-tailed woodrats in upland and stream-side forests without rock shelters in southwestern Oregon and absence from such areas elsewhere. Prey biomass and diversity was higher than in Doug-las-fir-western hemlock forests to the north (Carey et al. 1992). Abundance in Douglas-fir transition forests was lower than in interior-valley mixed-conifer forests and mixed-conifer-mixed-evergreen forests to the south. As prey biomass available to the spotted owl decreased northward, predation pressure on bushy-tailed woodrats may have increased. Similarly, predation pressure on bushy-tailed woodrats may have been more intense in transition forests than in mixed-conifer forests. Whereas northern flying squirrels (*Glaucomys sabrinus*) and bushy-tailed woodrats were the common prey in transition forests, they and dusky-footed woodrats, brush rabbits (*Sylvilagus bachmani*), and red tree voles (*Phenacomys longicaudus*) were abundant and were common prey in mixed-conifer and mixed-conifer-mixed-evergreen forests (Forsman et al. 1984, 1991; Carraway and Verts 1991; Gillesberg and Carey 1991; Carey et al. 1992). Multiple, abundant prey species allow spotted owls to use small home ranges (Carey et al. 1992) and may dilute predation pressure on any single species (or cause owls and other predators to focus on the most abundant and concentrated prey, the dusky-footed woodrat). In southern Oregon transition forests, intensive predation by spotted owls appeared to reduce dense populations of northern flying squirrels by 50% and locally extirpate bushy-tailed woodrats (Carey et al. 1992). In a dense population of dusky-footed woodrats in northern California mixed-conifer-

mixed-evergreen forest, predators killed 50% of juveniles and 30% of adults (Sakai and Noon 1997). Indeed, the large number of larger small mammals that serve as prey for strigids and mustelids and the presence of stick houses of dusky-footed woodrats (potential den sites for various prey species, including bushy-tailed woodrats) may have facilitated the occurrence of the bushy-tailed woodrat in forest without rock shelters *(see* Carraway and Verts 1991 for a list of species commensal with dusky-footed woodrats).

The climate of interior valleys is warm and dry; rock shelters are not necessary for protection from cold temperatures and rain nor are rock areas necessary for subnivean travel and storage of food for overwinter use as is necessary in areas of heavy snowfall. Bushy-tailed woodrats build their own stick houses (on the ground) and stick nests (in trees) in southwestern Oregon (Maser 1965, 1966; Maser et al. 1981; Carey 1991). Bushy-tailed woodrats also use cavities in trees extensively (Carey 1991, Carey et al. 1997; Maguire, unpublished data). With multiple species (northern flying squirrels; both species of woodrat; Douglas' squirrels, *Tamiasciurus douglasii*; western gray squirrels, *Sciurus griseus*; and red tree voles) using stick nests, tree cavities, and fallen trees as shelter (Maser et al. 1981; Carey 1991, 1996; Carraway and Verts 1991; Gillesberg and Carey 1991; Carey et al. 1997), competition for dens could be strong. Bushy-tailed woodrats are territorial and interspecifically aggressive. One of us (ABC) observed a male bushy-tailed woodrat kill one female dusky-footed woodrat and one female northern flying squirrel in a 1.2 by 1.2 by 2.4-m cage with a surplus of food and nest boxes. Thus, bushy-tailed woodrats may have been more common in old forest than managed competitive-exclusion stage forest because understory vegetation, fallen trees, and cavities in standing trees were more abundant in old forests than young, managed forest (Carey 1995; Carey et al. 1991b, 1997, 1999). In northern forests, cavities are less abundant (Carey et al. 1997), rainfall is higher and cool temperatures are more common, and we did not find stick nests built by bushy-tailed woodrats. Ground fires are less frequent than in southern forests, thus fewer hollow trees form as a result of fire scars. Abundances of cavities and

hollow trees may be too low to allow bushy-tailed woodrats to locate clustered housing for one to five woodrats central to one or more patches of abundant food. If clusters of cavities were found, travel to arboreal dens without the dilution effect of multiple prey species could make woodrats especially vulnerable to predation by owls. Dens in standing and fallen trees often do not have multiple entrances and exits and ability of long-tailed weasels (*Mustela frenata*) to prey on cavity-nesting mammals may be enhanced (Wilson and Carey 1996, Carey et al. 1997).

Abundance along streams may have been due to increased abundance of deciduous trees (*Alnus rubra* and *Acer macrophyllum*) and undergrowth and accumulation of coarse woody debris near streams, especially in very young and old forests. Colonization of stream-side areas in old forest by early successional species is common because of dense shrubby vegetation (Carey 1988). Stream noise can interfere with the ability of owls to detect prey by sound at night and might provide woodrats with some protection from predation. Neither the bushy-tailed woodrat nor the dusky-footed woodrat are particularly efficient at water conservation—both benefit from the availability of free water (Meserve 1974, Carraway and Verts 1991).

Abundances of the two species of woodrats were negatively correlated in mixed-conifer forests and bushy-tailed woodrats were rare in mixed-conifer-mixed-evergreen forests in the Klamath Mountains where dusky-footed woodrats were increasingly abundant. Bailey (1936) reported that dusky-footed woodrats could be found throughout the Upper Sonoran Life Zone (interior valleys and their margins) and the mixed-conifer and mixed-conifer-mixed evergreen forests of southwestern Oregon, particularly in shrub lands and areas of dense underbrush in forests; Maser et al. (1981) reiterated this distribution. Cudmore (1986) and Gilbert and Allwine (1991) caught dusky-footed woodrats (1 each) in the southern Western Cascades. Hooven (1959) reported that dusky-footed woodrats could achieve densities of 0.2-0.7/ha in dense Douglas-fir thickets. We trapped dusky-footed woodrats on 15 occupied sites; density ranged from 0.1/ha to 4.3/ha, averaging 1.2 ± 0.3/ha. Densities of dusky-footed woodrats increases in mixed-

conifer-mixed-evergreen forests and dusky-footed woodrats may be abundant enough there to exclude bushy-tailed woodrats. Densities reported for dusky-footed woodrats in California ranged from 5/ha to 45/ha (Carraway and Verts 1991). Sakai and Noon (1997), however, reported densities as high as 81/ha in ecosystem initiation stages of mixed-conifer-mixed-evergreen forests in northern California. Dusky-footed woodrats build their own houses and can live in large colonies; they seem to be limited more by food, water, and vegetative cover than by housing sites. In California, Raphael (1988), Ward (1990), and Sakai and Noon (1993, 1997) all found dusky-footed woodrats most abundant in early seral stages, with a secondary peak of abundance in a bimodal distribution in late-seral stages; none found bushy-tailed woodrats in their studies. One of us (CCM), however, did catch bushy-tailed woodrats in 350-yr old growth along a stream in Trinity County, California. The low densities and marginal environments we found in southwestern Oregon may reflect decreased habitat quality for dusky-footed woodrats at the northern limits of its range in upland forests. Low densities may explain the lack of correlation between numbers of stick houses and numbers of dusky-footed woodrats given the high correlations reported by Sakai and Noon (1993, 1997). However, Cranford (1977), Wallen (1982), and Lynch et al. (1994) did not report high correspondence between number of houses and number of individuals either.

Hard-leaved sclerophylls become increasingly less common the farther north of California (Franklin and Dyrness 1973). These plants, especially tanoak and other evergreen hardwood trees and shrubs can become extremely abundant in clearcuts (and even delay development of coniferous forest) in California. In stable, stream-side, alder (*Alnus*)/willow (*Salix*) and chaparral environments, dusky-footed woodrats colonies may persist >25 yr (Linsdale and Tevis 1951, Wallen 1982). In old forests, with canopy gaps and histories of frequent fires that produced open canopies, patchy but stable areas of brushy understories develop and provide habitat for dusky-footed woodrats. Dense, evergreen vegetation <3 m can provide food, cover, and travel ways for dusky-footed woodrats. Woodrat diets often

reflect local feeding specializations, but dusky-footed woodrats are particularly specialized (Atsatt and Ingram 1983). A series of adaptations allows dusky-footed woodrats to feed on evergreen leaves high in fiber, tannins, and phenolics. These include (1) digestive tract microflora that help maintain the woodrat's nitrogen balance, (2) reingestion of feces, (3) large, insulated houses that decrease energy expenditure, (4) location of houses near preferred food plants to decrease travel time and exposure to predators, (5) hoarding food that not only permits continuous, high volume feeding but also helps detoxify the food through enzymatic breakdown and release of toxic chemicals. In summary, dusky-footed woodrats appear limited by stable, densely brushy environments for food and cover from predation, materials for housing construction, dispersal ability, and climate. In mixed-conifer-mixed-evergreen forests both brush fields (chaparral; early, open stages of evergreen hardwood forests; and coniferous forests with well-developed sclerophyllous understories) and densely vegetated stream-sides provide stable, high quality environments. Stability and density of vegetation structure may be more important than vegetation composition. Dusky-footed woodrats are habitat specialists, which despite adaptations to high fiber, tannins, and phenolics, often exhibit generalized food habits (Meserve 1974). In mixed-conifer and transition forests, moderate to poor quality habitat for both dusky-footed woodrats and bushy-tailed woodrats can be found along streams and in some old-growth forests. In Western Hemlock Zone forests, there is no habitat for dusky-footed woodrats, and bushy-tailed woodrats are generally relegated to rocky areas and high elevations, along with some other larger small mammals (e.g., *Marmota* spp., *Ochotona princeps*, *Spermophilus saturatus*).

Hypotheses and Implications for Conservation

Our research suggests that woodrats are limited in distribution and abundance in southern Oregon forests because the highest quality habitat for dusky-footed woodrats—dense, shrubby, early stages of forest development—is scattered over large landscapes dominated by competitive-exclusion forest and is relatively ephemeral, suitable as habitat for only 5-10 yr. Competitive-exclusion forests may persist 30 yr under intensive management for timber and up to 200 yr without timber harvests. Colonizing potential habitat created by clearcutting thus requires hospitable intervening habitat, aggressive dispersal behavior, or well developed dispersal corridors. Old-growth forests with patches of dense cover provide moderate quality habitat. We hypothesize that the abundance of dusky-footed woodrats over a landscape could be increased by landscape-level management that includes variable-density thinning, in managed stands, that is designed to mimic spatial patterns characteristic of old-growth and niche-diversification forests (Carey and Curtis 1996). This hypothesis can be tested in adaptive management experiments at the landscape scale, with treatment units of small watersheds. Carey and Curtis (1996) provide guidance for multiple-objective management for biodiversity that is also appropriate for woodrats. Strategies include variable-density thinning combined with coarse woody debris management and creation of debris piles from thinning slash, management of stream side areas to restore coarse woody debris and complex vegetation structure, and management of mass-wasting areas to promote recruitment to streams of coarse woody debris and coarse rocky debris at failure. Treatments are designed to (1) allow colonization of managed forests by both woodrat species, (2) facilitate colonization through maintenance of sources of colonizers, i.e., populations along streams, and (3) contribute to a larger, more viable metapopulation in the landscape.

Our review suggests that lack of clusters of den sites in upland forests with developed understories and without rock outcrops limits the distribution of bushy-tailed woodrats in Washington by making occupancy impossible in some instances and allowing only small populations susceptible to extirpation by predation in other cases. Even abundant, scattered coarse woody debris is insufficient to allow woodrats to occupy old-growth forests in western Washington (Carey 1995, Carey and Johnson 1995). This hypothesis could be tested via experiments in which large piles of debris could be constructed from thin-

ning operations designed to enhance understory development. These experiments should be conducted within reasonable distances (e.g., < 1 km) of occupied woodrat habitat and cover large enough areas (ca. 6-10 ha) to be true tests of the hypothesis.

Acknowledgements

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