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Appendix. Stand and silvicultural characteristics of trapping sites for Townsend's chipmunks, Willamette National Forest, Oregon, 1988.

Stand ^a	Size (ha)	Age (yr)	Elevation (m)	Aspect	Slope (%)	Stand history
1107-86	55	60	900	NW	35	WF ^b , RIC ^c
1303-33	28	30	600	E	25	SPC ^d , SFL ^e , REF ^f , FBR ^g , HCC ^h
7115-16	59	30	800	S	25	SFL, SPC, REF, FBR, HCC
7115-31	52	40	500	SW	10	SFL, REF, FBR, HCC
7115-83	36	40	450	S	20	RIC
1109-43	97	>400	850	N	55	NPC ⁱ
1109-84	82	>400	500	NW	60	NPC
1110-90	48	>400	800	SW	20	NPC
1111-44	110	>400	900	SW	40	NPC
7116-08	23	>400	375	NW	20	SC ^j

^a Numbers represent USDA Forest Service compartment number followed by stand number (last 2 digits).

^b Stand originated from wildfire.

^c Forest Service records incomplete.

^d Precommercial thinning.

^e Fertilization.

^f Reforestation by planting.

^g Broadcast or spot burn.

^h Harvest clear-cut.

ⁱ No previous cutting; small amounts of salvage cutting may have occurred.

^j Selective cutting; not extensive.

DUSKY-FOOTED WOODRAT ABUNDANCE IN DIFFERENT-AGED FORESTS IN NORTHWESTERN CALIFORNIA

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Abstract: Because dusky-footed woodrats (*Neotoma fuscipes*) are important prey species of northern spotted owls (*Strix occidentalis caurina*), we estimated their abundance in Douglas-fir (*Pseudotsuga menziesii*)/tanoak (*Lithocarpus densiflora*) forests of different ages in northwestern California. We surveyed and trapped woodrats in 6–8 stands in each of 5 seral stages during the summers of 1988–90. We used belt transects to compute nest density, and livetrapped at nest sites to estimate woodrat numbers per nest. Combining these 2 sources of information provided an estimate of woodrat densities, which were highest in sapling/brushy poletimber stands, followed by seedling/shrub and large old-growth stands. Woodrats were not found in small sawtimber stands and rarely occurred in large sawtimber stands. Because of within- and among-stand heterogeneity in woodrat abundance, the combined method may provide a more reliable estimate of woodrat abundance within a seral stage than live trapping on a grid. Because woodrats cross ecotonal boundaries, sapling/brushy poletimber stands adjacent to mature and old-growth Douglas-fir/tanoak forests may be source areas for woodrats preyed upon by northern spotted owls. Our data suggest that adopting specific silvicultural procedures that provide source areas for woodrats adjacent to suitable spotted owl habitat may directly benefit spotted owl populations; we recommend that specific hypotheses regarding these procedures be tested.

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Populations of the northern spotted owl declined throughout their geographical distribution for at least a decade, and conservation strategies to arrest the species' decline have been

proposed (Thomas et al. 1990; USFWS Recovery Plan for the Northern Spotted Owl, unpubl. rep., 1992). Better understanding of the ecology of spotted owl prey may allow management to speed the owl's recovery. Food habit studies in mixed coniferous and mixed-evergreen forests of southern Oregon and northern California have shown that the dusky-footed woodrat is the ma-

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for prey species for owls below 1,250 m (Barrows 1980, Solis 1983, Forsman et al. 1984, Ward 1990, Carey et al. 1992). In northwestern California, Raphael (1984) found that abundance of dusky-footed woodrats increased with stand age. However, dusky-footed woodrats also were reported to be abundant in the shrub-sapling seral stage (Raphael 1988), a habitat in which owls rarely forage (Forsman et al. 1984; Gutierrez 1985; Carey et al. 1992; C. Zabel, U.S. For. Serv., pers. commun.). Old-growth forests supported the next highest concentrations of woodrats, whereas intermediate-aged forests supported low densities (Raphael 1988). To clarify these habitat associations, we estimated the abundance of dusky-footed woodrats in different-aged forest in northwestern California.

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STUDY AREA

A minimum of 6 study stands, from each of 5 seral stages, was located on the Lower Trinity and Big Bar Ranger districts, Six-Rivers and Shasta-Trinity National Forests of northwestern California. Douglas-fir conifers and tanoak hardwoods were the dominant tree species in this Mixed Evergreen Forest type (Sawyer et al. 1977). We defined the 5 seral stages as: seedling/shrub stands with annual and perennial grass-herbaceous ground cover and shrub vegetation between 0 and 12 cm dbh (diameter at breast height); sapling/brushy poletimber stands with dominant Douglas-firs 12.1–27.0 cm dbh and 15–40 years old; small sawtimber stands with dominant Douglas-firs 27.1–53.0 cm dbh and 41–80 years old; large sawtimber stands with dominant Douglas-firs 53.1–90.0 cm dbh and 81–180 years; and large old-growth stands with dominant Douglas-firs >90.1 cm dbh and >180 years.

METHODS

We determined initial seral-stage designations and stand size from Forest Service timber polygon maps. We selected a minimum of 25 stands for each seral stage by choosing the closest stand of a given seral stage from randomly selected UTM reference points plotted on timber polygon maps. Criteria for stand selections were: >10 ha in size, accessible by road or hiking within 15 minutes, dominant vegetation of Douglas-fir and tanoak, and elevation 300–1,200 m. We conducted vegetation surveys of each stand using 0.02- and 0.05-ha circular plots to characterize structural and compositional differences among the seral stages. We conducted nest surveys from May to June and livetrapped along transects and at active nest sites from June through early August, 1988–90.

We used nest counts and live trapping at nests to estimate woodrat abundance, and live trapping along transects as a test to check on the reliability of nest counts. Because dusky-footed woodrats have a patchy distribution even within a stand, it is difficult to determine their abundance through trapping alone. Although trapping is often conducted within large grids (e.g., 10 × 10 plots with 40-m spacing; Raphael 1984; Taylor et al. 1988; Carey 1989, 1991; Ward 1990), individual stands are often much larger. Nest counting is not as labor intensive, and nest counting can survey a larger portion of a stand more efficiently and quickly than trapping in grids. Nest counting is feasible because dusky-footed woodrats typically build conspicuous, dome-shaped stick houses on the ground (Linsdale and Tevis 1951). Occasionally less conspicuous nests are found in trees (English 1923), in hollow limbs, and in rock crevices (Gander 1929). Vogl (1967) used nest counts to estimate dusky-footed woodrat populations for a southern California manzanita (*Arctostaphylos glandulosa*) chaparral habitat. However, Vogl did not live trap at nest sites, but rather assumed that each nest was inhabited by 1 animal, except in the case of a female with young.

We used fixed-width belt transects (Seber 1982:28) to survey for woodrat nests and assumed that: dusky-footed woodrat nests within the belt transect had a probability = 1 of being detected; initial nest positions were fixed; no woodrat nests were counted more than once; and all woodrat nests were distinguishable and correctly identified. We met the second and third assumptions but may not have fully met the first

and fourth regarding cryptic, non-structured nests.

Size and shape of a stand determined the total number and length of transects. Distances between transects varied: 75 m in seedling/shrub stands, 55 m in sapling/brushy poletimber, and 100 m for small and large sawtimber and old-growth stands. Transect widths varied according to seral stage: 50 m wide for seedling/shrub stands, 20 m wide for sapling/brushy poletimber, and 60 m wide for small and large sawtimber and old-growth stands. Transect widths were wider in the older-aged stands than in younger-aged brushy stands because older stands provided greater visibility and easier mobility with less understory vegetation. We determined the initial transect placement within a stand by adding 10 m to half the transect width and moving this distance in from the stand's edge (the transition between 2 habitats).

We counted only active woodrat nests. All woodrat nests were examined and judged to be active or inactive based on characteristics described by Vestal (1938) and Linsdale and Tevis (1951). Although ground-level woodrat nests were most common in our study areas, we looked for atypical nests. Clipped branches found on the ground and adjacent to burrow entrances or log piles or snags, and branches gnawed off from surrounding shrubs were helpful in locating atypical nests. Branches gnawed by woodrats were readily identified by tooth marks, whereas a fibrous membrane remained at the base of branches browsed by other mammals. Three observers conducted nest surveys in unison; one walked the transect accompanied by one on each side. We crisscrossed the study area and kept in constant communication. Active nests were flagged, numbered, and mapped using transect stations as reference points.

We obtained an estimate of woodrat numbers per nest by live trapping (3 consecutive rain-free nights) all active nest sites from 2–3 randomly selected transects per stand for each seral stage in 1988, and by live trapping up to 14 randomly selected nests in 1989 and 1990. Three Tomahawk 201 traps were located at entrances to each nest or along active runways leading from a nest. We tagged all first-captured woodrats on both ears with identical numbered aluminum tags. Tagging prevented double counting of woodrats and also helped to identify instances where woodrats used 2 or more nests.

To test the reliability of nest counts, we again

livetrapped along the transect lines for 3 consecutive rain-free nights. Trapping stations along transects were at 20-m intervals along the midline of the belt transects. In 1988, we randomly selected 2 transects and livetrapped with 2 Tomahawk 201 traps placed 5 m either side of each trapping station. In 1990, we livetrapped the same stands as in 1989, and 2 additional old-growth stands, using ground and arboreal traps placed within 5 m of each 20-m interval station. We placed 1 live trap on the ground and one in a tree secured 1.5 m off the ground.

We estimated woodrat abundance as catch per unit effort for each stand by summing the number of first-captured woodrats and then dividing by the total number of available traps (Caughley 1977:20–22, Seber 1982:55–56). We calculated the total number of available traps by subtracting the number of traps tripped but empty, and one-half of traps occupied by animals other than woodrats from the total number of traps set (Nelson and Clark 1973).

We estimated nest density for each stand by dividing the total number of nest detections by transect area. We estimated woodrat density and its variance by combining information on the number of nests per ha with the number of woodrats per nest (Scheaffer et al. 1979:41). We assumed that captures at a nest represented woodrats from that nest. We used 1-way analysis of variance (ANOVA) to test for differences in nest-capture rates and density estimates among the different habitats where woodrat nests were located. Density estimates were log-transformed before analysis. A posteriori comparisons were based on the Newman-Keuls multiple range test (Zar 1984:190–191). We computed Pearson product-moment correlation coefficients to compare numbers of animals captured at nests with numbers of captures along belt transects.

RESULTS

Seral Stage Differences

There was a distinguishable relationship between the size and density of trees among the 5 seral stages of Douglas-fir/tanoak forest (Fig. 1). The mean dbh (with SD, *n*) for conifers > 12.1 cm dbh for the 5 seral classes were: zero cm dbh (0, 0) for seedling/shrub, 20.5 cm dbh (5.1, 206) sapling/brushy poletimber stands, 36.1 cm dbh (19.7; 1,036) small sawtimber, 48.7 cm dbh (30.8, 670) large sawtimber, and 88.7 cm dbh (50.5, 309) large old-growth stands. Few

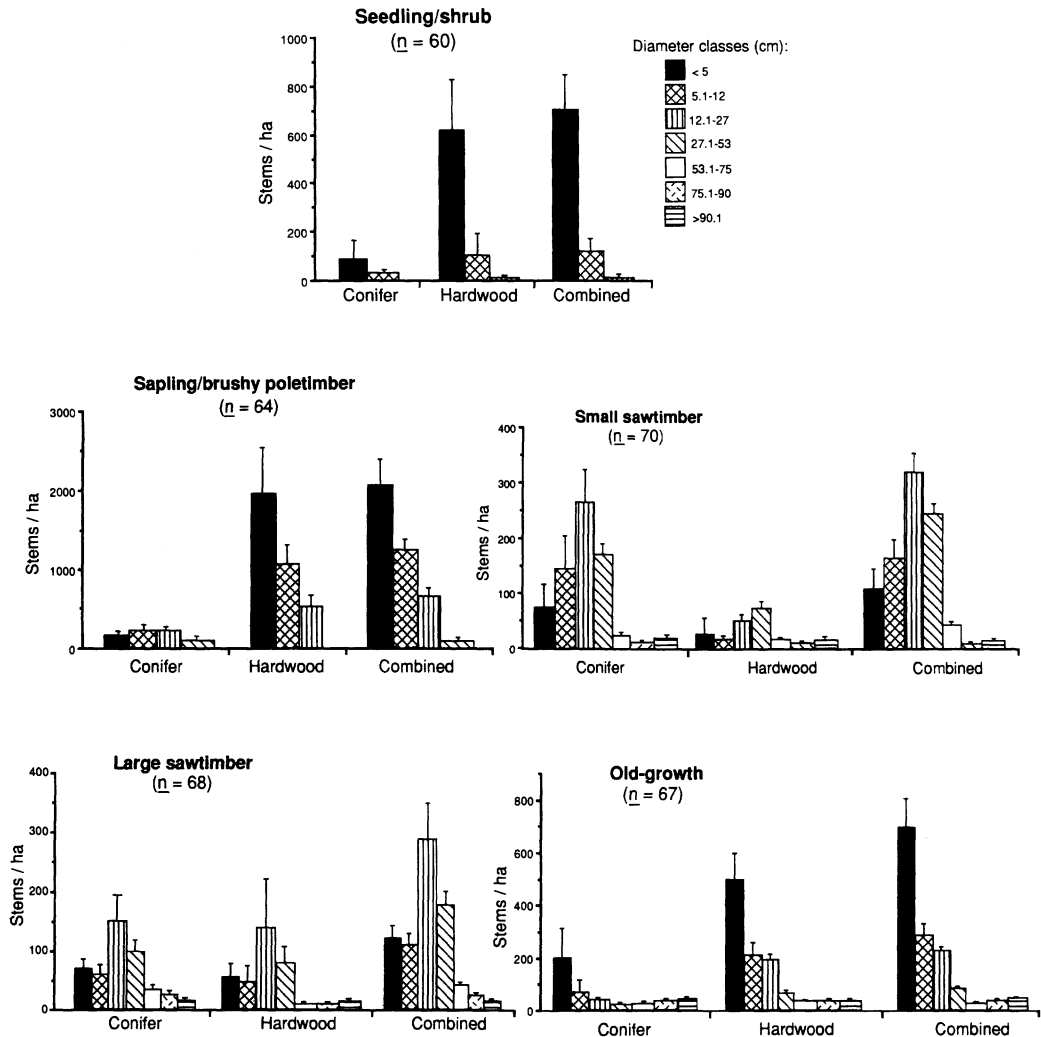


Fig. 1. Density estimates by diameter class for hardwood and conifer species for each of 5 seral stages within Douglas-fir/hardwood forest, northwestern California, 1989.

large-diameter conifers and hardwoods were found in the shrub/seedling and sapling/brushy poletimber stages (Fig. 1). However, the seedling/shrub stage had a distinguishable hardwood (mainly tanoak) component averaging <5.0 cm dbh. The sapling/brushy poletimber stage was characterized by high densities of conifers in the 5.1- to 12.0-cm-dbh class and a very prominent and dense hardwood layer consisting of trees ranging from <5.0 to 27.0 cm dbh (Fig. 1). A greater diversity of diameter classes of hardwoods and conifers was found in the small sawtimber, large sawtimber, and old-growth stages (Fig. 1). Small sawtimber stands were characterized by more conifers in the 12.1- to 27.0-cm-dbh classes and low densities of hard-

woods. Large sawtimber stands were characterized by larger conifers (12.1–90.0 cm dbh) and had the highest densities of hardwoods in the 12.1- to 53.0-cm-dbh classes. Old-growth stands had the highest densities of conifers >90.1 cm dbh, with a distinct hardwood tree component between <5.0 and 27.0 cm dbh.

Population Estimates

The occurrence and density of dusky-footed woodrats varied among seral stages (Table 1). Woodrats averaged >80 animals/ha in sapling/brushy poletimber stands and <1 woodrat/ha in all other seral stages (Table 1). No woodrat nests were located in small and large sawtimber

Table 1. Demographic characteristics of dusky-footed woodrats and their nests in various seral stages of Douglas-fir/hardwood forests, northwestern California, 1988-90.

Seral stages Stands	Total transect length (m)	Total adjusted trap nights	Total no. nests trapped	Total no. nests detected	Total captures	Average captures/ trap night	Average captures/ nest	Nest density/ ha	Woodrat density/ ha	95% C.I.
Seedling/shrub^a										
TT	800	8	1	1	2	0.25	2.00	0.25	0.5	^b
SL	700	0	0	0	0			0	0	
HR	920	0	0	0	0			0	0	
AP	520	43.5	6	6	10	0.23	1.67	2.31	3.9	2.0
EF	440	13.0	2	2	3	0.23	1.50	0.91	1.4	4.3
BM	360	0	0	0	0			0	0	
Total (\bar{x})	3,740	64.5	9	9	15	(0.24)	(1.72)	(0.58)	(0.97 A ^c)	(1.55)
Sapling/brushy poletimber^a										
ZP	1,240	18.5	3	3	3	0.16	1.0	1.21	1.2	3.0
SL	740	260.5	33	50	52	0.20	1.6	33.78	53.2	12.8
HR	880	225.5	27	31	41	0.18	1.5	17.61	26.7	7.1
SH	520	98.5	12	48	20	0.20	1.7	46.15	76.9	31.5
WR	440	119.5	14	75	39	0.33	2.8	85.23	237.4	43.9
HN	400	111.0	14	33	31	0.28	2.2	41.25	91.3	31.2
Total (\bar{x})	4,220	833.5	103	240	186	(0.22)	(1.8)	(37.54)	(81.12 B)	(20.96)
Small sawtimber^a										
SF	520	0	0	0	0			0	0	
ZP	1,380	0	0	0	0			0	0	
JH	480	0	0	0	0			0	0	
JL	500	0	0	0	0			0	0	
WR	1,220	0	0	0	0			0	0	
TT	940	0	0	0	0			0	0	
Total (\bar{x})	5,040	0	0	0	0			(0)	(0)	
Large sawtimber^a										
SL	1,260	0	0	0	0			0	0	
ZP	1,240	0	0	0	0			0	0	
HR	1,380	0	0	0	0			0	0	
GR	1,720	0	0	0	0			0	0	
WR	1,420	0	0	0	0			0	0	
SC	760	0	0	0	0			0	0	
Total (\bar{x})	7,780	0	0	0	0			(0)	(0)	
Large old-growth^a										
TT	1,220	18.5	1	1	2	0.11	2.0	0.14	1	^b
WR	1,340	0	0	0	0			0	0	
HR	1,300	39.5	6	6	7	0.18	1.2	0.77	0.9	0.8
SL	1,080	7.0	1	1	1	0.14	1.0	0.15	0.2	^b
SH	2,480	0	0	0	0			0	0	
TH	1,840	0	0	0	0			0	0	
OK ^d	360	45.5	7	7	8	0.18	1.1	1.08	1.2	1.5
SM ^d	600	9.0	1	1	0			0.28	0	
Total (\bar{x})	10,220	119.5	16	16	18	(0.15)	(1.3)	(0.30)	(0.41 A)	(0.42)

^a TT = Tish Tang, SL = Sugar Loaf, HR = Hennessey Ridge, AP = Ammon Prairie, EF = East Fork, BM = Brush Mountain, ZP = Ziegler Point, SH = Sharber, WR = Waterman Ridge, HN = Hennessey North, SF = South Fork, JH = Jimjam High, JL = Jimjam Low, GR = Grayll, SC = Surprise Creek, TH = Tishtang High, OK = Oak Knob, SM = Sugarloaf Mountain.

^b Sample size of 1 did not allow estimation of confidence interval.

^c Means within columns followed by the same letter do not differ ($P > 0.05$) Neuman-Keuls multiple range test.

^d Large old-growth stands with known breeding spotted owls.

stands. The densities of woodrats in sapling/brushy poletimber stands were greater ($P < 0.001$) than in seedling/shrub stands and old-growth stands. The seedling/shrub seral stage had the next highest density of woodrats but did not differ ($P > 0.50$) from the old-growth seral

stage. Woodrat captures along transect lines totaled 53 in the sapling/brushy poletimber seral stage, 36 in seedling/shrub, 19 in old-growth, one in large sawtimber, and zero in the small sawtimber seral stage. Nest densities and woodrat captures along transects and at nest sites

Table 2. Vegetation characteristics used to differentiate among the sapling/brushy poletimber stands within Douglas-fir/hardwood forest, northwestern California, 1989.

Stands ^a	% herbaceous ground cover	Density tanoaks/ha		Density conifer/ha	Density conifer/ha	
		<5.0 cm dbh	5.1–12.0 cm dbh	27.1–53.0 cm dbh	<0.5 m height	0.5–1.0 m height
HN	33.4	2,290	650	4	95	65
HR	3.7	970	1,035	0	0	35
SH	4.9	1,771	1,054	3	12	8
SL	22.1	1,012	687	0	75	71
WR	2.0	4,310	1,600	0	90	120
ZP	73.4	785	490	68	970	1,280

^a HN = Hennessey North; HR = Hennessey Ridge; SH = Sharber; SL = Sugar Loaf; WR = Waterman Ridge; ZP = Ziegler Point.

showed comparable differences among seral stages. For example, sapling/brushy poletimber stands had the highest captures and nest densities followed by seedling/shrub and old-growth stands.

The number of active nests and the density of woodrats varied among the sapling/brushy poletimber stands (Table 1). Density estimates ranged from 1.2 woodrats/ha (stand ZP) to 237.4/ha (stand WR). Although clearly a sapling/brushy poletimber stand, the vegetation structure and composition of ZP differed from the other stands in this seral stage. Stand ZP had the highest herbaceous ground cover, lowest density of sapling tanoaks, intermediate levels of sapling conifers, and the highest density of seedling conifers (Table 2). In some ways, the vegetation structure of this stand was transitional between the sapling/brushy poletimber and late stage poletimber to small sawtimber seral stages. Twenty years before our study, portions of this stand received herbicide to reduce competing vegetation and release the conifers. Portions of this stand also were salvage-logged, contributing to the high density of 27.1– to 53.0-cm-dbh poletimber-sized conifers (Table 2). The among-stand variation in woodrat density within this seral stage is reduced somewhat (26.7–237.4 woodrats/ha) if stand ZP is omitted (Table 1).

For seral stages with woodrats, the number of captures/nest averaged >1.0 woodrat/nest (Table 1). Adult and subadult woodrats made up >92% ($n = 200$) of the total ($n = 217$) captures. Juveniles were relatively uncommon in the capture sample ($n = 17$). The exclusion of juveniles when computing average woodrat captures/nest did not affect the results for any seral stage; captures still averaged ≥ 1.0 woodrat/nest.

Comparison Between Trapping Techniques

Four of 72 transects, representing 32 stands, had captures of ≥ 1 woodrat when no nests were found. Nine woodrats were captured along transects where no nests were found (6 subadults [5 males of which 3 were scrotal, 1 female] and 3 adult scrotal males). Total transect captures and total nests counted within belt transects were correlated ($r = 0.78$, $n = 65$, $P < 0.01$), as were total nest captures and total transect captures ($r = 0.80$, $n = 65$, $P < 0.01$), and captures at nests and along transects ($r = 0.58$, $n = 65$, $P < 0.01$).

DISCUSSION

Woodrat Abundance

The relationship between seral stage and woodrat captures per trap night and total woodrat captures at nests generally support the findings by Raphael (1988). Minor differences between our results and those of Raphael (1988) arise from differences in definitions of seral stages. Woodrats may have occurred in some of our early clearcut seedling/shrub stands and not in others because the presence of hardwood shrubs (e.g., tanoak) may have provided them with sufficient cover and food. Few or no woodrat captures in small and large sawtimber stands may have resulted from lack of understory plant cover. Cranford (1976:170) reported that woodrat use was low in areas with little plant cover.

Density estimates for our study were mostly lower than those reported by Ward (1990:52; $\bar{x} = 1.47$ woodrats/ha) for late seral stage forests (>180 yr) in northwestern California. As in our study, however, Ward (1990) found density varied greatly among his sites. Differences among our mean density estimates could be attributed to: true differences in density among study ar-

eas; differences in the methods of estimation, since Ward's estimates were based on the cumulative number of individuals caught during 8 nights of trapping from plots averaging 4.56 ha; and our failure to discover cryptic nests despite specific attempts to find them.

Our study showed that the average woodrat captures/nest, from June through mid-August, can be substantially greater than Vogl's (1967) assumption of 1 woodrat/nest. Our estimate of the average woodrat captures per nest does include juveniles, but because juveniles made up a very small proportion (only 8%) of the total captures, exclusion of juveniles does not change our findings.

Despite the abundance of woodrats in sapling and brushy poletimber stands, these stands are seldom used by foraging spotted owls (Forsman et al. 1984; Gutierrez 1985; Carey et al. 1992; C. Zabel, U.S. For. Serv., pers. commun.), probably because the woodrats are inaccessible to them. However, these stands may be source areas for woodrats that subsequently disperse throughout older seral stages used by foraging owls. Sightings of spotted owl pellets littering the forest floor of a sapling/poletimber stand in southwestern Oregon led Carey et al. (1992) to hypothesize that spotted owls were attracted to dusky-footed woodrat concentrations. Spotted owls may hunt along edges between old stands and young stands with high woodrat abundance (Ward 1990; C. Zabel, U.S. For. Serv., pers. commun.). Because woodrats are arboreal (Linsdale and Tevis 1951), owls may also capture woodrats from trees in sapling/brushy poletimber type stands. We know of no published studies that substantiate natural woodrat movement between different-aged habitats. However, we trapped 9 woodrats along transects with no detectable nests or signs of foraging, suggesting that individuals disperse or wander outside their natal areas. Several radio-tagged woodrats that occupied some of the sapling/brushy poletimber stands we studied moved short distances (<52 m) into adjacent large old-growth stands at night, then subsequently returned to their nest sites (H. F. Sakai and B. R. Noon, unpubl. data). We documented dispersal of 2 tagged woodrats from one of our brushy sapling stands, where 1 subadult male dispersed to an adjacent old-growth forest and the other adult male traveled through an adjacent old-growth forest before settling into a neighboring brushy stand.

Inventory Technique

Estimates of nest density derived from the belt-transect method are less affected by habitat variation than line-transect methods (Morrison and Kennedy 1989), where detectability problems arise in dense, heavily vegetated habitat or from obstruction by large objects (e.g., snags, trees, downed logs) or steep slopes. We addressed variation in the detectability of nests in different habitats by using fixed-width belt transects, overlapping the search areas of observers within the transect belt, and decreasing transect width in very dense stands. However, some atypical nests may have been missed, violating two of our assumptions and leading to a negative bias in the estimates. For example, Humphrey (1988) reported that simply counting nests or piles of droppings or burrows to estimate Key Largo woodrat (*N. floridana smalli*) abundance led to negatively biased estimates.

Nest counting and subsequent live trapping at a random sample of nests provides an indirect estimate of woodrat abundance. However, the method may provide more reliable information on their relative abundances in different habitats than more extensive trapping on grids. Abundance estimates from trapping grids depend on grid size and placement and therefore may not reflect the patchy distribution of dusky-footed woodrats, especially if stands are large and the grids are small. Several long belt transects can sample within-stand variation better than typical trapping grids. Much heterogeneity occurs among stands within a seral stage, necessitating a degree of replication that may not be attainable with fixed grids. Another advantage of nest counting is that money and time are saved by not having to measure and lay out grids. Use of this technique, however, requires observers to be especially aware of visual cues (e.g., gnawed branches, piled sticks at burrow entrances) as well as checking log jams, earth mounds, brush pile, snags, and brushy understory shrubs (especially in older-aged stands) for signs of occupancy by woodrats.

Indirect density estimates (based on nest counts and no. of animals trapped/nest) are biased to the extent that any cryptic nests go uncounted. We believe this bias to be minor. First, trapping along transects showed that in only 4 of 32 stands did we catch ≥ 1 woodrat when no nests were found. We speculate that most of these woodrats

were either transients from adjacent stands or residents missed because of their use of non-stick nests. We believe the majority of the 9 captured woodrats were transients because none were juveniles, 67% were subadults (5 males [3 of which were scrotal], 1 female), and only 3 were adult males in breeding condition. Second, habitats occupied by woodrats show evidence of foraging on the understory vegetation or clipped branches on the ground. We found such sign even for some dispersing woodrats. We exhaustively sought evidence of woodrat foraging in all stands. If a bias remained, it would have been most pronounced in the sawtimber and old-growth stands.

Woodrat Abundance and Spotted Owls

Radio-telemetry studies indicate that northern spotted owls are seldom located within brush-stage clearcuts even though these habitats occur within or adjacent to the home ranges of most radio-tagged birds (Sisco 1990; Solis and Gutierrez 1990; Carey et al. 1992; C. Zabel, U.S. For. Serv., pers. commun.). Owls do not forage in these habitats, presumably because the abundant prey are unavailable to them. To create brushy poletimber stands that do benefit owls, some demographic rate of owls, such as reproduction, must be limited by prey availability; woodrats within brushy poletimber stands must travel from source areas into older stands; and the brushy poletimber stands must be adjacent to stand types used for foraging by spotted owls. Data exist to support the last 2 criteria; no data exist for spotted owls to support the first. Data from other raptors, however, do demonstrate a relationship between prey abundance and reproductive performance (e.g., Cade 1960; Cave 1968; Hagen 1969; Newton 1979, 1991; Wendland 1984).

If these criteria are met for spotted owls, the question shifts to the appropriate amount and spatial pattern of young and old seral stages needed to support breeding pairs. Since most foraging is restricted to large sawtimber and old-growth stands, it is clear that some minimum acreage is needed in these seral stages to maintain a given pair of owls. Any compensatory relationship between the size and juxtaposition of habitats with large woodrat populations and the late seral stage area requirements of spotted owls remains unverified. Most forests in this region have been clearcut, converting the landscape from old to young forest. Even through

these areas may support much larger woodrat populations than in the past, spotted owl populations in the Douglas-fir/hardwood region of northwestern California are declining (Franklin et al. 1990, Franklin 1992). In addition, spotted owl home-range size and social behavior may be adversely affected by extensive amounts of young forest in the landscape (Carey et al. 1992).

RESEARCH AND MANAGEMENT IMPLICATIONS

Our findings suggest that some level of timber harvest may benefit spotted owls because dusky-footed woodrats reach their highest abundance in sapling/brushy poletimber stands. This inference does not extend to areas where woodrats are not the primary prey (see Thomas et al. 1990:Appendix J), and even in woodrat-dominated areas, such a hypothesis must be tested.

If spotted owls benefit from being adjacent to woodrat source areas, we believe there are management options to maintain or enhance woodrat populations. Although we base these options on our current understanding of the ecology of dusky-footed woodrats, hypotheses based on them should be rigorously tested using replicated control and treatment plots. For example, when regenerating clearcuts are treated to remove competing vegetation, retention of hardwood brush and patches (≥ 5 –10 m wide) that do not significantly suppress conifer growth could provide suitable habitat for woodrats. In young sawtimber stands, implementing specific silvicultural treatments, such as precommercial thinning operations to maintain small patches or strips of brushy vegetation, may support small woodrat populations in a seral stage in which they are normally rare. Other hypotheses that should be tested include the patch sizes required to maintain self-sustaining woodrat populations, widths of brush strips needed to yield dispersal rates high enough to sustain a pair of owls, and the best silvicultural treatment schedules needed to maintain woodrat habitat within regenerating clearcuts. Finally, if regenerating stands are eventually scheduled for a complete removal of competing, brushy vegetation, we suggest that the treatment be timed to displace woodrats only after these stands have acted as source areas for a number of years.

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EFFECT OF SNOW DEPTH ON PREDATION AND SCAVENGING BY GRAY WOLVES

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Abstract: Snow can affect wolf predation rates, diet composition, and scavenging, which are important components in understanding and managing wolf-prey systems. Thus, I located elk (*Cervus elaphus*) killed by gray wolves (*Canis lupus*, hereafter referred to as wolves) in Banff National Park, Alberta for 5 winters, and I followed one pack of wolves intensively throughout 1 winter to determine the effects of snow depth on wolf predation. Kill rate increased ($P < 0.001$) from 1 ungulate/5.4 days with no snow to 1 ungulate/1.1 days in snow 60 cm deep. Similar ($P > 0.5$) numbers of calves ($n = 24$) and adults ($n = 28$) were killed in shallow snow; predominantly calves (9 of 11) were killed at intermediate snow depths that hindered calves but not adults; and only adults ($n = 9$) were killed in deep snow that hindered both age classes of elk. Scavenging of ungulate carcasses occurred at shallower ($P < 0.01$) snow depths than did kills. At shallow snow depths, wolves likely encountered carcasses more frequently because they had a lower kill rate and moved farther between kills. My data indicate snow depth could add substantial, density-independent variation to wolf-prey interactions and affect which classes of prey are killed.

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Snow is a ubiquitous component of the northern environment in winter and has complex effects on the behavior of wolves and their prey (Telfer and Kelsall 1984, Fuller 1991). Deep snow can hinder the movements of both wolves and ungulates, but wolves have lighter foot loadings than most ungulates (Mech et al. 1971, Telfer and Kelsall 1984) and often can travel on top of a snow crust that will not support their prey (Peterson 1977). Hunting success of wolves generally increases in deep snow unless it is very soft (Kolenosky 1972, Peterson and Allen 1974, Haber 1977), and kill rate may increase as the snow depth increases (Nelson and Mech 1986). Correspondingly, the proportion of a carcass wolves eat before abandoning it declines with increasing snow depth (Pimlott et al. 1969, Mech et al. 1971, Carbyn 1983, Potvin et al. 1988), but generally remains greater than 80%. Snow also affects the diet composition of wolves, but a consistent pattern is not obvious (Fuller 1991). In several studies calves became a larger component of the diet in deeper snow (e.g., Peterson 1977, Ballard et al. 1987), whereas in others adult females became more vulnerable (Mech and Frenzel 1971, Haber 1977), or there was no

apparent effect of snow on diet composition (Fuller 1991). By affecting kill rates, diet composition, and perhaps carcass use and scavenging, snow may alter the functional response of wolves and influence wolf-prey dynamics. Additionally, because food intake in winter affects pup production and survival, snow may influence the numerical response of the wolves (Nelson and Mech 1986).

Herein, I examine the effect of snow depth on the kill rate and diet composition of wolves in Banff National Park, Alberta. Elk were the main prey, but 5 other ungulate species also were hunted by wolves, and ungulate carcasses were available for scavenging. I also use changes in kill rates to determine whether scavenging was avoided by wolves relative to hunting, and consider the implications of the results for predator-prey dynamics.

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