BETWEEN-HABITAT MOVEMENT OF DUSKY-FOOTED WOODRATS AND VULNERABILITY TO PREDATION

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Abstract: Management of northern spotted owls *(Strix occidentalis caurina)* in northwestern California is aided by knowledge of its prey base, the dusky-footed woodrat *(Neotoma fuscipes).* From late April through September 1990, we radiotracked 25 dusky-footed woodrats representing both sexes and a cross section of age classes (ad, subad, and juv). Animals were captured in sapling/poletimber shrubfields resulting from past clear-cut timber harvest. In northwestern California woodrats reach their highest densities in this seral stage. During evening radiotracking sessions, we detected intermittent, short distance movements of juvenile and subadult males and females, and adult females from shrubfields into adjacent old-growth forests occupied by spotted owls. None of the radiotagged woodrats permanently emigrated to older-aged forests during our study period. Between-year emigration frotn shrubfield to old forest, however, was documented for marked individuals. Our telemetry results indicate that woodrats are not averse to crossing sharp ecotonal boundaries from shrubfields into adjacent old forest, into canopy openings in these forests, or into natural openings within dense shrubfields. A substantial number of our radiotagged woodrats were killed by predators, with carcasses most often (5 of 9 depredated woodrats) found in adjacent old forest. These observations suggest that during these between-habitat forays, woodrats may be more vulnerable to avian and mammal predators. Therefore, to some degree, the existence of brushy shrubfields adjacent to older forest may increase the availability of woodrats to predators, such as spotted owls, that exploit prey from a variety of habitats but spend the majority of their time hunting in late seral stage forests.

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The dispersed clearcut method of forest management (Franklin and Forman 1987), as practiced in northwestern California and throughout the range of the northern spotted owl, has resulted in a sharply contrasting landscape mosaic of young (< 30-yr) and old (> 200-yr) forest patches (Spies et al. 1994). These patch types are intermixed in a complex mosaic, and characterized by abrupt edges between stands of different ages. At a landscape scale, the recent and extensive harvest of old-growth forest (since about 1950 on public lands) has resulted in a largely disjunct distribution of northern spotted owls (Thomas et al. 1990, Murphy and Noon 1992, Noon and McKelvey 1996).

Dusky-footed woodrats are nocturnal, polygynous, arboreal herbivores (Gander 1929, Linsdale and Tevis 1951). In the interior forests of northwestern California woodrats occur in highest abundance in 15-30-year-old brushy stands (dominated by *Ceanothus* sp., *Ribes* sp., sapling Douglas-fir [*Pseudotsuga menziesii*] and tanoak [*Lithocarpus densiflorus*]) resulting from past clearcut timber harvest (Sakai and Noon 1993). One behavioral characteristic that aids in their detection is the construction of large nests, usually composed of sticks, that may reach 2 m in height (Ingles 1965). The nest is usually the focal point of the home range, and is actively defended against conspecifics (Linsdale and Tevis 1951).

Below about 1,250 m in southern Oregon and northern California, dusky-footed woodrats are often the most important prey species (both in frequency and biomass) of northern spotted owls (Barrows 1980, Solis 1983, Forsman et al. 1984, Ward 1990, Carey et al. 1992, Zabel et al. 1995). Northern spotted owls nest almost exclusively in old-growth stands in interior forests (second-growth stands with residual old trees in the coastal redwoods), and forage primarily in mid- and late-seral stage forests (rev. in Thomas

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et al. 1990, U.S. Dep. Inter. 1992). Even though woodrats are most abundant in brushy shrubfields, northern spotted owls rarely forage in these habitats, presumably because the vegetation is impenetrable and the woodrats unavailable (Forsman et al. 1984, Gutiérrez 1985). Northern spotted owls forage more frequently than expected near the edge (< 100 m) between late and early successional forest (Zabel et al. 1995), suggesting greater prey availability in these areas. Since woodrats are primary prey in this region of the owl's range, presumably they are not averse to moving to adjacent forested habitats, use edges, and cross openings.

Linsdale and Tevis (1951:348) documented woodrat movements across open ground in oak woodland forests, and Cranford (1976) documented 9 woodrats dispersing from riparian woodland habitat into adjacent redwood forests following extensive flooding of nest sites. Whether woodrats occupying shrubfields display similar movement patterns across habitat boundaries was unknown. To distinguish exploratory movement by woodrats from dispersal events, we estimated home range size and location. Earlier studies suggest that woodrats have the potential for dispersing long distances from brushy shrubfields (Linsdale and Tevis 1951, Cranford 1976) but data were lacking to support this speculation.

The primary objective of our study was to investigate the lack of concordance between the low abundance of dusky-footed woodrats in old-growth forests (Sakai and Noon 1993) and the dominance of woodrats in the diet of northern spotted owls (Thomas et al. 1990, Carey et al. 1992, Zabel et al. 1995). To gain insights to this relation, we determined if woodrats were averse to crossing the usual sharp ecotonal boundary between sapling/poletimber shrubfields and adjacent late seral forested stands occupied by spotted owls.

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STUDY AREA

From late April through September 1990, we conducted our study in 2 sapling/poletimber shrubfields at 1,090 m elevation on the Lower Trinity Ranger District, Six Rivers National Forest, northwestern California. We selected shrubfield stands within the elevational range of woodrats (300-1,200 m), < 5 ha in size, accessible by road or limited hiking. Both shrubfields were surrounded by older-aged forests, and their boundaries were characterized by sharp ecotones. A strip of old-growth forest, measuring 60 m at its narrowest width, separated the 2 (1.2 ha and 4.5 ha) shrubfields. The selected shrubfields consisted of a mixture of Douglas-fir conifer, tanoak hardwood, and shrubs (deer brush, [*Ceanothus* sp.] and manzanita, [*Arctostaphylos* sp.]) with the majority of Douglas-firs and tanoaks measuring < 12 cm diameter-at-breast-height (dbh). Both sites had a closed canopy, averaging 88.9% ± 8.3 SD and 92.2% ± 8.3 SD, with canopy height ranging between 8 and 10 m. The denseness of the hardwood and brush layer in the sapling stage contributed the most to vertical cover; few trees > 27.1 cm dbh were present in both study sites (1.7 and 18.3 trees/ha).

METHODS

We systematically surveyed both stands for woodrat nests (methods described in Vestal 1938, and Linsdale and Tevis 1951), and consecutively numbered all active nests. We operated 3 livetraps (Tomahawk # 201 traps) at each active nest for 2 consecutive nights. We ear-tagged all woodrats captured with uniquely numbered aluminum tags and recorded mass, sex, reproductive condition, and age. We aged woodrats following methods in Lindsdale and Tevis (1951). Juveniles were defined as animals with gray pelage, subadults with intermediate brownish-gray pelage, and adults with cinnamon-brown pelage.

Animal locations were determined by radiotelemetry. We stratified our sample on the basis of age (i.e., juv, subad, and ad) and sex, and randomly selected 25 woodrats to wear radio-collars. Adults and subadults were collared in late April-early May, and juveniles in mid-June (when they emerged from nests). We attached neck collars, weighing 4.5-5.8 g with transmitters, on the ventral side of the neck.

Patterns of woodrat movement were based on radiotelemetry locations and live captures within a 36 ha, 15- X 15-study grid with 40-m spacing. The study plot included both shrubfields and adjacent old forest. All active nest sites found within the surrounding old-growth stands were livetrapped to determine if any woodrats previously eartagged in an unpublished 1989 study had dispersed from the brushy shrubfield. We used the strongest signal method (Bendel and Gates 1987, Cranford 1976) to radiotrack (hereafter, track) collared woodrats. Three observers, using walkie-talkies to communicate, took simultaneous locational fixes (hereafter, fix). We obtained 1 fix/collared woodrat/night. Paths 1 m wide were cut to gain access to grid corners for nighttime triangulation in both shrubfield study plots. We verified all fixes outside the shrubfields by walking toward the triangulated location and listening for a change in signal or by making visual or audio contact with the animal. For locations within forest, the perpendicular distance from the shrubfield/forest ecotone to the estimated location was then measured.

Tracking began each evening 15-30 minutes following sunset, in all weather conditions, for 4 nights/week during the initial month of the study, then tracked 5 nights/week for the remainder of the study. A triangulation polygon <25 m^2 was considered a valid fix since this was within the 1% error of accuracy for an average female home range (Cranford 1976). We determined the accuracy of observer triangulations at least once a month throughout the study period by taking a minimum of 3 simultaneous daytime fixes of nesting, collared woodrats and hidden transmitters placed up to 2 m aboveground within the study grid. Accuracy of day fixes averaged 1.7 m (SD = 1.3, range = 0.7-6.0, n = 17) and was determined as the mean difference in distance between the center of the triangulated polygon and the collared nesting woodrat or the hidden collar location.

We discriminated temporary movements within estimated home range boundaries from true dispersal behavior. Following Lidicker (1975), we defined dispersal as the complete and permanent emigration from an individual's home range, excluding short-term exploratory movernents or inclusion of a former home range area. Following Burt (1943) and Blair (1953), we defined home range as the area, including the nest site, over which a species normally travels to search for food, mates, and care for young. We used the 100% minimum-convex-polygon (MCP; Bekoff and Mech 1984, Mohr and Stumpf 1966) and the 95% adaptive kernel (AK; Worton 1989) algorithms to estimate home range boundaries for individual woodrats with >50 independent locations. The AK method discriminates areas within the home range on the basis of probability of utilization.

To compare home range estimates arnong different age/sex groups for woodrats tracked for ≥ 5 months, we used analysis of variance, and considered a probability value of 0.05 as statistically significant. We used 2-sample t-tests with 95% confidence interval for pairwise comparisons of home range estimates between breeding and nonbreeding periods. For simultaneous pairwise comparisons, we adjusted the Student's t-value at the $100(1 - 0.05/k)$ percent level, where $k = c(c - 1)/2$ and c = number of age/sex groups.

We differentiated between mammal and raptor predation based on a combination of criteria: (1) mammal-teeth marks on the radiocollar; collar located in a woodrat nest or underground; (2) raptor-location of carcass found at the base of a perch site with hair balls, viscera, and excrement (white wash).

RESULTS

Home Range

Based on animals with >50 locations, MCP home range size estimates for the age/sex groups were: adult female, 2,632 m^2 (SE = 1,149, n = 2); adult male, 5,338 m^2 (SE = 937, n = 4); subadult female, 1,927 m^2 (SE = 670, n = 3), subadult male, 4,186 m^2 (SE = 2,833, n = 2), and juvenile male 2,604 m^2 (SE = 1,800, n = 2) (Table 1).

No significant differences in home range size (MCP estimates) were detected among age/sex classes of woodrats tracked for the entire period of our study (F = 1.96, $P > 0.24$), or for those with > 50 locations (F = 1.30, $P > 0.34$; Fig. 1). Lack of statistically significant differences in home range size among age/sex classes is attributable to the large within-class variability (Table 2). Home range sizes of adult and subadult woodrats did not differ significantly between age classes for breeding (defined as Apr-Jun; t = 0. 95, 6 df $P > 0.38$) and post-

Table 1. Home range estimates, with the minimum convex polygon and adaptive kernel methods, for different age/sex groups of radiocollared woodrats in 2 brushy shrubfields of northwestern California, 1990.

Age/sex individual	Total locations	100% min. convex polygon (m^2)	95% adaptive kernel (m^2)
Ad/F			
661	74	1489	1494
751	75	3786	2569
756	36	756	1281
777	34	2645	5499
606	21	1019	1635
Ad/M			
417	18	2686	5996
608	77	7645	6546
686	78	4453	4354
763	60	5934	3262
766	56	3321	5038
Subad/F			
662	76	3263	4830
807	54	1811	1541
807 (2nd home range)	24	1132	1100
700	78	1337	1253
Subad/M			
634	48	1372	1308
754	16	4834	6036
811	52	7020	7942
811 (2nd home range)	32	3555	6711
684	76	1353	2334
Juv/F			
629	11	1166	2147
639	46	2600	3081
641	35	3903	5578
643	35	1164	1930
Juv/M			
638	51	803	859
640	22	1066	1596
645	23	1908	2672
753	76	4404	3424

breeding (defined as Jul-Aug; $t = -1.53$, 5 df, $P > 0.19$) periods.

An average of 5.1 ± 2.5 SD subadult and adult female locations were found within the home range of radiocollared subadult and adult males. The home range of a single adult male overlapped an average of 6.2 ± 2.6 SD female locations. We estimated a minimum average of 3.1 ± 1.3 SD subadult and adult females nesting within a 15.6-m radius, for each trapped adult male.

Movement

Radiocollared woodrats moved short distances from shrubfields into adjacent old-growth forests during the evenings. In our sample, movement into adjacent forest varied by age/sex group, and by individual animal (Table 2). Juvenile females were the age/sex group observed most frequently outside of shrubfields (0.8% of total locations). Subadult and juvenile males also traveled outside shrubfields (0.5%) but were observed less frequently than juvenile females. Adult and subadult females were detected much less frequently (0.2%) outside shrubfields and adult males were never observed outside the shrubfield. Due to small sample size, we were unable to test the statistical significance of these differences. Therefore, the generality of these apparent age/sex differences to the larger population is unknown.

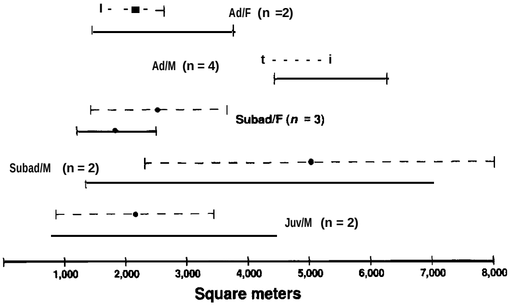

Fig. 1. Mean home range size by age and sex of woodrats radiotracked in northwestern California in 1990 and with >50 independent locations. Estimates are based on the adaptive kernel (AK) and minimum convex polygon (MCP) algorithms, with standard errors (SE) represented as dash and solid lines.

None of the 25 collared woodrats emigrated permanently during our study period. Dispersal was documented, however, by the recapture of 2 woodrats tagged in a previous study (H. F. Sakai, unpubl. data). Both were scrotal adult males first captured as subadults in 1989. One dispersed a straight line distance of 217 m through an adjacent old-growth stand, crossing an 8-m-wide dirt road before settling in a new nest in a brushy hardwood patch (11 X 14 m) located in the middle of an old-growth stand. The second, dispersed a straight line distance of 134 m through a 74-m-wide strip of old-growth stand to a neighboring brushy shrubfield.

Behavior indicative of true dispersal was observed for 2 other subadult males. One male moved 31 m, crossing an 8-m dirt road, from its brushy shrubfield nest to a nest in an adjacent old-growth stand and remained there for 2 days before returning to its former nest. This animal was preyed upon within a week of moving back to the shrubfield. The second male,

Table 2. Age and sex, distances moved from shrubfield habitat edge into adjacent forest, and predation status of 25 radiocollared dusky-footed woodrats. Study conducted in 2 Douglas-fir/tanoak dominated brushy shrubfields in northwestern California, 1990.

Age/sex individual	Total locations	Distance (m)	Preyed upon (what and where)
Ad/F			
661	74	39	no
751	75	0	yes (raptor; forest)
756	36	0	no
777	34	4	yes (raptor; shrubfield)
606	21	2	no
Mean(SD)		15(20.8)	
Ad/M			
417	18	0	yes (mammal; forest)
608	77	0	no
686	78	0	no
763	60	0	no
766	56	0	no
Mean(SD)		0	
Subad/F			
662	76	6	no
807	78		no
700	78	0	no
Mean(SD)		3.5(3.5)	
Subad/M			
634	48	2	no
754	16	52	yes (raptor; forest)
811	83	3, 7, 3, 5	no
684	76	0	yes (mammal; forest)
Mean(SD)		12(19.7)	
Juv/F			
629	11	2, 5	yes (mammal; shrubfield)
639	46	0	yes (mammal; shrubfield)
641	35	1, 1, 5, 12, 22, 10, 1	no
643	35	0	no
Mean(SD)		6.6(7.0)	
Juv/M			
638	51		no
640	22	0	yes (mammal; shrubfield)
753	76	2, 4, 1, 18	
645	23	0	FZs (mammal; forest)
Mean(SD)		4.5(6.7)	

tracked for 51 days in its original home range, moved 207 m to a new nest within the same shrubfield. Before establishing a new home range (based on 33 days of tracking), this male traveled repeatedly back and forth between its original and new nest.

Of our collared animals, juvenile woodrats had the highest predation rate (50%) followed by adults (30%) and subadults (29%; Table 2). Three of 9 woodrat mortalities were attributed to avian predators, and both sexes of juveniles were depredated by mammalian predators (as determined by teeth marks on the transmitter collars). Five of 9 collars from depredated woodrats were found in the adjacent older-aged forest.

DISCUSSION

Home Range

In our study, home range size estimates, by age/sex class, varied from 0.19 to 0.53 ha. These estimates are closely comparable to those of Cranford (1976) who based his estimates on similar age/sex classes. Perhaps what is most notable about our home range size estimates is their extreme variability. This finding, however, supports previous observations that dusti-footed woodrats may center their lifetime activity around a single tree, or range over 18 ha (Linsdale and Tevis 1951).

Movement

Our study indicates dusky-footed woodrats residing in successional shrubfields display exploratory behavior by making short distance forays into adjacent older-aged forests during night-time hours. By doing so, they leave a habitat where they are presumably less accessible to avian predators relative to woodrats residing in, or moving through, more open older-aged stands. Further, our results suggest dense woodrat populations in shrubfields (Sakai and Noon 1993) are a source of colonists to less dense woodrat populations residing in surrounding forested stands. Our recapture results of 2 marked adult male woodrats from a prior study parallel those of Cranford (1976) who also observed adult and subadult male woodrats disperse across discrete habitat boundaries. Similar to black-tailed prairie dogs (*Cynomys ludovicianus* and Belding ground squirrels (*Spermophilus beldingi* (Garrett and Franklin 1988, Hoogland 1982, Holekamp and Sherman 1989), subadult male woodrats showed a high frequency of exploratory movements-second only to juvenile females who were observed most frequently outside of shrubfields. Two subadult males changed home ranges within the same stand; we captured adult and subadult males in shrubfields, and in large sawtimber and old-growth stands where there was no evidence of active or inactive nests (Sakai and Noon 1993).

Home range overlap was extensive suggesting that woodrat movement may be motivated, in part, by density-dependent effects. Alternatively, exploratory movements may be an adaptive response to the ephemeral nature of shrubfield habitat-the structural features of the stand change and no longer provide suitable habitat following ecological succession. Successional processes involve a gradual decline in habitat suitability for woodrats, but at a rate much slower than the average lifespan of a woodrat. However, exploratory movement by juveniles and subadults woodrats would facilitate discovery of early successional habitats as occupied stands gradually declined in suitability. Data from Sakai and Noon (1993) suggest that this occurs when the dominant trees (usually Douglas-fir) begin to over top and eventually suppress the low-to-mid-canopy level vegetation (< 3-6 m). In the inland forests of northwestern California, the decline in habitat quality occurs at about 40-50 years following clearcut timber harvest.

Observations of movement from shrubfields into adjacent old-growth forests partially explain the occurrence of woodrats in the diet of spotted owls. Spotted owls seldom forage in shrubfields (Forsman et al. 1984, Gutiérrez 1985), yet woodrats are most abundant there (Sakai and Noon 1993). Some evidence exists that spotted owls may hunt along edges between old stands and regenerating stands where woodrats are more abundant (Zabel et al. I995, Carey and Peeler 1995). If this is a common foraging behavior, then shrubfields may be a potential source of woodrat prey for foraging owls. During an evening tracking session on 20 July 1990, a male northern spotted owl exhibited potential foraging behavior as it was observed actively searching from its perch site in a remnant mature live tanoak tree growing 5 m inside of the shrubfield edge. Additional observations of spotted owls potentially searching for prey while perched within 5-10 m from the edge of brushv shrubfield sites were made on 3 and 6 July, and on 2 July a spotted owl was observed sitting in the middle of a dirt road that bisected 2 shrubfields. Observations of foraging spotted owls suggests that woodrats may be vulnerable when crossing openings or moving into older-aged stands. In support of this hypothesis, Metzgar (1967) reported that wandering or transient white-footed mice (*Peromyscus leucopus)* were more vulnerable to predation by eastern screech owls (*Otis asio*) than resident mice. Transient white-footed mice moved about more frequently and became more active while traveling through unfamiliar habitat, thus increasing their conspicuousness and chances for being preyed upon (Metzgar 1967). Woodrats living in dense shrubfields probably reduce the risk of avian predation by being less accessible. Transient dusky-footed woodrats traveling through openings, along shrubfield edges, and into adjacent older-aged forests, however, would be more vulnerable to predation. Over a dozen visual observations during evening tracking sessions provided evidence of subadult and adult male and female woodrats using or crossing open areas where they would be more vulnerable to predation.

If woodrats are less vulnerable to predation within dense shrubfields, why would they move outside of these areas? Several hypotheses have been proposed to explain proximal causes of distance movement among sciurid rodents. These include the food-demand hypothesis (Dunford 1977, Dobson 1979, Dobson and Kjelgaard I985), limited availability of nest sites (Carl 1971), conspecific aggression (King 1955, Steiner 1972, Sheppard and Yoshida 1971, Festa-Bianchet and King 1984), inbreeding avoidance (Festa-Bianchet and King 1984), and ectoparasite load (Holekamp 1986). We have no evidence that these, or other, factors strongly influenced woodrat movement. However, male biases in natal dispersal is common across mammalian taxa (Lidicker 1973, Greenwood 1980, Dobson 1982, Holekamp and Sherman 1989) and dusky-footed woodrats follow this pattern (Kelly 1989). High costs associated with female dispersal and reproduction favors female philopatry since they require nests for successful rearing of young (Kelly 1989). Female woodrats, unlike males, usually spend their entire life in their natal area (Kelly 1989), suggesting that established nests are important for their survival and reproductive fitness. Under some circumstances, nests or available nest material, may limit population density (Linsdale and Tevis 1951:83). In our study area, woodrats appeared to have an abundant supply of available nesting material-the brushy stands were densely packed with dead branches. Woodrat density ultimately may be limited by the availability of sufficient food to meet their annual per capita requirements, especially in shrubfields with declining habitat quality. We speculate that some of the movements we observed were motivated by density-dependent factors, as well as adaptive, exploratory behaviors associated with successional declines in habitat quality. The tradeoff for these otherwise adaptive behaviors may be an increased risk of predation.

MANAGEMENT IMPLICATIONS

The movement of dusky-footed woodrats from early seral shrubfields' into adjacent late seral forest stands may directly benefit spotted owls by increasing the availability of a preferred prey species. To enhance duskv-footed woodrat populations, Sakai and Noon (1993) propose retaining brush patches during precommercial thinning of regenerating clearcuts, creating brush patches in young sawtimber stands, and scheduling treatment of regenerating clearcuts only after the stands have acted as woodrat source areas for a number of years. Based on this study and our current understanding of the habitat distribution and behavior of dusky footed woodrats, we further suggest leaving remnant islands (min. size 1 ha) of mid-canopy conifers and hardwoods (> 15 cm dbh) in otherwise clearcut areas to serve as perch sites for diurnal and nocturnal raptors. These forested islands will also afford northern spotted owls some protection from great horned owls (*Bubo virginianus*) when foraging in open areas. Because woodrats will cross openings (e.g., roads, natural openings in brushy stands, and natural breaks in mature forests), interior forest gaps could be created and maintained adjacent to perch sites in shrubfields for the benefit of avian predators (i.e., northern spotted owls). Based on our findings of woodrat use of natural openings in brushy stands and actual road widths, we recommend gaps ranging in size from 3 to 10 m. A final recommendation is the retention of perch sites adjacent to created openings to increase the availability of prey to avian predators.

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