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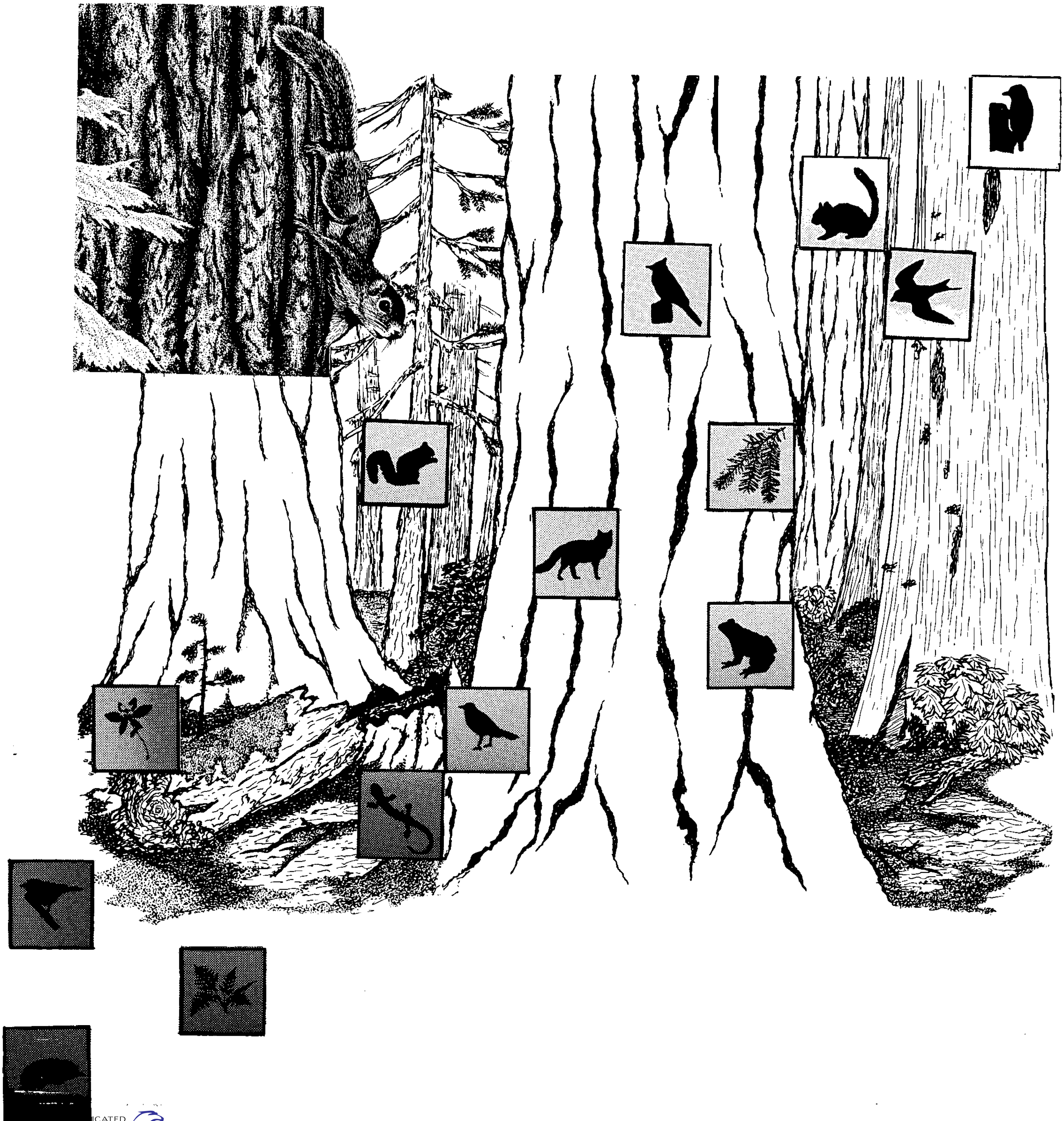

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Biology and Management of Old-Growth Forests

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Keith B. Aubry, Technical Coordinators

The Biology of Arboreal Rodents in Douglas-Fir Forests

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Abstract

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Arboreal rodents in Douglas-fir forests west of the Cascade crest in Oregon and Washington include (listed in decreasing order of dependence on trees) red tree vole (Phenacomys longicaucfus), northern flying squirrel (Glaucomys sabrinus), Douglas' squirrel (Tamiasciurus *douglasii),* dusky-footed woodrat (Neotoma *fuscipes),* bushy-tailed woodrat *(Neotoma cinerea),* and Townsend's chipmunk *(Tamias townsendi).* The arboreal rodents constitute an ecological community-a group of species that interact and influence one another's pattern of abundance and use of resources. All but the Douglas' squirrel and Townsend's chipmunk are important prey of the spotted owl (Strix *occidentalis).* The arboreal squirrels are mycophagists and have important functions in ecosystem processes. Individual species exist in many habitats, but the arboreal rodent community reaches its highest diversity and abundance in old-growth forests. The rodents are not evenly distributed, however, across the Pacific Northwest; maximum diversity and abundance in the community occurs in mixed-conifer, old-growth forests that contain streams. Although the species differ in life histories and ecologies, all seem sensitive to timber harvesting because of both elimination of habitat and creation of barriers to dispersal.

Keywords: Bushy-tailed woodrat, Douglas' squirrel, dusky-footed woodrat, northern flying squirrel, old growth, red tree vole, Townsend's chipmunk, Oregon, Washington.

Preface

Information about old-growth Douglas-fir forests and the wildlife species associated with them is critical to forest managers in the Pacific Northwest. Management of these forests has become a major public policy issue. Extremely high levels of concern have been expressed for a broad variety of values associated with old-growth forests. These include ecological, social, and religious values as well as commodity values derived from timber production. Forest managers are faced with a need to devise balanced strategies that retain all these values at levels acceptable to the public and consistent with the National Forest Management Act.

Forest acreage in the "old-growth" stage of development has declined rapidly in the Pacific Northwest during the past three decades. This has caused increasing concern about species' associations with old forests and maintenance of viable populations for those species most closely associated. Decisionmakers need to know which species show strong associations with old-growth forests, and understand the ecological requirements of those species. They need methods and tools to effectively manage and monitor these species and their habitat.

The purpose of this series of publications on the "Biology and Management of Old-Growth Forests" is to summarize the life history characteristics and habitat relations of species showing strong associations with old-growth forests in Washington, Oregon, and northern California, and to suggest options for their management. University and Federal scientists who collaborated in the USDA Forest Service, Pacific Northwest Research Station old-growth research program have produced a comprehensive list of associated species. Their technical research results were presented at a symposium in March 1989 in Portland, Oregon, and published in a book entitled *"Wildlife and Vegetation of Unmanaged Douglas-fir Forests."* We offer this series of management publications as a sequel to their research and to address other issues surrounding the management of late-seral ecosystems. The series is funded by the Wildlife Habitat Relationships Program, Pacific Northwest Region, USDA Forest Service. Our goal is to provide timely information to managers so they can make well-informed decisions about the management of old-growth forests.

Mark H. Huff
Richard S. Holthausen
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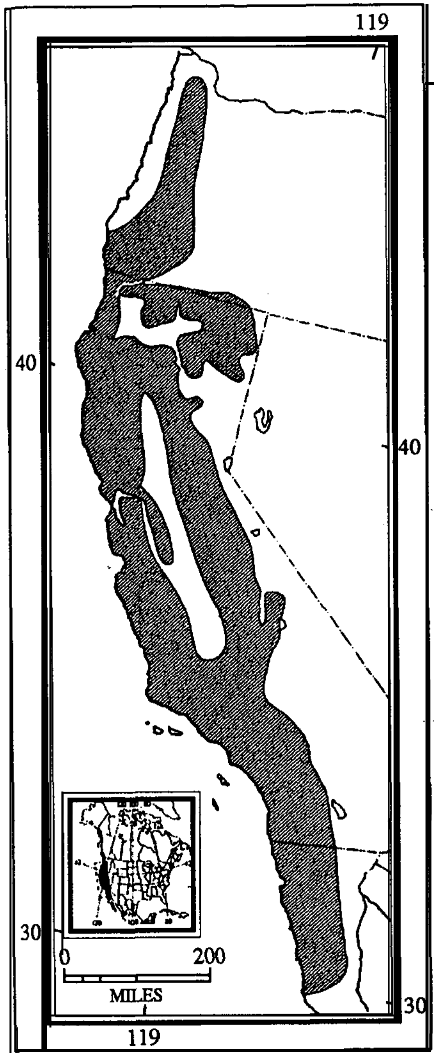
Introduction

The word "arboreal" means inhabiting or frequenting trees. Few mammals confine their activities to trees, and many mammals occasionally climb trees. We consider rodents to be arboreal when their nests are usually in trees, when they routinely forage in trees, or when they use trees as avenues for travel. Pacific Northwest rodents show a wide range of dependence on trees; the extent of dependence on trees of six species is listed in table 1. The geographic ranges of these species are shown in figure 1. West of the Cascade crest, there are three highly arboreal rodents: Douglas' squirrel, northern flying squirrel, and red tree vole. The Douglas' squirrel nests, forages, and travels among trees and travels and forages on the ground. The Douglas' squirrel changes its foraging emphasis with season, thereby reflecting the abundance of cones and fungi. The flying squirrel nests in trees, glides from tree to tree, runs and climbs among boles and branches, travels on the ground, and forages primarily on the ground for fungi and secondarily in trees for lichens. The red tree vole rarely ventures onto the ground, unless harassed in a tree. When harassed, the vole often will escape to the ground by running down the tree or by deliberate free falling (Maser and others 1981b). The red squirrel replaces the Douglas' squirrel in forested environments east of the Cascade crest and north of Washington and is similar to the Douglas' squirrel in habits. The western gray squirrel usually is not found in coniferous forests and prefers deciduous and evergreen hardwood forests.

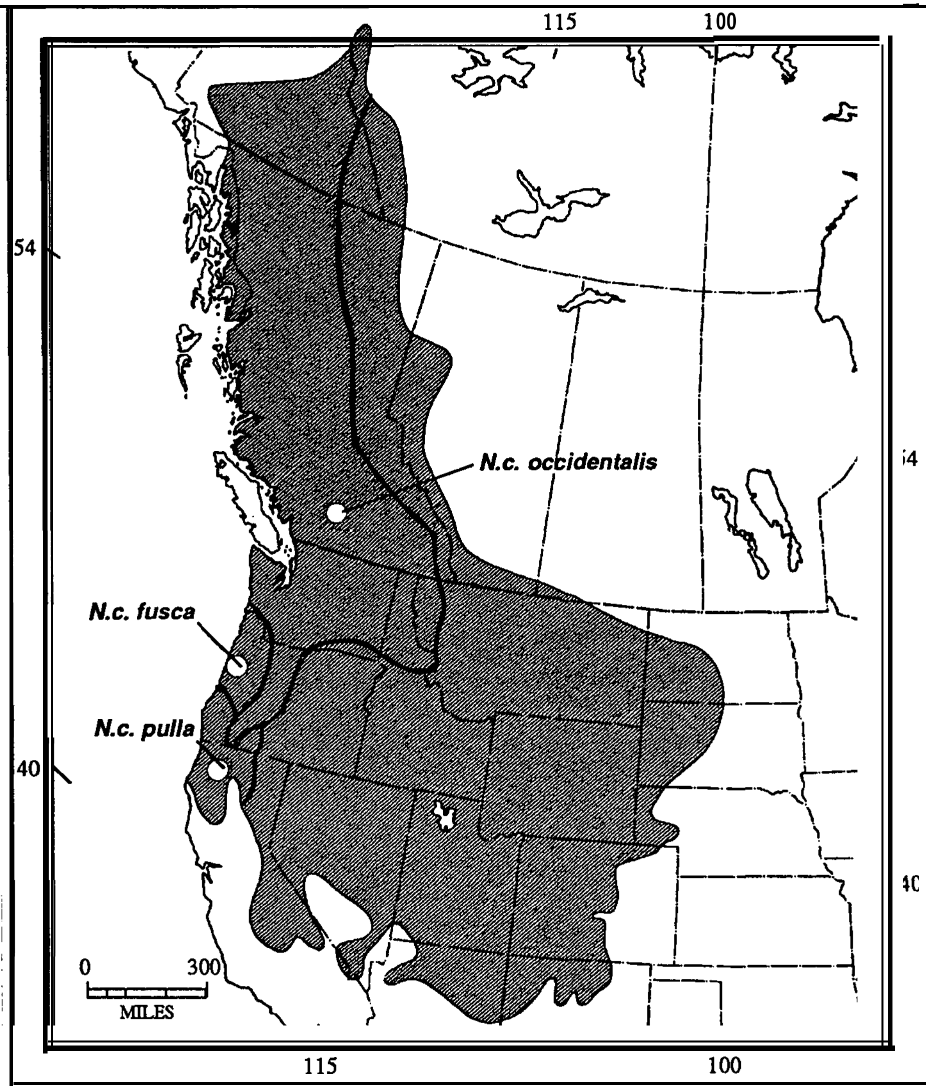
Table 1—Degree of dependence on trees of selected species of rodents in the Douglas-fir forests of the Pacific Northwest[a]

	Species[b]					
Activity	RTVO	FLSQ	DOSQ	DFWR	BTWR	TOCH
Travel:						
Ground		*	**	*	**	***
Trees/shrubs	****	***	**	***	**	*
Nest:						
Ground			*	**	**	***
Trees/shrubs	****	****	***	**	**	*
Forage:						
Ground		***	**	**	**	**
Trees/shrubs	****	*	**	**	**	**
Arboreality[c]	12	8	7	7	6	4

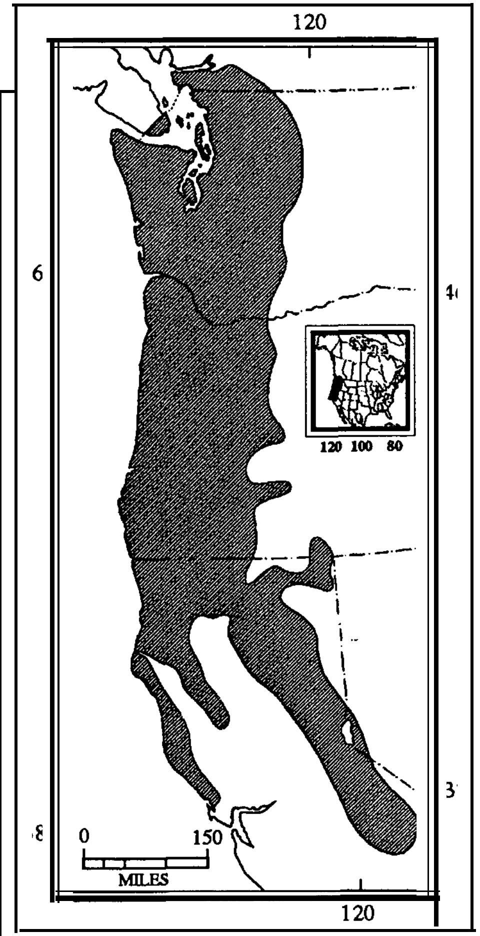
[a] Ratings are subjective.
[b] * Occasional, ** common, *** dominant, **** almost exclusive; RTVO, red tree vole; FLSQ, northern flying squirrel; DOSQ, Douglas' squirrel; DFWR, dusky-footed woodrat; BTWR, bushy-tailed woodrat; TOCH, Townsend's chipmunk.
[c] Sum of arboreal asterisks.



Dusky-footed woodrat *(Neotoma fuscipes)*

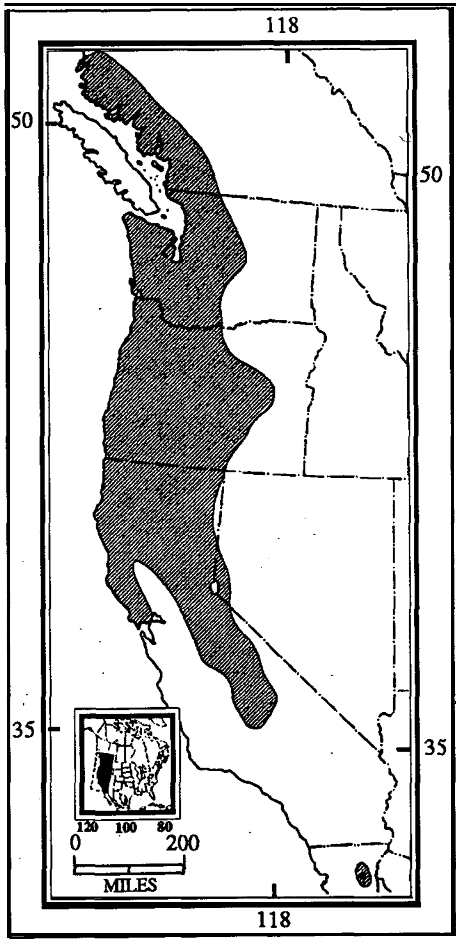


Bushy-tailed woodrat *(Neotoma cinerea)*

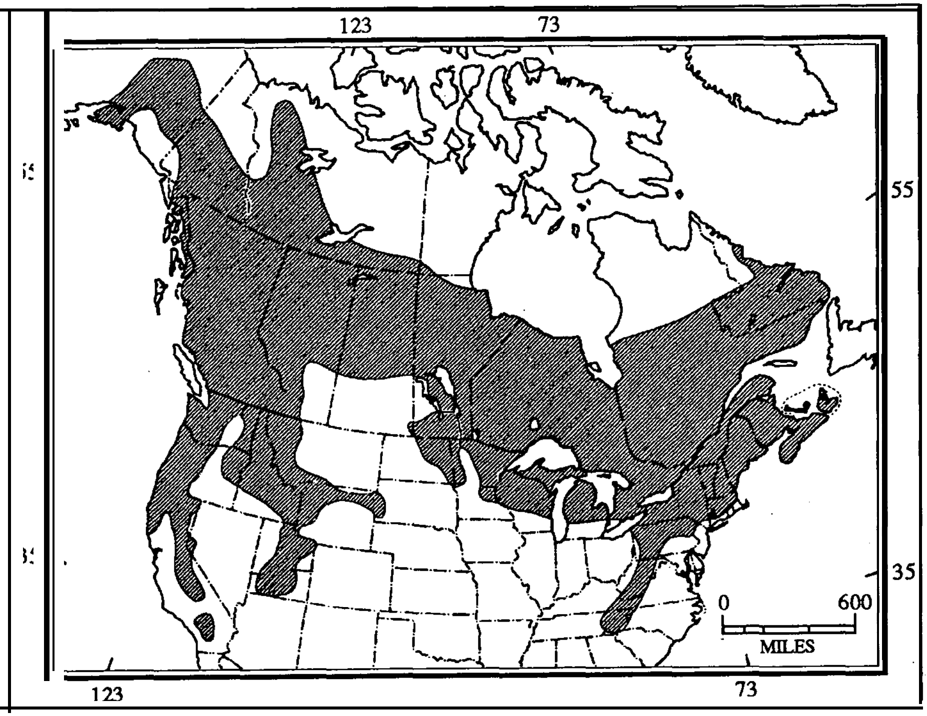


Townsend's chipmunk *(Tamias townsendii)*

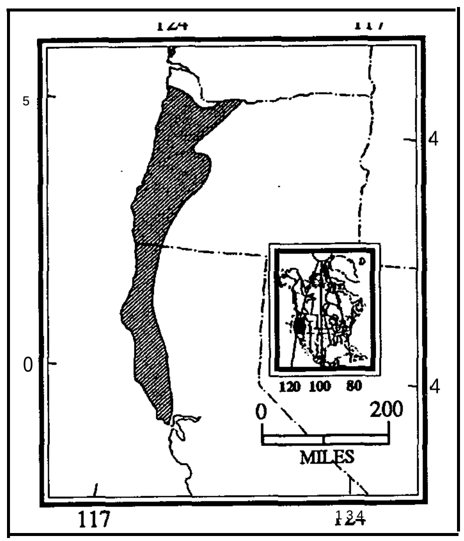
Figure l-The geographic ranges of the arboreal rodents commonly found in Douglas-fir forests of the Pacific Northwest.



Douglas' squirrel *(Tamiasciufus douglasii)*



Northern flying squirrel *(Glaucomys sabrinus)*



Red *tree* vole *(Phenacomys longicaudas)*

Figure I-Continued

The dusky-footed woodrat, the bushy-tailed woodrat, and Townsend's chipmunk are less arboreal than the tree vole, flying squirrel, and Douglas' squirrel. The dusky-footed woodrat builds nests of sticks in trees (up to 50 feet or more aboveground) and lodges of sticks and debris on the ground around the bases of trees, fallen trees, or stumps. The bushy-tailed woodrat usually travels and forages on the ground and nests in rock outcrops, fallen trees, stick nests in trees, or in cavities in trees. The chipmunk climbs well, forages (for cones), and sometimes nests in trees. It generally forages on the ground and in shrubs (for fungi, cones cut by Douglas' squirrels, and fruits of vascular plants), and nests in burrows. The semiarboreal rodents use some of the same foods, structures, and space as the arboreal rodents. The dusky-footed woodrat and the bushy-tailed woodrat have similar diets and may compete with each other for food and for space. Bushy-tailed woodrats and northern flying squirrels both use cavities in trees as well as stick nests, which also may be used by Douglas' squirrels, dusky-footed woodrats, and red tree voles.

The relation of arboreal rodents with trees makes them sensitive to timber harvest. Sensitivity reflects the degree of dependence on trees for food and shelter and the ability of the species to travel on the ground and across nonforested environments. This latter ability is crucial for colonizing young forests as they develop into suitable environments for arboreal rodents.

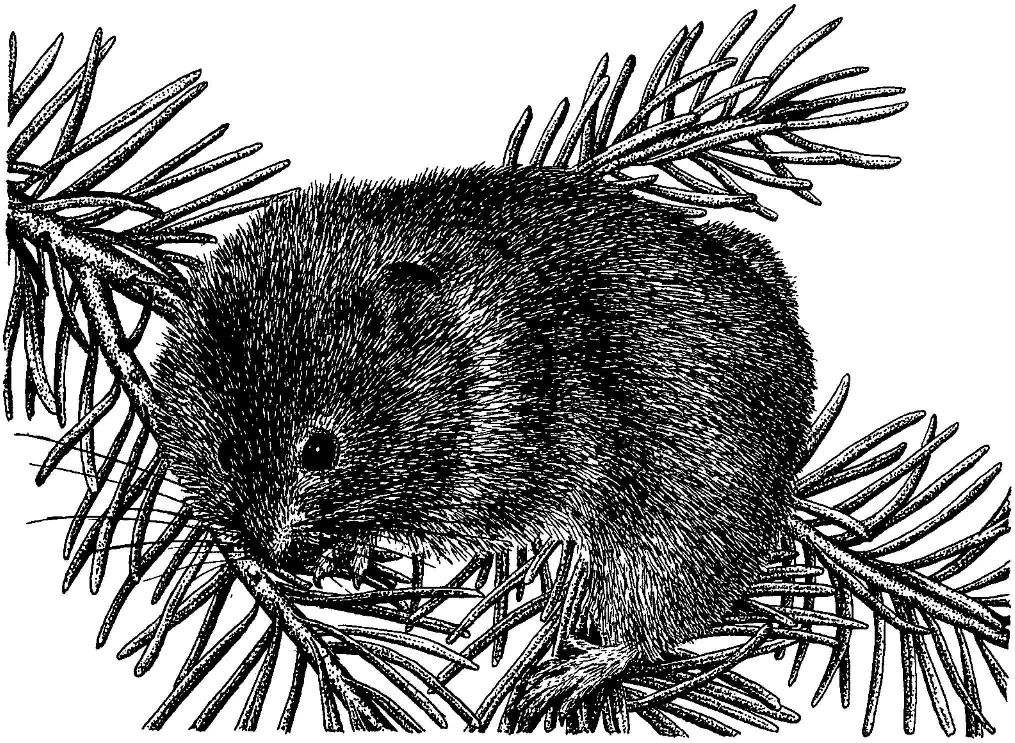
The red tree vole is associated with old growth for reasons not readily apparent and may be limited in ability to traverse nonforested areas. Ruggiero and others (1991) conclude that the red tree vole is closely associated with mature and old-growth forests and that significant reduction in these old forests will lead to a marked reduction in tree vole populations. The cavity-using flying squirrels are closely associated with old forests perhaps because of the greater abundance of cavities in old as opposed to young forests; "closely associated" means that loss of old-growth forest will precipitate a significant decline in flying squirrel numbers (Carey 1989, Carey and others 1991a). The conifer seed-eating Douglas' squirrels apparently benefit from the abundance of conifer seed in old growth; Buchanan and others (1990) conclude that loss of old-growth forests in western Washington will adversely affect populations of Douglas' squirrels. The relation between forest age and the abundance of Douglas' squirrels is not entirely clear, however, because of regional differences in forest composition, conifer seed variety and abundance, and perhaps abundance of hypogeous fungi and Townsend's chipmunks.

Arboreal rodents constitute an ecological community: a group of species interacting and potentially influencing one another's pattern of abundance and use of resources. Of particular significance is that four of the arboreal rodents (flying squirrel, red tree vole, and the two woodrats) constitute a major portion of the prey of the spotted owl. Thus, they influence and are influenced by spotted owl populations. The flying squirrel, Douglas' squirrel, and Townsend's chipmunk are of additional ecological significance because they eat the sporocarps of ectomychorrizal hypogeous fungi and disseminate the spores of the fungi and nitrogen-fixing bacteria (Li and others 1986; Maser and others 1978a, 1978b, 1985, 1986). The ectomychorrizal fungi are essential to nutrient uptake in trees; inoculation of the soil with the fungi and bacteria through rodent feces is an important part of the nutrient cycling process in the forest.

The Douglas' squirrel, red squirrel, and the woodrats will under certain circumstances cause damage to trees (Fisch and Dimock 1978, Franklin 1964, Maser and others 1981b). The Douglas' squirrel, red squirrel: and Townsend's chipmunk consume large quantities of conifer seed and once were considered a problem by foresters. They no longer seem to be of concern, perhaps because planting seedlings has become more routine than reliance on natural seeding for regeneration.

This paper summarizes the information on the life histories of the arboreal rodents, describes how the community might function in relation to the sere of forest development, and identifies those species and processes that seem to be affected by forest management. I emphasize especially the conversion of naturally regenerated, unmanaged stand-old growth and stands with old-growth components-to managed stands. The terminology used is from Brown (1985) for plant communities and stand conditions and Franklin and Dyrness (1973) for physiographic provinces and vegetation zones; the correspondence between the terminology used by the Old Growth Forest Wildife Habitats Research and Development Program (USDA Forest Service, Pacific Northwest Research Station) and Brown (1985) is provided in appendix 1. In addition, I examine both stand-level and landscape-level effects. I attempt to identify the critical elements of the habitat of each species to allow managers to determine where management can be used to ameliorate the effects of harvesting natural stands.

There is limited information in the-published literature on arboreal rodents in the Pacific Northwest; much of the life history information I present comes from a few, faunistic references: Bailey 1936, Brown 1985, Dalquest 1948, Hall 1981, lngles 1965, and-Maser and others 1981b. Because these references draw on much of the same primary literature and therefore are redundant, I usually do not specifically reference them in the text. I do reference pertinent primary literature, and I summarize the findings of my own studies that are in different stages of analysis and publication and those of the Old Growth Forests Wildlife Habitats Research and Development Program (Ruggiero and others, in press). Where information is lacking, I intentionally speculate about factors that might be limiting to a species to provide managers with at least a subjective basis on which to make recommendations. This paper emphasizes west-side Douglas-fir forests of Washington, Oregon, and northern California. Where I can, I incorporate information on the species pertinent to the east-side forests and Alaska. Monitoring and inventory techniques are presented by Carey and others (in press a).



Species Descriptions and Habits

Red Tree Vole

The nocturnal red tree vole is the smallest and least studied of the arboreal rodents of Douglas-fir forests in the Pacific Northwest. Maser and others (1981b) provide the best single description of the species. There is some doubt about the red tree vole being only one species; future taxonomic work could result in recognition of two species (Hall 1981). The red tree vole is about 7.5 inches long, including a 3-inch tail. It averages just under 1 ounce in weight. The pelage is thick, long, and soft, brown red to bright brown to orange brown on the back, and light gray below. The long, hairy tail is black to brown. The ears are almost hairless.

Life history-Red tree voles breed throughout the year but generally produce a litter of one to four (usually two or three) young from February to September. Gestation is 28 days but may be extended to 48 days in lactating females. Females can breed immediately after parturition. Reproduction in red tree voles is characterized by a long reproductive period, small litter size, slow development of young, and extended nursing of young all of which may be interpreted as physiological adaptations to the difficulties of converting conifer needles into energy for metabolism. I know of no information on the longevity, population structure, population density, or social behavior of red tree voles. In captivity, voles will not drink free water but do drink from water-saturated moss or sponge. They eat only conifer needles. Brown (1985) lists the home range as one or more trees. Red tree voles may spend their entire lives in tree tops (they move easily from tree to tree through the canopy). Terrestrial activity is reported by Corn and Bury (1986) and Raphael (1988); the nature of this activity is unknown.

Distribution and habitat—Red tree voles are confined to western Oregon and northwestern California (Hall 1981). Populations are widely scattered and are disappearing in many localities because of logging (Benson and Borell 1931, Howell 1926, Maser and others 1981b, Zentner 1977). Early mammalogists reported that red tree voles occupied only areas of extensive forest or areas of recently isolated forest (Bailey 1936). Brown (1985) states that the primary habitat of the red tree vole is closed sapling-pole-sawtimber, large sawtimber, and old-growth temperate coniferous forest stands. Secondary habitat includes large sawtimber and old-growth high temperate coniferous forest, closed sapling-pole, large sawtimber, and old-growth coniferous wetlands, and closed sapling-pole, large sawtimber, and old-growth mixed-conifer forest. But Corn and Bury (1988, 1988) report that red tree voles are three times more abundant in old growth than in younger stands along the west side of the Cascade Range. Red tree voles are rare in closed sapling-pole-sawtimber and large sawtimber stands but relatively abundant in old growth in the Cascade and Coast Ranges of Oregon (Carey 1989; see also Corn and Bury, 1991). In California, Zenter (1977) and Meiselman and Doyle (in press) found red tree voles are more abundant in old growth than in younger forests.

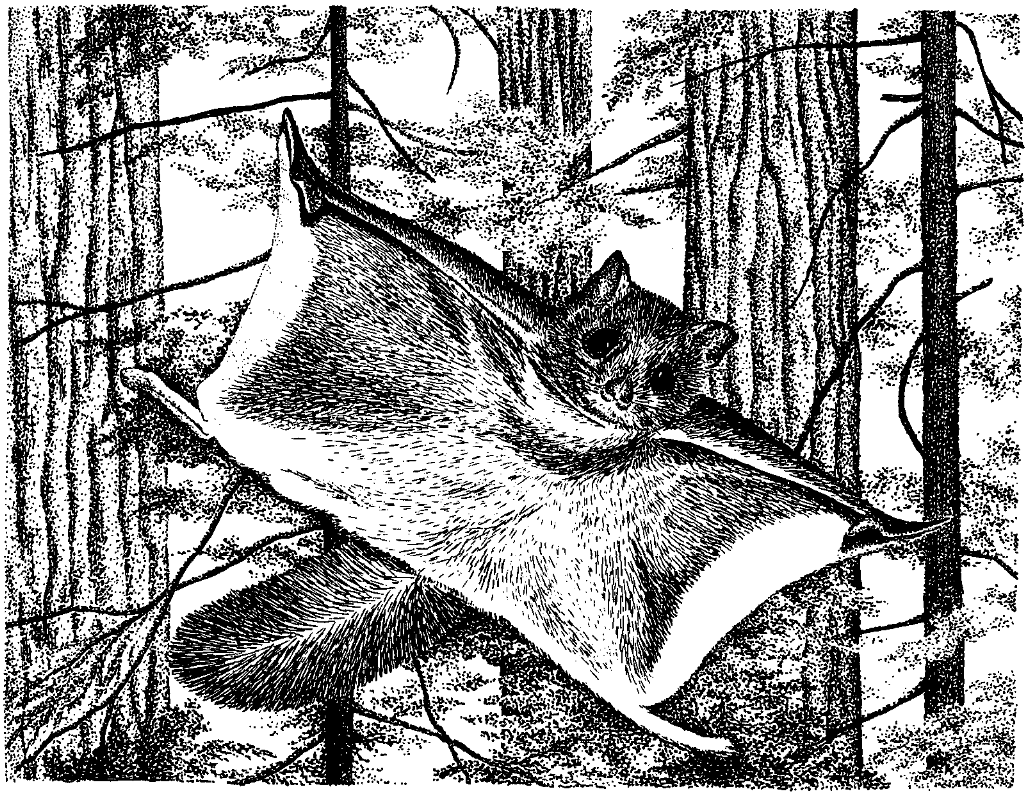
Nests and shelters—Red tree voles build nests wherever there is a suitable foundation and a readily accessible food supply; nests range from 6 to 160 feet aboveground (Benson and Borell l931, Maser and others 1981b). Nests may be placed at any height in trees of any size (Howell 1926). Recent studies suggest, however, that the voles prefer old-growth trees (Meiselman and Doyle, in press; Zenter 1977). Whorls of branches provide support in young trees; single, large branches in old-growth trees can support large nests. Nests are constructed of resin ducts, lichen, feces, conifer needles, and fine twigs. In old-growth trees, nests may be covered with a heavy layer of moss and are firmly attached to the tree. The vole also will use nests constructed by other species and sometimes will make nests within hollow trees. In California, males sometimes nest, in burrows under fallen trees or coarse woody debris. Arboreal nests used by red tree voles may have been used or constructed by western gray squirrels, Douglas' squirrels, northern flying squirrels, dusky-footed woodrats, bushy-tailed woodrats, deer mice, and various birds (Maser and others 1981b).

In southwestern Oregon, red tree voles select the largest available trees for nesting, even in old growth. Nest tree d.b.h. (diameter at breast height) and number of nests per tree are correlated; the sample with the highest mean d.b.h. (46 inches) had 4.1 nests per tree, and the sample with the smallest mean d.b.h. (28 inches) had 1.8 nests per tree. Nests were distributed throughout the live canopy but were most abundant in the lower third of the canopy (Gillesberg and Carey 1991). Meiselman and Doyle (in press), Vrieze (1980),and Zenter (1977) reported the same for red tree voles in California. Food and cover are abundant in the lower canopy where the crown interweaves with adjacent trees, thereby effectively increasing forage abundance and escape routes (Vrieze 1980). Half the nests were on branches and half were against boles, similar to what Zentner (1977) reports. Single, large limbs of old-growth trees provide not only support for nests but also escape routes from predators, access to mates, and proximity to green foliage (Maser and others 1981 b). Large trees can accommodate more than one vole, which thereby may promote colony formation and increased access to mates.

Food-The principal food of the red tree vole is Douglas-fir needles. The voles occasionally eat the needles of grand fir, white fir, Sitka spruce, and western hemlock. Water is obtained by licking dew, rain, or condensation from fog off needles.

Predators-The chief predator of the red tree vole is the spotted owl (Maser and others 1981 b); the northern saw-whet owl (Forsman and Maser 1970) and the long-eared owl (Reynolds 1970) also prey on the vole. Far more important than predation in limiting vole abundance are forest fires and logging. Clearcutting "decimates entire populations and is responsible for the disappearance" of the vole in many areas (Maser and others 1981b).

Limiting factors-The red tree vole is the most highly specialized vole in the world (Maser and others 1981b). Its dependence on Douglas-fir for shelter and food and its restricted diet have resulted in life history characteristics that permit only slow growth of the population and that are adaptive only in a relatively stable environment. Old growth provides such stability; trees in young forests are continuously growing and presumably require continual nest relocation. Primary production is high in old growth, and leaves are concentrated on fewer individuals, thereby providing maximum food availability. The tall, multilayered canopies have high water-holding capacity, humidity, and fog interception, thus providing free (chemically unbound) water for the voles. Large branches and boles provide stable nest sites within green foliage that allow construction of large nests that may be used by generations of tree voles, thereby promoting formation of colonies and maximizing access to mates. Thus, limiting factors of importance within its preferred environment (old growth) would seem to be the size of the old-growth stand, the length of time it has been colonized by red tree voles, and the noncatastrophic influences of fire, windstorms, and predation by owls. Limiting factors within the landscape that determine the pattern of abundance and persistence of red tree vole colonies are the major catastrophes (fire, windstorm, clearcutting) that destroy stable old growth and result in rapidly developing (changing, unstable) younger forests.



Northern Flying Squirrel

The single best reference on northern flying squirrels is Wells-Gosling and Heaney (1984). Most published information on the northern flying squirrel in the Pacific Northwest, however, is anecdotal (see Maser and others 1981 b). Only the diet of the squirrel has been reported in detail (Maser and others 1985, 1986; McIntire and Carey 1989).

The northern flying squirrel is nocturnal and rarely seen by people. But it is readily recognizable from its large dark eyes, fine, soft hair that is dark reddish brown on the back and tan to white on the belly, its wide and horizontally flat tail, and the flaps of skin (patagia) that extend from the wrists to the ankles. Dorsal pelage changes color with age (Davis 1963) but the changes are subtle and not readily evaluated in the field. Flying squirrels do not fly by flapping the patagia, rather they glide. They maneuver well while gliding and can make sharp, right-angle turns. Glides can be long, in excess of l00-150 feet. The squirrels are graceful flyers and can land gently on a tree trunk; sometimes, however, they deliberately crash onto the leafy surface of a shrub or small tree.

The squirrels average just under 12 inches long, including 5 inches of tail. The ears are prominent, about 0.8 inch high. Adult northern flying squirrels average 4.3 ounces in Washington and Oregon. Flying squirrels are not highly vocal and do not sound alarm or territorial calls, but they do sometimes make a high-pitched chitter while flying and guttural sounds when threatened or angry.

Life history-Flying squirrels breed during late April through early July; the peak of breeding is from late May to early June; young are born from mid-June through mid-August and are not weaned until mid-October or mid-November. One litter of two or three young is produced per year. Most yearling females do not breed. About 25 percent of the adult females do not breed in any one year. Young squirrels may disperse in the fall or they may spend the winter with their mother. Sex ratio is approximately 1 to 1. Little is known about the social behavior, mating system (promiscuous vs. monogamous), or dispersal behavior of northern flying squirrels. Often several adult flying squirrels occupy the same nest. Aggregations are usually segregated by sex (Maser and others 1981a, Osgood 1935). Life expectancy is probably less than 4 years; Davis (1963) reports a mean of 1.8 years.

Distribution and habitat-Northern flying squirrels occur across northern North America in areas of coniferous forest. Their range is continuous through Canada and extends to the edge of the continuous forest, to Alaska, southward in the lower United States through the Appalachian Mountains, the Black Hills, the southern Rocky Mountains, and the Sierra Nevada. The squirrel is associated primarily with coniferous forest and mixed coniferous-deciduous forest and occasionally broadleaf-deciduous forest (Wells-Gosling and Heaney 1984). In the Pacific Northwest, flying squirrels are associated primarily with large sawtimber and old-growth temperate, high temperate, subalpine, and mixed conifer-coniferous forest types. Hardwood, pine, and riparian/wetland types are considered to be secondary habitats (Brown 1985).

Within the Pacific Northwest, densities of flying squirrels differ greatly. On the Olympic Peninsula, I found densities to average 0.2/acre in old-growth Douglas-fir/western hemlock and climax western hemlock/Sitka spruce forests and only O.O8/acre in managed, small Douglas-fir or western hemlock sawtimber. Some small sawtimber stands had no flying squirrels. In southwestern Oregon, densities averaged 0.8/acre in old-growth Douglas-fir and mixed-conifer stands (with densities averaging O.4/acre where predation by spotted owls was high and reaching 1.5/acre where owl predation was low) and O.4/acre in managed, small Douglas-fir and mixed-conifer sawtimber stands. In the Oregon Cascade Range, densities averaged 0.8/acre in both old-growth and managed Douglas-fir/western hemlock sawtimber in a preliminary analysis (with owl predation not considered). The average movements by squirrels differed with each stand; overall, the mean maximum distance moved between subsequent recaptures was about 325 feet (Carey and others 1991a). Thus, an estimate of home range size (for a 10-day period) is 1.9 acres. In Alaska, density was 0.3/acre, and home ranges were over 70 acres in 150-year-old white spruce-paper birch forests (Mowrey and Zasada 1984). The squirrels moved in 1.2-mile circuits around their home ranges. In North Carolina and Tennessee, northern flying squirrels used many distantly spaced nests and moved more than 1,600 feet in a night in spruce-fir/northern hardwoods ecotones (Knowles and others 1990).

Nests and shelters-Flying squirrels use two types of nests: nests in cavities in trees and nests on limbs. The cavities may be natural cavities formed by mechanical damage to the tree or rot or cavities excavated by woodpeckers or other birds. The cavities may be in live or dead trees. External nests are generally built of moss and lichen by the squirrels or may be abandoned nests of birds or other arboreal mammals. External nests usually are used only in summer. Each individual flying squirrel will use several dens, cavities, or external nests (Cowan 1936). The number of cavities or nests required by northern flying squirrels is not known. Mowrey and Zasada (1984) report individuals used between 1 and 13 dens. In Oregon, I found individual northern flying squirrels using up to seven nest sites. Snags containing nest cavities averaged 35 inches in d.b.h.; live conifers with nests averaged 49 inches d.b.h. Cavity trees used in small sawtimber stands were obviously trees carried over from the preceding old-growth stand. Large (>20 inches d.b.h.) snags are 10 times more abundant in old growth than in small sawtimber (Carey and others 1991 b). Use of multiple dens by northern and southern flying squirrels is common (Cowan 1936, Jordan 1948). Carey and Gill (1983) found that southern flying squirrels in captivity used up to four nest boxes, Doby (1984) reports use of multiple nest boxes and natural dens, and Bendel and Gates (1987) report southern flying squirrels use an average of four dens in a l00-day period.

Food-In the Pacific Northwest (including Alaska), the diet of flying squirrels is primarily fungi and lichens (Maser and others 1986, Mclntire and Carey 1989, McKeever 1960, Mowrey and others 1981); lichens are important east of the Cascade crest and in Alaska. Flying squirrels consume a large variety of fungi including Basidiomycetes, Ascomycetes, and Zygomycetes; Maser and others (1986) report 20 taxa annually, and Mclntire and Carey (1989) report 12 taxa from two stands in one season in 1 year. In contrast, the principal diurnal consumer and disperser of fungal spores, Townsend's chipmunk, consumed only 7 of the 12 taxa of fungi (Mclntire and Carey 1989). Year-round consumption was documented in southwestern Oregon (Maser and others 1986) despite marked seasonal (fall and spring) production of sporocarps; there are substantial differences among years in sporocarp production also (Fogel 1976, Hunt and Trappe 1987, Luoma 1991). Similar studies have not been completed for the Olympic Peninsula where densities of flying squirrels are low. But the diversity of hypogeous fungi apparently increases markedly from the peninsula (8 species) to the Oregon Cascades (47 species) to southwestern Oregon (97 species).

Predators-The major predator of the northern flying squirrel in the Pacific Northwest is the spotted owl. Spotted owls can reduce the flying squirrel population around nest groves by 50-67 percent-from 0.8-1.2/acre to O.4/acre. Great horned owls also could be an important predator in the Pacific Northwest: In some areas, the barred owl is becoming abundant and could be an important predator. Where marten are abundant, they prey on flying squirrels and other arboreal rodents. Other species may prey on flying squirrels too, but I found no documentation that their predation is significant.

Limiting factors-Limiting factors for flying squirrels seem to be food, shelter (cavities), and the spotted owl. It is not clear how limiting food and shelter are. I found no apparent relation between the abundance of Townsend's chipmunks and Douglas squirrels and the abundance of flying squirrels. The three species use the same food resource (hypogeous fungi). Townsend's chipmunks often outnumber flying squirrels; Douglas: squirrels can be equally abundant. This would suggest that food is not limiting continually; it does not suggest that food might not be limiting at certain times of the year (for all three species) or in certain years. Marked variability in the production of fungi affects all the mycophagists by periodically reducing their densities; such variation in resource abundance allows species of similar habits to coexist. The chipmunk and Douglas' squirrel have conifer seed as a major part of their diet. Like fungi, conifer seed abundance differs markedly among seasons and years. I found no information on differences in abundance of hypogeous fungi between old growth and managed, small saw-log stands.

I found no negative correlation between the abundance of flying squirrels and bushy-tailed woodrats, even though both use tree cavities. The bushy-tailed woodrat seems to be limited in abundance more by its social behavior and, perhaps, the presence of rock outcrops (perhaps predation, too) than by the abundance of tree cavities (Escherich 1981). Although the red tree vole, Townsend's chipmunk, and Douglas' squirrel use cavities in trees too, they more often use external nests (I doubt they provide competition to the flying squirrel for tree cavities). Flying squirrels will use the abandoned external nests of other mammals as well as bird nests and, thus, may benefit from the presence of these other species. Most of the cavities used by flying squirrels seem to be abandoned woodpecker holes; the presence of woodpeckers may be essential for high populations of northern flying squirrels. Woodpeckers are three times more abundant in old growth than in young forests in southwestern Oregon (Carey 1989, Carey and others 1991b, Lundquist 1988, Nelson 1989); throughout the Pacific Northwest, woodpeckers are more abundant in old growth than in younger forests (Carey 1989, Huff and Raley 1991). Placing nest boxes in young stands in southwestern Oregon led to increases in flying squirrel populations but this research is not complete. In many other areas, nest boxes have led to increases in squirrel populations (Carey and Gill 1983, Carey and Sanderson 1981).

It seems that flying squirrel populations are constrained by at least three different factors: food, shelter, and predation. These factors differ in importance with year, season, habitat type, and individual stand. Of these factors, the one most easily ameliorated by management is shelter. Provision of snags for woodpeckers, retention of live trees with top rot, artificial creation of cavities in trees, and provision of nest boxes are ways to provide shelter for cavity-using wildlife. The greatest potential for increasing flying squirrel populations with these techniques lies in young stands. Management for diversity and abundance of fungi in closed canopy forests has not been attempted. It seems to me that retention of coarse woody debris, enhancement of tree species diversity, the diversity of herbs and shrubs (perhaps through thinnings that open the canopy), and mycophagous rodent populations should lead to increased fungal diversity and abundance. Thinnings, however, will retard natural snag production. Thus, management prescriptions for flying squirrels must be thoughtfully formulated to achieve the right combination of management practices.

Douglas' Squirrel

The Douglas' squirrel has been a subject of intensive investigation (Koford 1982; Sanders 1983; Smith 1965, 1968a, 1970, 1978,1981; Smith and Balda 1979; Smith and Reichman 1984; and others). The Douglas' squirrel is a diurnal, conspicuous resident of coniferous forests in the Pacific Northwest. It calls attention to itself with its loud, repeated territorial calls: the long, trilling "burr" or "rattle," a "screech," a "growl," and a "buzz;" it also gives an alarm call (chirp) in response to predators and people (Smith 1978). The Douglas' squirrel is about 13 inches long, including 5 inches of bushy tail. Its ears are 0.9 inch tall; the squirrel averages 9 ounces. Pelage color can differ among individuals, geographic locations, and seasons but tends to be dusky olive on the back, white to orange on the belly, with a dark stripe on each side.

Llfe hlstory-The breeding season is March-August, sometimes with two peaks and a lull in May (Koford 1982; Smith 1965, 1968a). Reproduction differs markedly with food (cone) abundance; breeding may be delayed or deferred, and litter size differs. Up to two litters of 4-8 young may be produced in one year with births peaking in June and with young leaving the nest before September. The young are weaned 2-3 weeks later in mid-September. Young squirrels begin giving their first territorial calls in mid-September and establish territories by late September or October. Families have been observed together as late as December, however, perhaps a reflection of second litters. Woods (1980) reports that mortality is high for juvenile Douglas' squirrels and that life expectancy for adults is less than 3 years.

Both male and female Douglas' squirrels defend individual territories with calls and chases. Territories are relaxed during the 1 or 2 days per year that the female is in estrus. Mating is promiscuous. Territories may also be relaxed in the spring when male cones are abundant and may be abandoned in years of food shortage. Territories are small (0.53 acres) and average 425 feet in diameter. Size may differ with food abundance; territories usually contain 0.7-2.9 times the annual energy requirements of the squirrel. Territories are exclusive and contiguous. Douglas' squirrel densities average 0.6-0.9 per acre. Territories are defended not only against other Douglas' squirrels but also against Townsend's chipmunks.

Distribution and habitat-Douglas' squirrels are found from southwestern British Columbia through the western half of Washington, the western two-thirds of Oregon, northern California, and the Sierra Nevada. The Douglas' squirrel may intergrade with the red squirrel along the eastern edge of its range. If this occurs, the four subspecies of the Douglas' squirrel will be reclassified as additional subspecies of the red squirrel (Hall 1981). Within the Pacific Northwest, Douglas' squirrels are found in the open sapling-pole, closed sapling-pole, large sawtimber, and old-growth stands in the temperate and high temperate coniferous forests, mixed-conifer forests, and subalpine forest parks. Secondary habitats include hardwood and shrubby wetlands, coniferous wetlands, and lodgepole pine, shorepine, and conifer-hardwood forests (Brown 1985). In northern California, Raphael (1984) found a positive correlation of Douglas' squirrel abundance and stand age (55-315 years), as did Ralph and others (1991). But in riparian areas in the Oregon Cascades, Anthony and others (1987) found no differences in the abundance of Douglas' squirrels among young (closed sapling-pole), mature (large sawtimber), and old-growth forests in the spring. There were no differences in Douglas' squirrel abundance in the spring among closed sapling-pole-small sawtimber, large sawtimber, and old-growth Douglas-fir forests in southwestern Oregon, the Oregon Cascades, and the Washington Cascades (Carey 1989). In a small sample of stands in the Washington Cascades in the winter, however, Buchanan and others (1990) found Douglas' squirrels to be more abundant in old-growth stands than in closed sapling-pole-small sawtimber and large saw-log stands. It is not clear why these results differ; the results Carey (1989) reported included spring samples from the stands sampled by Buchanan and others (1990). The Douglas' squirrel is not known to routinely switch territories with seasons; however, immigration to areas of high food abundance has been reported (Sullivan and Sullivan 1982). The spring population is that surviving the period of lowest food abundance and is generally the lowest population of the year (Sullivan and Sullivan 1982). If old growth provides more diverse and abundant food than younger forests, then the spring population should demonstrate differences more markedly than winter populations; but winter populations are composed of adults and juveniles. Perhaps the differences observed were due to old growth providing better overwintering habitat for juveniles than young forests can. If most of the juveniles died by spring, or dispersed in spring into young stands, then the different results would be accounted for. Sullivan and Moses (1986) report that young stands serve as a dispersal sink for juvenile and yearling red squirrels.

Nests and shelters-Douglas' squirrels use various shelters: tree cavities, hollow trees, hollow logs, nests of grass, lichens, and sticks in trees, and burrows in the ground (Maser and others 1981 b, Smith 1968a). Most commonly used are loosely constructed stick nests in summer, hollow trees or tree cavities in winter, weathertight nests in dense foliage as alternate winter nests, and an underground nest in the main midden (cone cache) pile during prolonged, severe weather. Den sites do not seem limiting to Douglas' squirrels. Douglas' squirrel external nests may be used by red tree voles and northern flying squirrels, but there is no evidence suggesting that other arboreal rodents expropriate the nests of Douglas' squirrels.

Food-Douglas' squirrels are behaviorally and anatomically adapted toward exploiting their primary foods: conifer seed and fungi (Smith 1970, 1981). The genus *Tamiasciurus* is known for storing cones in caches. The caches of the red squirrel may be very large: one red squirrel in Ontario picked and cached at least 1,000 cones in 1 day (Clarke 1939); caches in Alaska contained up to 8,500 cones each with individual squirrels cutting and caching 12,000-16,000 cones (Smith 1968b); caches in Michigan averaged 4 bushels or 1,300 cones (Yeager 1937); caches in the Rocky Mountains were 20-30 feet across and 1-1.5 feet deep (Finley 1969); and in Arizona, caches contained 8-24 bushels of cones and were 15 by 30 feet in area (Patton and Vahle 1986). Red squirrels may cache enough cones to support themselves through one or more years of poor cone crops. Douglas' squirrels also are capable of harvesting cones at a high rate and storing them in a centrally located cache; for example, 277 cones in 23 minutes (Smith 1981). But caches of Douglas' squirrels seem to be smaller than those of red squirrels. Caches of 1,800-2,500 cones were cached in springs and seeps in the Sierra Nevada, but more commonly, cones were cached in groups of 1-20, averaging 6, under fallen trees (Shaw 1936); in Oregon, caches were 0.5 bushels (200 cones) along streams, in moist depressions, in or under fallen trees, and under moss on the ground (Lavender and Engstrom 1956). Caches are in moist, cool locations to keep the cones from drying, opening, and spilling their seeds. I could not find any large caches in southwestern Oregon, but I did find a few small caches (<30 cones); squirrels in the areas I studied seemed to be scatterhoarding (hiding small groups of cones). In California, Koford (1982) found that Douglas' squirrels cached only enough cones to last 6-9 months; enough to carry them through the winter and spring only. Fungi also may be cached (by both species). The Douglas' squirrel is adept at finding hypogeous fungi; Fogel and Trappe (1978) report that Douglas' squirrels ate more species (89 species) of fungi than any other mycophagist; however, they do not report data on the northern flying squirrel (and Maser and others [1981a] thought Townsend's chipmunk was the foremost diurnal consumer of hypogeous fungi).

Both species of Tamiasciurus depend on caches of cones (and sometimes fungi) for winter food (Lindsay 1986). Why then the absence of large caches? The nocturnal flying squirrel will raid caches of fungi, and Townsend's chipmunks are abundant and raid caches of cones. It may be too difficult for the Douglas' squirrel to defend single, large caches in the face of other Douglas' squirrels, flying squirrels, and Townsend's chipmunks. I found small caches and observed squirrels scatterhoarding among fallen trees. Koford (1982) describes similar behavior in

California, and Sanders (1983) notes that cache locations were near fallen trees. It also may be that hemlock and Douglas-fir cones do not retain their seed as long as lodgepole pine cones do aboveground or above-water.

Both fungi and cones differ markedly in abundance among seasons and among years. Fruiting of hypogeous fungi peaks in spring and fall (Fogel 1976), but seasonality differs by species with up to sixfold changes in annual production (Luoma 1991). The abundance of hypogeous fungi also seems related to the amount of decaying wood in forest stands (Maser and others 1986). Young, managed stands do not have the coarse woody debris accumulations that old forests have; thus, young forests may provide a greater seasonality and a lower overall abundance of hypogeous fungi than do old forests, with the summer drought having a greater influence on soil moisture in the absence of large amounts of decaying wood.

Cone production differs among species of tree, years, seasons, age classes of stands of trees, sites, and individual trees (see Eis and others 1965, Fowells 1965, Garman 1951, Hoffman 1924, Lowry 1966, Ruth 1955, Schopmeyer 1974, Smith and Balda 1979). The great fluctuations in seed production by conifers west of the Cascades result in parallel fluctuations in Douglas' squirrel populations (Smith 1970, Buchanan and others 1990). Variability is accentuated by synchrony among species of trees: Douglas-fir, grand fir, western hemlock, and western redcedar are generally synchronous in cone production. Production is not truly cyclic but peaks occur with an interval of 1-5 years. There is at least one failure and two light to medium crops every 5-7 years (Fowells 1965); failures occur every 4 years on the average in western Oregon and Washington (Lowry 1966). In all species, heavy cone crops are typically followed by one or two off years. Cone and seed production are physiologically expensive and result in reduced height and diameter growth. Variability and synchrony in cone production not only reflect tree physiology and weather but also are adaptations to seed predation. Crop failures among years of heavy seed production lead to dramatic reduction in populations of seed predators (five orders of insects, six families of birds, and two orders of mammals) and allow a large percentage of the seeds in productive years to go uneaten (Smith and Balda 1979).

Ability of a tree to bear cones increases with age up to 300 years. An old-growth tree may produce 14 times more seed than a 40-year-old tree. Young old growth (275 years) produces 24 times more seed than a 40-year-old stand, but still produces much less seed than old growth that is 300-350 years old. Seed production may decline at 600 years. Old stands also produce cone crops in years that young stands do not. There seems to be a much greater variation in cone production among individuals in old stands than in young stands. Thus, there is a more consistent minimum seed production in old stands than in young stands.

Conifer species differ in amount of seed produced and seasonality of seed fall. Douglas-fir may produce averages of 0, 300, 1,500, or 2,000 cones per tree per year, depending on the year; good producers may produce 5,000-12,000 cones (with a maximum of 20,120) in good years. Years of poor cone production also have low numbers of seeds per cone. Western hemlock produces more seed than Douglas-fir or grand fir; western redcedar is second only to western hemlock. Western hemlock also produces some seed, every year and will have seed-bearing cones throughout the winter, with greatest seed fall occuring in March. Grand fir, western redcedar, and Douglas-fir seed fall peaks in September-October; western redcedar may retain some seed throughout the winter; and Douglas-fir will have a secondary seed fall in March in some areas.

Old-growth forests, especially old-growth Douglas-fir/western hemlock/western redcedar forests, provide a more abundant,. more consistent, less seasonal (due to the great variety of species in old growth), and more diverse seed resource for Douglas' squirrels (and Townsend's chipmunks and the seed-eating birds) to exploit than does a young Douglas-fir forest. In addition, the multilayered canopies of old growth also include other seed- and mast-producing species, especially deciduous species such as maples and huckleberries, that can be of great importance in years of conifer cone crop failure. Old growth, then, provides the best environment available to Douglas' squirrels. But the key question remains unanswered: Is old growth necessary for the continued existence of Douglas' squirrels? This question and its corollary (Are young forests just dispersal sinks for Douglas' squirrels?) can be answered only after research during a major cone crop failure, and perhaps a failure followed by another failure or poor cone crops.

Predation-The principal predators of the Douglas' squirrel in the Pacific Northwest are the northern goshawk and the great homed owl; the marten may be an important predator in some areas (Smith 1965, Woods 1980). I could find no quantitative measures of predation on the Douglas' squirrel; all references to predation seem to be anecdotal or speculative.

Limiting factors-Food seems to be the single-most limiting factor for Douglas' squirrels. Of particular importance seems to be the large difference in seasonal and -annual cone production. Sullivan and Sullivan (1982) show that supplemental food can increase Douglas' squirrel populations in forests of 45-110 years by 5 to 10 times through immigration, increased reproduction, and increased survival of juveniles. In a related study, Sullivan and Moses (1986) show that decreasing a stand's production of cones through silvicultural thinning reduces red squirrel densities (they observed a twofold reduction). Certain thinnings, however, may increase seed production in Douglas-fir over time. Other factors do not seem nearly as important as food in regulating numbers of Douglas' squirrels.

Dusky-Footed Woodrat

The dusky-footed woodrat is primarily nocturnal but sometimes forages during the day; it may be considered crepuscular, with peaks of activity at dawn and dusk. It is actually more arboreal than the bushy-tailed woodrat (Escherich 1981, Walters 1949). Walters (1949) felt that the dusky-footed woodrat is more proficient at traveling through trees and shrubs than on the ground; he found parts of plants remaining from feeding activity scattered below the arboreal pathways used by the woodrats. Linsdale and Tevis (1951) thought the woodrat is equally proficient on the ground and in branches. They report that woodrats follow well-established travelways both on the ground and in the foliage of trees and shrubs.

The dusky-footed woodrat is about the same size (12.5-inch body, 3.5-inch tail) and weight (10 ounces for males, 8 ounces for females) as the bushy-tailed woodrat. The pelage is soft and long, red to yellow brown on the back and tan to white on the undersides. The feet are grayish brown with white toes and claws. The tail is covered with short, black hair. The feet and tail are the best field characteristics distinguishing the dusky-footed woodrat from the bushy-tailed woodrat.

The dusky-footed woodrat seems to have a vocal repertoire limited to an alarm chatter, squeal of rage, and squeal of distress. When agitated, it vibrates its tail against vegetation or parts of its house, producing a rattle. It is quite noisy in its movements; its footfalls on its trails *often can* be *heard, and it can be heard moving* through vegetation. The dusky-footed woodrat is often reluctant to move through plant litter because of the noise that would result, and it prefers to use branches and limbs rather than the ground when traveling (Linsdale and Tevis 1951).

Life history--The social biology of the dusky-footed woodrat is markedly different from that of the bushy-tailed woodrat. The dusky-footed woodrat lives in colonies-groups of houses. Each house that is a residence is occupied by one adult and is vigorously defended against other adults, but there is extensive overlap among home ranges (foraging areas) and amicable interactions outside the houses. Not all houses are used equally. About 80 percent are occupied by single animals; some are infrequently used and in disrepair; some are "common" houses, used by many individuals. Adults generally have more than one house. Individuals will visit one another, with most of the visits being meetings of a male and female. About one-fourth as frequent are meetings of two females; with meetings of males being rare. Most visits take place at common houses. Males initiate more visits than do females. Individuals know and recognize each other. Females investigate other individuals (familiars or strangers). Males avoid familiars (other than visits to females) and are antagonistic to strangers (Wallen 1982).

Pair-bonding for mating is temporary; fighting increases during the breeding season (Caldwell and others 1984, Cranford 1977). In Oregon, breeding begins in January and February; partuition takes place during February-May. There is generally one litter per year, sometimes two. There are one to four young per litter, generally two or three (Maser and others 1981b, Walters 1949). Juveniles disperse to establish home ranges in or adjacent to the maternal range before establishing home ranges in unoccupied but suitable areas. Juvenile home ranges may overlap those of adults by 62 percent. Juvenile dispersal distances are generally less than 50 feet (Linsdale and Tevis 1951).

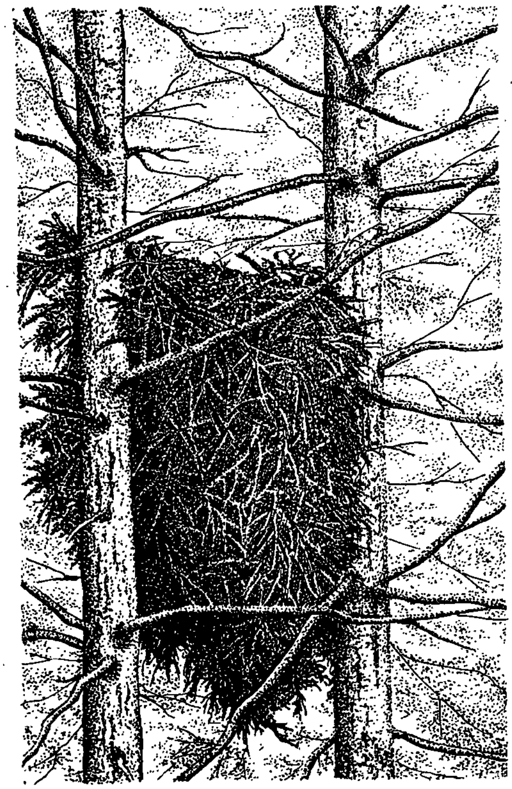
In a stable environment (for example, streamside alder and willows in California chapparal), colonies and houses may be occupied for more than 25 years (Wallen 1982). The social group (colony) is fairly stable; the number of adults remains fairly constant. Females usually stay near their houses: males travel farther than females, but distances traveled still are short. The restriction to small home ranges allows only a slow spread of the colony into new areas. In addition, new houses are rarely constructed outside an occupied colony. individual houses will be used by a succession of woodrats-sometimes by a dozen individuals, sometimes by hundreds (Linsdale and Tevis 1951). Disruption of a colony (for example by flooding) can lead to dispersal from the colony (Cranford 1977). Population density can be as high as 8-18/acre (Cranford 1977, Wallen 1982). In Oregon, densities ranged from 0.2/acre to O.6/acre in my study areas and 0.6-2.1/acre in Hooven's (1959) study areas. In California, annual home (ranges average 0.6 acre for males and 0.5 acre for females; males may expand their ranges to 1.O acre on average in November and December; females reduce their ranges during lactation. Home range overlap between males averages 15 percent; between females, 25 percent; and between males and females, 28 percent. During the breeding season, overlap may increase to 57 percent between males and females. But in the preferred foraging areas, there is no overlap. Individuals average four such centers of activity within their ranges; these areas are high in value for both food and cover. Individuals average 1.8 houses per home range; mean residence time per house is 34 days (Cranford 1977). In Oregon, recaptures suggest seasonal home ranges of 0.7 acre (Walters 1949), 1.1 acres (Hooven 1959), and in my studies, 1.0 acre.

Distribution and habitat-The dusky-footed woodrat is found south of the Columbia River in the dry interior valleys of the Willamette, Umpgua, and Rogue Rivers in western Oregon, throughout the Siskiyou Mountains of southwestern Oregon, through California, to Mexico. Whereas the bushy-tailed woodrat is associated with northern coniferous forests, the dusky-footed woodrat is a more southern species, generally associated with chapparal types.

Although the dusky-footed woodrat generally is considered to be an animal of the chapparal, even in chapparal types it is most abundant along brushy creek bottoms (for example, in wooded canyons) and in chapparal characterized by a dense mixture of trees and shrubs (Linsdale and Tevis 1951). It also thrives in the mixed-evergreen and mixed-conifer forests of southwestern Oregon and northern California. Brown (1985) lists their primary habitats in Oregon as shrub-old-growth stages of deciduous hardwood, conifer-hardwood, mixed-conifer, and temperate coniferous forests; hardwood and shrubby wetlands and coniferous wetlands; and shrub-closed sapling-pole stages of alder and shorepine forests. In southwestern Oregon, I found dusky-footed woodrats to be relatively abundant in mixed-conifer, streamside saw-log stands (0.6/acre), managed pole stands (O.2/acre), old growth (0.2/acre), and managed saw-log stands (0.2/acre). They generally were absent from Douglas-fir types in the Western Hemlock Zone (Franklin and Dyrness 1978). Raphael (1984) reports a bimodal pattern of abundance in northern California: woodrats were more abundant in young-growth (<150 years) and old-growth (>250 years) forests than in the intervening age class.

Walters (1949) surveyed several habitat types ranging from grasslands and pastures to old growth in the Willamette Valley. He found the distribution of the dusky-footed woodrat to be sporadic and discontinuous. The woodrats were absent from isolated pockets of seemingly good habitat. Woodrats were abundant where there was heavy cover: fir-oak-brush, fir-brush, oak-fir-brush-willow, fence row thickets, and willow strips. In areas with little understory or brushy ground cover, woodrats were absent. Hooven (1959) also reports an association with dense underbrush. The components of the underbrush may differ, but include hawthorns, blackberries, snowberry, poison oak, and tree saplings-overstory can be absent or composed of Douglas-fir, oaks, madrone, ash, or other trees. Habitat may be markedly different in east-side Oregon forests; Hammer and Maser (1973) link dusky-footed woodrats with junipers.

In summary, in west-side Oregon the dusky-footed woodrat is found in the interior valleys (which have Upper Sonoran Life Zone characteristics) and in the Klamath Mountains Province (which includes the Siskiyou Mountains). Within these areas the woodrat favors environments characterized by dense understories or underbrush. These conditions exist most often in streamside areas, sapling-pole stands, brushy patches within old-growth and sawtimber stands of coniferous forest, in mixtures of brush and forest, and in thickets in the dry valley types.



Nests and shelter--Dusky-footed woodrats build houses in trees and shrubs and on the ground. Terrestrial houses are large, conical, and composed of sticks and debris. The construction is shinglelike, which aids in shedding water. In the Willamette Valley, houses ranged from 1 to 11 feet high and averaged 5 to 6 feet high and 4 to 5 feet wide (at the base). Terrestrial houses are generally built over a stump, around a clump of sprouts, or over a log. The house may have seven to eight chambers, including up to five sleeping nests when young are present. The nests are made of grass and shredded bark. Terrestrial houses often have a ground retreat or burrow system beneath them. The woodrats can move into the burrow system when the house is disturbed; they even can survive complete destruction of the house by fire when in the ground retreat. Houses may be built in clumps of sprouts and multistemmed shrubs; tree houses may be up to 50 feet high in a tree. The aboveground houses are smaller, on average, than the terrestrial houses but still are well constructed. Tree houses are necessarily absent from nonforested areas. Terrestrial houses may be absent in areas subject to seasonal flooding. Along the Oregon Coast, the dusky-footed woodrat often does not build conspicuous houses. The dusky-footed woodrat prefers to build its large houses in thickets; for example, in Douglas-fir saplings 20 feet tall. At one time, it was thought that the arboreal houses were used primarily by males, but that has been proven untrue (Cranford 1977, Hammer and Maser 1973, Hooven 1959, Linsdale and Tevis 1951, Maser and others 1981b, Walters 1949).

The houses of dusky-footed woodrats may be used concomitantly by other species such as deer mice and western spotted skunks; in California, the presence of woodrat houses significantly increased the deer mouse population (Cranford 1983). Other inhabitants of woodrat houses include arthropods-74 species in Oregon and 90 species in California (Ashley and Bohnsack 1974). As with the bushy-tailed woodrat, the house is critical to the survival and lifetime reproductive success of the dusky-footed woodrat, even to the extent of influencing the social biology of the species (Caldwell and others 1984, Wallen 1982).

Food-The diet of the dusky-footed woodrat is general. Maser and others (1981a) summarize the diet for Oregon: leaves and cambium of Douglas-fir, western redcedar, Port-Orford-cedar, rhododendron, wax myrtle, salal, blackberries and thimbleberries; leaves and fruit of California laurel; tanoak acorns; and fronds of bracken and deer fern. Walters (1949) examined food stored in houses and found green clippings of red alder, oceanspray, willow, hazelnut, white oak, ash, cascara, serviceberry, snowberry, blackberry, vine maple, and poison oak; maple samaras; and ash seed. White oak clippings were the most common item found; clippings of Douglas-fir were common as were green cones of Douglas-fir. Hooven (1959) conducted studies of food acceptance by captive dusky-footed woodrats; they accepted the foliage of oak, snowberry, maple, and poison oak and acorns, berries, and fruit. Hooven (1959) also examined food in houses and found leaves of madrone and blackberry. Linsdale and Tevis (1951) found that fungi (hypogeous and epigeous) can be a significant part of the diet of the woodrat. This evidence of general food habits may be misleading, however.

Atsatt and Ingram (1983) state that despite apparently generalized food habits, woodrat diets often reflect local feeding specialization. The dusky-footed woodrat is particularly specialized. The dusky-footed woodrat in captivity can maintain its weight on a pure diet of evergreen oak leaves. Evergreen oak leaves are high in fiber, phenolics, and tannins; other woodrats (for example, the desert woodrat) cannot exist on such a diet. Atsatt and Ingram (1983) also observed that in the natural environment the dusky-footed woodrat selectively feeds on evergreen sclerophyll (hard-leaved) vegetation high in fiber, tannins, and related polypeptides. There are a series of adaptations that allow dusky-footed woodrats to survive on a diet of toxic plants. These adaptations increase the feeding efficiency and energy efficiency of the woodrats allowing them to minimize the amount of toxin that must be ingested. The adaptations include:

- Dietary uniformity that increases microflora efficiency permits increased ingestion rates necessary to maintain a nitrogen balance.
- Reingestion of feces reinoculates the gut flora.
- Large houses insulate against temperature extremes and decrease energetic requirements.
- Houses established in or near preferred food plants decrease foraging time (and energy).
- Hoarding of food is a detoxification mechanism that permits relatively continuous, high-volume feeding.

Ability to digest sclerophylls in conjunction with other, less toxic, plants might account for the ability to maintain such high population densities and small home ranges compared to the bushy-tailed woodrat. It might also be part of the reason for their occupation of northern California mixed-conifer and mixed-evergreen forests almost to the exclusion of the bushy-tailed woodrat.

Predators-Linsdale and Tevis (1951) list 11 significant predators of the dusky-footed woodrat in southern California. In Oregon, the primary predators seem to be the spotted owl and the bobcat; hawks, other owls, coyotes, long-tailed weasels, and western spotted skunks also may prey on dusky-footed woodrats. Bubonic plague has been found in dusky-footed woodrats in northern California (Clover and others 1989) and in southeastern Oregon and northeastern California (Maser and others 1981 b). The significance of plague to woodrat populations is unknown, however.

Limiting factors--The dusky-footed woodrat seems to be limited by the extent of dense, brushy environments that are stable in nature and by its limited ability to disperse and establish new colonies in recently developed brushy plant communities. Stable environments seem to be brushy streamsides in plant communities ranging from chapparal to mixed-conifer forests. Old-growth mixed-conifer forests with brushy understories also are stable environments. Late, brushy clearcuts through closed sapling-pole stands provide suitable environments but generally are not stable (they develop to small saw-log stands that usually are not suitable). The mechanisms and frequency with which dusky-footed woodrats find and colonize such stands has not been determined. Streamsides could be the source for colonization of these areas. Similarly, brushy roadsides through areas of intense timber activity may function as dispersal routes to old clearcuts and other brushy types for dusky-footed woodrats. Linsdale and Tevis (1951) state that the dusky-footed woodrat lives where low-growing woody vegetation provides protection from carnivores, shelter from the elements, and shade. Such a mass of plants ensures sufficient food, suitable limbs for runways between houses, materials for houses and nests, and the vertical, anchoring woody support necessary for the stability of a large house.

Bushy-Tailed Woodrat

The nocturnal bushy-tailed woodrat is large: body length is 11-18 inches, tail length is 5-9 inches, and ears are 1.0-1.5 inches in height. Weights from southwestern Oregon averaged 9.7 ounces for 27 males and 9.0 ounces for 47 females. Males may grow to weigh 21 ounces, almost twice the maximum weight for females (Escherich 1981). Their pelage is soft, dark-gray brown to reddish on the back and gray to white on the underside; the tail is bushy with hairs longer than 0.8 inch; the large ears have little hair. Pelage color differs with subspecies but still tends toward gray brown. Bushy-tailed woodrats do not use territorial or alarm calls like the Douglas' squirrel or Townsend's chipmunks, but they do communicate by stamping their feet.

Life history-The bushy-tailed woodrat is the only polygynous woodrat-males keep harems of one to three females. Males are territorial and aggressive and defend both dens and foraging areas. Scent marking is used to define territories. Males may engage in serious fights; members of pairs may begin fighting after the breeding season ends in July or August (Escherich 1981). Dixon (1919) aptly describes them as "quick in movement" and "fierce"; they fight vigorously when captured. Their territoriality may be interspecific; a male bushy-tailed woodrat in captivity killed both a dusky-footed woodrat and a northern flying squirrel (even with surplus nest boxes and food present). The distribution of woodrat families is patchy, and the families are generally well separated. These well-separated concentrations of woodrat biomass attract predators; the loss of a few individual woodrats from these small family groups may lead to the extinction of the colony (Escherich 1981). Thus, dispersal of offspring is an important component of population viability; frequent recolonization of vacated habitats is necessary. Dispersal may occur shortly after weaning or after several years. Dispersal distances of 1.4-2.0 miles have been recorded. My studies in southwestern Oregon confirmed Escherich's (1981) observations of woodrats in California. I found 2.3 females per male where bushy-tailed woodrats were present; in areas of old-growth Douglas-fir forest that I studied for 5 years, woodrats were present only 50 percent of the time. In mixed-conifer old growth, however, populations seemed more stable and larger than in the Douglas-fir areas. Spotted owls preyed heavily on bushy-tailed woodrats in both areas.

Along the Oregon coast, bushy-tailed woodrats begin breeding in January or February, and young are born in March. There is generally one litter per year, but sometimes there are two; litter size ranges from one to six, and averages two to four (Maser and others 1981b). In California, parturition occurred from March through July or August (Escherich 1981): In my studies in southwestern Oregon, 55 percent of the females were lactating or just postlactating throughout the summer and fall, which suggested more extended breeding than Maser and others (1981b) report. In California, Dixon (1919) reported one litter per year with a mean size of four.

Dlstribution and habitat-The bushy-tailed woodrat occurs throughout the greater Pacific Northwest, from Yukon to North Dakota, northern New Mexico, and the Sierra Nevada. Brown (1985) lists its primary habitats as shrub through closed sapling-pole red alder forests, shrub through old-growth mixed-conifer forest, and closed sapling-pole through old-growth temperate, high temperate, and coniferous wetland forests. Almost all other stand conditions and plant communities are considered to be secondary habitats. He lists coarse woody debris as a special habitat feature of primary importance. Cliffs and talus are listed as having secondary importance.

There are four subspecies of bushy-tailed woodrats in the Pacific Northwest (Hall 1981). I will discuss each of the three west-side subspecies briefly because I believe their ecologies differ significantly. *Neofoma cinerea occidentalis* occurs from Yukon Territory through British Columbia, Washington, northern Idaho, and the Oregon Cascade Range. In Washington, it is common in all mountainous areas wherever high altitude or steep slopes result in accumulation of talus or outcrops of broken rock (sea level to 10,000 feet), but it is most abundant in the Columbia River canyon (Dalquest 1948). These woodrats also will inhabit buildings, caves, tunnels, mines, and railroad beds (Dalquest 1948, Maser and others 1981). During extensive trapping in managed and old-growth forests around the Olympic Peninsula, I did not catch woodrats in areas without rock outcrops or talus. Bushy-tailed woodrats occur in rocky areas and rocky streamsides on the Olympic Peninsula. It seems that rock or talus is of primary importance to this species and that, in some places at high elevations, log piles also can be important.

The bushy-tailed woodrat in the Oregon Coast Ranges is N. c. *fusca.* This subspecies seems to be able to substitute hollow trees, tree cavities, and fallen trees for rock outcrops. There are few areas of extensive rock outcropping or heavy talus in the Coast Ranges. In my studies in southwestern Oregon, the woodrats were most abundant in mixed-conifer, streamside, saw-log forest (O.4/acre), the one rocky site I could find (0.2/acre), Douglas-fir, streamside saw-log forest (0.2/acre), managed mixed-conifer pole stands (0.2/acre), and mixed-conifer old growth (0.8/acre). They were irregularly (in space and time) abundant in Douglas-fir old growth (averaging 0.2/acre) and rare in large saw-log stands on ridgetops and upland managed saw-log stands. Densities in other types were less than O.O3/acre. These densities seem low because of the wide distance from one family group to another. Dixon (1919) reports average densities of O.O5/acre in California. In southwestern Oregon, rock outcrops and talus did not seem to be a requirement. Bailey (1936) states that the woodrat in Oregon generally occurs in heavily timbered forests among rocks overgrown with vegetation; where there is a scarcity of rocks, buildings, old logs, and log piles suffice.

In southwesternmost Oregon and northern California, is N. c. *pulla.* Many studies have been conducted in northern California and most associate N. c. *pulla* with rocky environments. Dixon (1919) describes the bushy-tailed woodrat as a member of the rockslide community. Escherich (1981) states that bushy-tailed woodrats are associated with rock outcrops, rockslides, caves, and buildings. Raphael (1984, 1988), in extensive studies of forest wildlife in northern California, did not find bushy-tailed woodrats away from rock outcrops. Ward (1990) did not find bushy-tailed woodrats in the wide array of mixed-conifer stands he studied in northern California. Tevis (1956) found that although bushy-tailed woodrats were rare in the mixed-conifer forests, they did occur in redwood forests. And Maguire (1983) caught bushy-tailed woodrats along a stream in mixed-conifer old growth in northern California.

In summary, throughout most of the Pacific Northwest, bushy-tailed woodrats are associated primarily with rocky environments. But in the transition zone between the Douglas-fir/western hemlock forests and the mixed-conifer forests in southwestern Oregon, the bushy-tailed woodrat persists without rock outcrops or talus. There, streamside forests provide the best environment followed by mixed-conifer closed sapling-pole stands and old growth. Woodrat populations fluctuate markedly in Douglas-fir old growth. Upland managed saw-log stands contain few woodrats. It is not clear whether persistence in nonrocky environments is limited to the transition zone; there have been few studies in the Cascade Range. Throughout their range, bushy-tailed woodrats seem to occur in small family groups, the groups often widely separated. I could find little information on their home ranges. Dixon (1919) states the bushy-tailed woodrat will forage up to 450 feet from its den (a 15-acre home range). But I recorded movements of up to 1,250 feet (within trapping grids that were only 1,300 feet wide) which suggests a maximum home range of about 110 acres. Average mean maximum distance moved was 280 feet-possibly an under-estimate because of grid size (Carey and others 1991a). Brown (1985) lists the minimum habitat per family group as 80 acres.

Nests and shelters-Woodrat shelters consist of two parts, the house (external structure-rock outcrop; hollow tree and woody debris plug; loose collection of sticks, woody debris, and other material) and the nest (internal nest cup). Bushy-tailed woodrats build small, open (cuplike) nests; like most packrats, the nest may be surrounded by a remarkable array of items the woodrat has collected. The nests often are in rock crevices or burrows under overhanging rock. In these cases, the woodrat often will accumulate sticks and woody debris in front of the entrance to the nest. Nests in rocky areas are often easily found by distinctive urine stains on the rocks. Nests also may be placed in hollow trees; I have seen the ground-level entrances to such trees jammed with woody debris-in the case of one old-growth tree having a fire-scar opening 3 feet high and 2 feet wide at the base, the entire opening was packed with woody debris. Cavities in trees, hollow logs, log piles, and burrows under logs also may be used. Bushy-tailed woodrats along the Oregon coast and in the Coast Ranges also will build arboreal nests up to 50 feet aboveground that are loosely constructed of sticks and twigs (Maser 1965, 1966). Apparently, these nests are not especially common and should not be confused with the tightly constructed nests of dusky-footed woodrats.

Food-The bushy-tailed woodrat has a broad, flexible diet (Escherich 1981). Food includes the leaves and cambium of Douglas-fir, Sitka spruce, and western hemlock, the leaves of western redcedar, the green parts of Pacific bleeding heart, angled bittercress, red elderberry, waterleaf, trailing blackberry, Himalaya blackberry (Maser and others 1981 b), and many other plants.

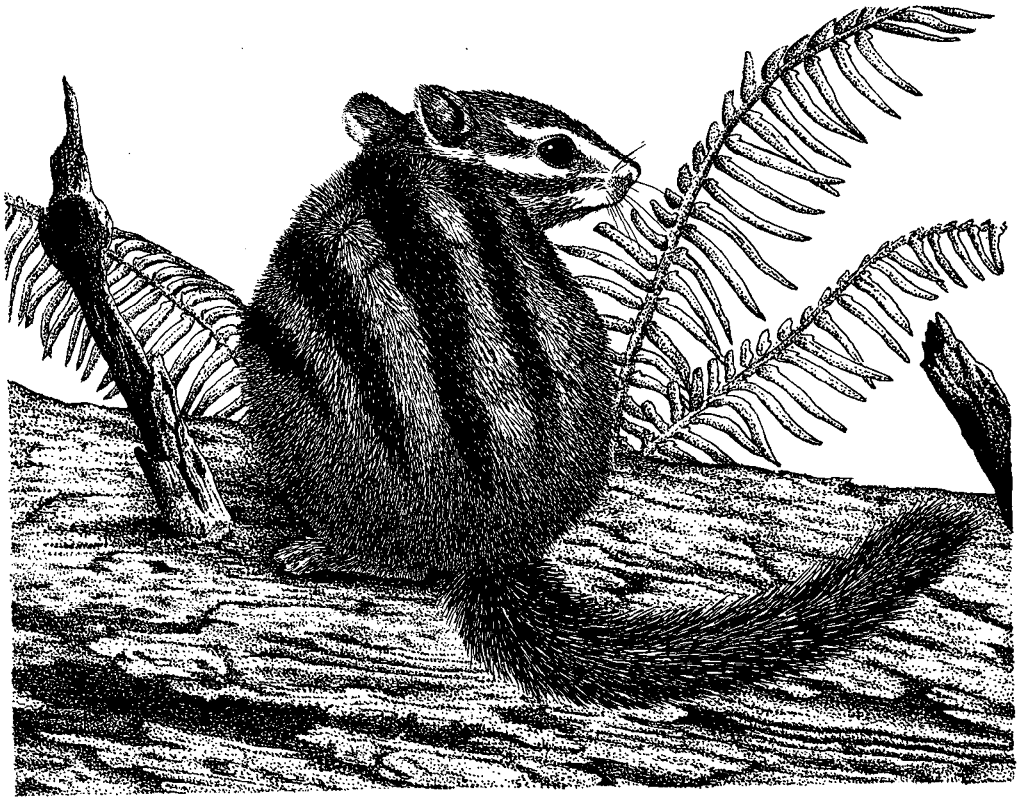
Predators-Bushy-tailed woodrats are prey for many predators: spotted owls, great horned owls, marten, and bobcats are thought to be important. Other, perhaps more incidental, predators include long-tailed weasels, coyotes, western spotted skunks, and large hawks.

Limiting factors-Escherich (1981) states that adequate rock shelter is the most important resource for the bushy-tailed woodrat, especially in areas that have cold weather and heavy snowfall. Stick houses are inadequate shelters in such areas. In areas of mild climate without rock housing available, hollow trees, tree cavities, and fallen trees might be the limiting resource. In such areas, stream cuts might also provide rock crevices that would be suitable shelters. The house is a defensible resource. Possession of a house is so important to woodrat survival that a high level of aggression and solitary house occupancy are basic to the genus.

Bushy-tailed woodrats will defend food resources near their houses from exploitation by other bushy-tailed woodrats. The strong territoriality of the bushy-tailed woodrat over food and shelter leads to separation of family groups. Isolation leads to greater threat of local extinction through predation, immigration, and stochastic (random) demographic processes (lack of births, deaths of individuals). Persistence, then, depends on routes of connectivity among the family groups.

Streamside zones might play a key role in providing dispersal corridors for recolonization of discrete habitats vacated by local extinction. Heavily timbered streamsides are characterized by a diversity of plant species and vertical diversity of vegetation that includes forbs, shrubs, and deciduous trees. These provide food, and together with the noise of the stream, some protection from predation. One of the major preferred habitats, closed pole-sapling stands, is relatively ephemeral-it is replaced by small saw-log stands in a relatively short time and appears (as a result of timber harvesting) at a frequency and in a pattern unpredictable by woodrats. Managed, upland saw-log stands seem poorly suited to bushy-tailed woodrats. Saw-log stands might lend to the ecological isolation of family groups. Mixed-conifer old growth provides, however, a stable environment and might act as a source of dispersing colonizers. Densities in Douglas-fir old growth may be lower than in the preferred habitats, and local extinctions may be common within parts of a greater stand. But extensive areas of Douglas-fir old growth may be capable of maintaining a viable population of bushy-tailed woodrats. Populations in large tracts of old growth are not as subject to local extinction as populations in small, managed stands or short stretches of suitable streamsides because barriers to dispersal and recolonization are minimal. Within spotted owl home ranges, especially near nest groves, the rate of predation may be very high. Thus, it would seem that rock housing, old growth, and heavily timbered streamsides are the limiting factors on the “metapopulation’-the group of woodrat populations present in the landscape.

In southwestern Oregon, I found the abundances of bushy-tailed woodrats and dusky-footed woodrats to be inversely related among jointly occupied sites. The inverse relation suggests a degree of competitive exclusion. All jointly occupied sites were in mixed-conifer zones. As one proceeds southward into mixed-conifer forest dominated landscapes, it seems the bushy-tailed woodrat disappears from the forest in the absence of rock outcrops. It is not clear to me whether the rocks are important in conferring a competitive advantage or whether they only occur in plant communities or at elevations not suited to the dusky-footed woodrats. The bushy-tailed woodrat seems restricted to the higher mountains of eastern and northern California.



Townsend's Chipmunk

There are 11 species of chipmunks in the .Pacific States; they are difficult to distinguish by external characteristics, and the present taxonomy is not clear, especially in southwestern Oregon, where there may be three or more species. But, presently, Townsend's chipmunk may be confused with the least chipmunk and the yellow-pine chipmunk in the Washington and Oregon Cascade Range and the Sonoma chipmunk in southwestern Oregon and northern California (Ingles 1965, Jones and others 1986). Townsend's chipmunk is the largest, darkest, and most arboreal chipmunk in Washington and Oregon. Its sides are tawny with black to dark-brown stripes and pale, whitish to cinnamon stripes that are not sharply defined. The underside of the tail is tawny; other underparts are dull white. There is a prominent white patch on the back of each ear. The ears are prominent and 0.8 inch tall. Townsend's chipmunk is 10 inches long-with a 5.5-inch body and 4.5-inch tail. The average weight of 625 Townsend's chipmunks from southwestern Oregon that we measured was 3 ounces. Weights in the north and central Cascades were slightly less than 3 ounces (Gashwiler 1976). Townsend's chipmunk gives a quiet, birdlike call ("PO-PO-PO"). The chipmunk is an expert climber and may forage, hide, or sun itself in bushes or trees.

Life history-In the coldest parts of their geographic range, Townsend's chipmunks hibernate. Along the west side of the Cascades, males are active from March through October and females are active from April through October; juveniles may stay active a month or two longer than adults (Gashwiler 1976).

Along the Oregon coast, chipmunks may stay active all year (Maser and others 1981b). Breeding activity begins in March in the Cascades and peaks in May, with lactation from June through August. One litter of two to six young (averaging four) is produced per year (Gashwiler 1976). In southwestern Oregon, I found that females were in estrus from April through June, pregnant from late April through June, and lactating from early May through June (I did not collect late summer data). Litter size was three to seven, averaging 4.4. Sex ratios tend to be even. Townsend's chipmunks may live up to 7 years in the- wild (Brand 1974).

Distribution and habitat-Townsend's chipmunk occurs on the southeastern tip of Vancouver Island, along the southwestern border of British Columbia, and throughout western Washington and Oregon. Hall (1981) considers the Townsend's chipmunk in the Siskiyou Mountains to be a separate species: the Siskiyou chipmunk. Similarly, he considers the chipmunk along the east side of the Cascades in Oregon (and northern California and the Sierra Nevada) to be a separate species: the California chipmunk. For the purposes of this paper, I will follow the checklist by Jones and others (1986), which does not recognize the Siskiyou chipmunk. If this subspecies becomes recognized as a distinct species, it may become of greater concern than it is now because of its restricted geographic distribution.

Brown (1985) lists the primary habitat of the Townsend's chipmunk to be the open sapling-pole through old-growth seral stages of temperate coniferous, high temperate coniferous, conifer-hardwood, and mixed-conifer forests and subalpine forest parks and the open and closed sapling-pole shorepine and the large sawtimber and old-growth, deciduous-hardwood forests. Almost all other forest categories are listed as secondary habitat. Raphael (1984) found, however, that Townsend's chipmunks increase in abundance with stand age (55-315 years) in northern California. I found Townsend's chipmunks to be 1.7 times more abundant in old growth than in young, managed stands in southwestern Oregon. Studies in the Oregon Cascades also found chipmunks to be more abundant in old growth than in managed, young forests. In riparian zones, Townsend's chipmunks are more abundant in young (small sawtimber) forests than in old growth and more abundant in old growth than in large sawtimber (Anthony and others 1987). Doyle (1990) found that the densities of chipmunks do not differ between upland areas and riparian areas. She reports exceptionally high mean densities: 4.9-5.3/acre. Densities in upland sites in a subsequent study were 1.5-50/acre. Densities may get as high as 2/acre, with home ranges of less than 2.5 acres in Canada (Woods 1980); the average densities I found in old growth in southwestern Oregon were 0.6/acre in spring and 0.8/acre in fall. The differences in density among these studies may reflect technique: Doyle used small grid sizes (which often lead to inflated densities). The chipmunks' ranges (as measured by mean maximum distances moved between subsequent recaptures, 338 feet) averaged 2 acres. Like flying squirrels, Townsend's chipmunks were very low in abundance in the western hemlock and Douglas-fir forests on the Olympic Peninsula.

Nests and shelter-Maser and others (1981 b) state that Townsend's chipmunk nest primarily in burrows. Brand (1974) found Townsend's chipmunks nesting 40 to 90 feet aboveground in trees; all but one of the nests he found were occupied by a female and her young. In the laboratory, he found that Townsend's chipmunks selected the highest nest boxes available, thereby indicating an innate preference for elevated nests. Broadbooks (1974) discussed the arboreality of chipmunks in general. He noted that the home ranges of chipmunks have an important vertical dimension and that chipmunks seem to occupy niches intermediate between the strictly arboreal tree squirrels and the terrestrial ground squirrels. Whereas many authors have noted that chipmunks forage on the ground, in shrubs, and in trees (Brand [1974] reports that Townsend's chipmunks will even cache food in trees and shrubs), most have assumed that chipmunks nest in burrows. Broadbrooks (1974) concludes that chipmunks are the only squirrels, and perhaps the only rodents, that have substantial nests both underground and in trees in a given year. Burrows generally are used in winter. The tree nests of chipmunks can be mistaken for bird nests or may be in cavities. All species of chipmunks use fallen trees and rock crevices for nest sites (Callahan and Estep 1982). Western chipmunks dig their own burrows. Entrances to burrows are inconspicuous (without dirt around the entrance). Chipmunks are quiet while entering or leaving the nest;, even when nursing is required, the family will visit the nest only once per day for a silent, brief period (Broadbooks 1974).

Food-Townsend's chipmunks consume many foods: fruits (evergreen huckleberry, red huckleberry, salal, blackberry, and others), seeds (acorns, maple seeds, laurel thistles, grasses, Douglas-fir, western hemlock, Sitka spruce), fungi, and insects (Maser and others 1981b). Townsend's chipmunk is the only chipmunk with a tendency to open western hemlock cones to get the seeds (Smith 1968a, Woods 1980).

Predation-Species most commonly listed as preying on Townsend's chipmunk are long-tailed weasels and mink. Western spotted skunks, bobcats, and great horned owls are potential predators. I know of no quantitative data on predation on Townsend's chipmunks. During my live-trapping studies, predation on chipmunks in traps by long-tailed weasels and spotted skunks often was heavy.

Limiting factors-l assume that food is the most limiting factor on Townsend's chipmunk populations. The marked annual difference in conifer seed production and fungi production can lead to marked changes in population density. Hooven and Black (1976) report fourfold changes in abundance in 3 years in a 125-year-old Douglas-fir stand. Population changes in a recent clearcut were even more variable; marked reduction was seen in the same year in a recent clearcut, an advanced clearcut, and a large saw-log stand, which suggested to me a cone crop failure was responsible. Sullivan and others (1983) were able to increase Townsend's chipmunk population by 40 to 50 percent in second-growth forests by providing supplemental food; withdrawal of the supplemental food precipitated a decline in the population, which led them to conclude that food limits the size of Townsend's chipmunk populations.

Maintenance of the Arboreal Rodent Community

My species accounts provide the basis for some generalizations about arboreal rodents. Zoogeography limits arboreal rodent communities in Washington; the red tree vole and the dusky-footed woodrat do not occur north of the Columbia River (fig. 1, table 2). The west-side forests of the Pacific Northwest differ markedly with geographic location (physiographic province). Northern forests tend more toward dominance by western hemlock; for example, on the western Olympic Peninsula. Southern forests are composed of a mixture of conifers and, in the southernmost areas, a mixture of conifers and evergreen hardwoods, which reflect climatic influences. Concomitant with the changes in the tree flora seems to be parallel changes in the abundance and diversity of hypogeous fungal communities. These changes seem to influence the overall abundance of the mycophagous northern flying squirrel and Townsend's chipmunk. Dusky-footed woodrats seem confined to the mixed-conifer and mixed-conifer-mixed-evergreen types. Bushy-tailed woodrats seem especially dependent upon rock outcrops or talus in the colder areas, but are able to persist in the absence of rock outcrops in the transition from the Western Hemlock Zone to the Mixed Conifer Zone. Deep into the Mixed Conifer Zone, however, the bushy-tailed woodrat once again seems dependent on rock outcrops or talus. These zoogeographic, physiographic, and climatic effects are beyond the control of the manager.

Table 2—Zoogeography of arboreal rodents in Douglas-fir forests of the Pacific Northwest

	Species abundances [b]					
Physiographic province [a]	DFWR	RTVO	TOCH	BTWR	FLSQ	DOSQ
Northern Cascades	–	–	+	*	+	**
Olympic Peninsula	–	–	*	*	*	**
Puget Trough	–	–	+	+	+	+
Southern Washington Cascades	–	–	+	+	+	**
Washington Coast Ranges	–	–	+	+	+	+
Oregon Coast Ranges	–	**	**	**	**	**
Interior valleys [c]	**	**	**	**	**	**
Western Cascades	–	**	**	*	**	**
Klamath Mountains	**	**	+ [d]	*	**	**

[a] From Franklin and Dyrness (1973).
[b] Codes: –absent; + present, but no information on relative abundance; * present, low abundance; ** present, relatively high abundance; RTVO, red tree vole; DFWR, dusky-footed woodrat; TOCH, Townsend's chipmunk; BTWR, bushy-tailed woodrat; FLSQ, northern flying squirrel; DOSQ, Douglas' squirrel.
[c] Rogue, Umpqua, Willamette and perhaps other river valleys.
[d] Replaced by other species.

Within a physiographic province, stand condition plays an influential role in structuring the arboreal rodent community. The influence of stand condition reflects both the degree of dependence on trees of the members of the community (table 1) and the habitat elements used by the rodents (table 3). Maximal diversity, abundance, and stability of the arboreal rodent community are achieved in old growth, especially old growth with streamside zones. The ameliorative physical, botanical, and climatic effects of old growth may be offset to a major degree by predation when the stand is a primary foraging area of a breeding pair of spotted owls.

Table 3—Habitat elements of recognized importance to arboreal rodents in Douglas-fir forests in the Pacific Northwest[a]

	Species[b]					
Habitat element	RTVO	FLSQ	DOSQ	DFWR	BTWR	TOCH
Large, live trees[c]	x-nest cavity food	Cavity nest	Cavity nest		Cavity	Cavity x-nest
Large snags		Cavity	Cavity		Cavity	Cavity
Fallen trees		Fungus (food)	Fungus cache	House site	Den	Fungus den
Woody debris				House material		
Multilayered canopy		Cover		Nests travel cover	Nests cover	Cover
Overstory diversity		Fungus	Seeds fungus		Seeds	Seeds fungus
Understory diversity		Fungus	Seeds fungus	Cover food	Cover food	Seeds
Epiphytes	Nest material	Nest food	Food			Nest material
Fog interception	Water					
Stability[d]	Important			Important	Important	
Connectedness[e]	Very important	Important	Important	Very important	Important	
Special features:						
Rock and talus					High value	
Dense underbrush		Cover		High value		
Streamsides				High value	High value	

[a] From table, x-nest means an external big leaf, twig, or lichen nest.
[b] RTVO, red tree vole, FLSQ, northern flying squirrel; DOSQ, Douglas' squirrel; DFWR, dusky-footed woodrat; BTWR, bushy-tailed woodrat; TOCH, Townsend's chipmunk.
[c] Includes live trees with broad limbs, broken tops, and cavities; >30 inches; x-nest is an external nest.
[d] Long-lasting stand condition; late seral stage.
[e] Large, contiguous areas of suitable habitat or corridors connecting areas of suitable habitat.

Members of the arboreal rodent community differ in their ecological flexibility (also referred to as niche breadth and width) and in their ability as colonizers. Landscapes can be viewed as being composed of elements that can be classified as ecological sources of dispersers, dispersal sinks, unsuitable for occupancy, and barriers to dispersal (table 4). To interpret the table, it is important to understand that there is considerable variability in the structure of plant communities in each of the stand conditions. Not only does the structure differ with forest type (for example, western hemlock vs. mixed conifers) but also with site (aspect, elevation, soils), presence of seeps, streams, and rock outcrops, stocking of canopy trees (both density of stems and canopy closure), and history (fire, windstorm, and insect damage). Thus, I list old forest as a source and sink for bushy-tailed woodrats. Mixed-conifer old growth with a stream seems to provide a good, stable environment (a source) for bushy-tailed woodrats. Other types of old forest with rocks or talus might do the same. But, Douglas-fir old growth within a spotted owl home range often fails to support a stable population of bushy-tailed woodrats and thus functions as a sink. Perhaps an extensive area of Douglas-fir old growth, one capable of supporting multiple local populations (in other words, a metapopulation), might be a source with the metapopulation composed of local populations that become established, send out colonizers, go extinct, and get recolonized.

Table 4-Habitat ratings for stand conditions in Douglas-fir forests In the Pacific Northwest relative to 6 arboreal rodents

		Species[b]					
Stand condition[a]	Years	RTVO	FLSQ	DOSQ	DFWR	BTWR	TOCH
Grass-forb	2-5	U,B	U,B	U,B	UB	+	U,B
Shrub	3-10	B	U	U	Sink-source	t	Source-sink
Open sapling-pole	8-20	B	U	U	Sink-source	+	Source-sink
Closed sapling-pole	20	Sink-B	U	Sink	Sink-source	Source-sink	Source-sink
Small sawtimber	60	Sink-B	Sink	Source-sink	Sink-source	Sink	Source-sink
Large sawtimber	100	Sink-source	Source-sink	Source-sink	Sink-B	Sink	Source-sink
Old forest	700	Source	Source	Source	Source	Source-sink	Source

[a] From Brown (1985); old forest includes old growth and old growth mixed with younger stand types.
[b] RTVO, red tree vole; FLSQ, northern flying squirrel, DOSQ, Douglas' squirrel; DFWR, dusky-footed woodrat, BTWR, bushy-tailed woodrat, TOCH, Townsend's chipmunk; U, unsuitable for occupancy; B, barrier to dispersal and population growth; sink is defined as an environment capable of maintaining a population for a while but either permitting only low reproduction or subject to periods in which the sink becomes unsuitable for occupancy; source is defined as an environment capable of sustaining a viable population that produces a surplus of offspring that are potential colonizers of unoccupied suitable environments or sinks; + indicates that the species has been found in the stand conditions, but the rating is unknown.

An innate feature of stand condition is stability, or the duration over which the stand remains in that condition (table 4). Early stages of forest development change more rapidly than late stages. Thus, I list shrub stages as sinks and sources for the dusky-footed woodrat. Only shrub stages of mixed-conifer or mixedconifer-mixed-evergreen forest function in this way. And only shrub stages with a dense cover of shrubs are suitable environments for dusky-footed woodrats. Shrub stand conditions can support dense colonies of dusky-footed woodrats. But eventually the stage will pass to an environment unsuited for the woodrat. In the interim, presuming successful colonization, the stand may function as a source of dispersing and potentially colonizing woodrats.

I list closed-canopy, early stand conditions as sinks and barriers for red tree voles. I have found colonies (both active and inactive) in such stages: it does not seem that colonization of these types is common. Creation of early seral stages within or adjacent to old forests probably would serve to inhibit the continued growth (or even persistence) of a colony of red tree voles.

Of major significance is my conclusion that old forest can serve as sources for five of the six rodents (and a source and sink for the sixth species) with no other stand condition being as consistently amenable to the rodents; Small or large sawtimber, or both, can serve as a source and a sink for three of the species-the flying squirrel, the Douglas squirrel and Townsend's chipmunk. Two other species-the dusky-footed woodrat and the bushy-tailed woodrat-find suitable habitat in younger stages. The value of these habitats as population sources is reduced by their ephemeral status in the successional. process. Possibly the most significant finding is that non-old-forest types do not seem to be sources of red tree voles-only old growth seems to do that. And other types might routinely function as barriers to red tree voles. Given the patchy, relatively uncommon abundance of red tree voles and the susceptibility of the voles to timber harvest, immediate action should be taken to identify and protect existing colonies of red tree voles. The status (numbers, sizes, and locations) of red tree vole metapopulations (and local populations) along the west side of the Cascades, in interior valleys, in the Coast 'Ranges, and in the Klamath Mountains is not known. Continued timber harvesting could threaten the persistence of red tree voles, either locally or on a larger scale, unless steps are taken for inventory and conservation of the species.

Scientific Names

Common name*	Scientific name
Mammals:	
Bobcat	*Felis rufus*
Bushy-tailed woodrat	*Neotoma cinerea*
California chipmunk	*Tamias obscurus*
Coyote	*Canis latrans*
Deer mouse	*Peromyscus* spp.
Desert woodrat	*Neotoma lepida*
Douglas' squirrel	*Tamiasciurus douglasii*
Dusky-footed woodrat	*Neotoma fuscipes*
Least chipmunk	*Tamias minimus*
Long-tailed weasel	*Mustela frenata*
Marten	*Martes americana*
Mink	*Mustefa vison*
Northern flying squirrel	*Glaucomys sabrinus*
Red squirrel	*Tamiasciurus hudsonicus*
Red tree vole'	*Phenacomys longicaudas*
Siskiyou chipmunk	*Tamias townsendii siskiyou*
Sonoma chipmunk	*Tamias sonomae*
Southern flying squirrel	*Glaucomys volans*
Townsend's chipmunk	*Tamias townsendii*
Western gray squirrel	*Sciurus griseus*
Western spotted skunk	*Spilogale gracilis*
Birds[b]	
Barred owl	*Strix varia*
Great horned owl	*Bubo virginianus*
Long-eared owl	*Asio otus*
Northern goshawk	*Accipiter gentilis*
Northern saw-whet owl	*Aegolius acadicus*
Spotted owl	*Strix occidentalis*
Microorganisms:	
Bubonic plague	*Yersinia pestis*
Plants[c]	
Angled bittercress	*Cardamine* L.
Ash	*Fraxinus latifolia* Benth.
Blackberry	*Rubus* L.
Bracken fern	*Pteridium aquilinum* (L.) Kuhn
California laurel	*Umbellulatia californica* (Hoot. & Am.)
Cascara	*Rhamnus purshiana* DC
Deerfem	*Blechnum spicant* (L.) With.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco.
Evergreen huckleberry	*Vaccinicim ovatum* Pursh.

Commonname	Scientific name
Grand fir	*Abies grandis* (Dougl.) Lindl.
Hawthorn	*Crataegus* L.
Hazelnut	*corylus* L.
Himalaya blackberry	Rubus *procerus* Muell.
Juniper	*Juniperus* L.
Laurel	*Umbellularia californica* (Hook & Am.)
Lodgepole pine	*Pinus contorta* Dougl. ex Loud.
Madrone	***Arbutus menziesii*** Pursh.
Maple	*Acer* L.
Oak	*Quercus* L.
Oceanspray	*Holodiscus disco/or* Pursh.
Oregon ash	*Fraxinus latifolia* Benth.
Pacific bleeding heart	*Dicentra* Bernh.
Pacific madrone	*"Arbutus menziesii* Pursh.
Paper birch	*Betula papyrifera* Marsh.
Poison oak	*Rhus diversiloba* T. & G.
Port-Orford-cedar	*Chamaecyparis lawsoniana* (A.Murr.) Parl.
Red alder	*Alnus rubra* Bong.
Red elderberty	*Sambucus racemosa* L. var. *arborescens* (T. & G.) Gray
Red huckleberry	*Vaccinium parvifolium* Smith
Redwood	*Sequoia sempervirens* (D. Don) Endl.
Rhododendron	*Rhododendron* L.
Sal al	*Gaultheria shallon* Pursh.
Serviceberry	*Amelanchier alnifolia Nutt.*
Shorepine	*Pinus contorta* Dougl. ex Loud.
Sitka Spruce	*Picea sitchensis* (Bong.) Carr.
Snowberry	*Symphoricarpos* L.
Tanoak	*Lithocarpus densiflorus* (Hook. & Am.)
Thimbleberry	*Rubus parvilorus Nutt.*
Trailing blackberry	*Rubus ursinus* Cham. & Schlect.
Vine maple	*Acer circinatum* Pursh.
Waterleaf	*Hydrophyllum* (Tourn.) L.
Waxmyrtle	*Myrica californica* Cham.
Western redcedar	*Thuja plicata* Donn.
Western hemlock'	*Tsuga heterophylla* (Raf .) Sarg.
White fir	*Abies concolor* (Gard. & Glend.) Lindl.
White oak	*Quercus garryana* Dougl.
White spruce	*Picea glauca* (Moench) Voss
Willow	***Salix*** L.

[a] Jones and others 1666:
[b] ***American Ornithologists' Union 1962.***
[c] **Common** names are those used by the authors cited; scientific names are from Franklin and Dyrness 1973.

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Appendix

Stand condition categories and their Old Growth Forest Wildlife Habitats Research and Development Program (OGWHP) equivalents.

Stand condition	Description [a]
Grass-forb	Shrubs <40 percent cover and <5 feet tall; ranges from no vegetation to dominance by herbs; tree seedlings <5 feet tall and <40 percent cover. **OGWHP:** clearcut, late clearcut
Shrub	Shrubs >40 percent cover; trees <40 percent cover and <1 inch d.b.h. **OGWHP:** late clearcut, shrub stage of forest development
Open sapling-pole	Average d.b.h. >1 inch and tree cover <60 percent; saplings 1-4 inches d.b.h.; poles, 4-9 inches d.b.h. **OGWHP:** late clearcut-sapling stage of forest development
Closed sapling-pole-sawtimber	Average d.b.h. 1-21 inches, crown cover >60 percent. **OGWHP:** sapling-pole; young forest (sawtimber)
Large sawtimber	Average d.b.h. >21 inches; crown cover <100 percent; decay and decadence lacking. **OGWHP:** mature forest.
Old growth	Stand >200 years old, at least 2 tree layers, decay in living trees, snags, fallen trees. **OGWHP:** old growth.

[a] Most stands studied by the OGWHP were naturally regenerated; however, most of the young stands studied in the arboreal rodent studies were regenerated through timber harvesting. Naturally regenerated young forest and mature forest often had substantial carryovers of old-growth components from the previous stand, including coarse woody debris, snags, and large trees. When such components were major parts of stands studied in the arboreal rodent studies, I designated the stand "old forest" when the components were major parts of the stand and "mixed-age" forests when they were minor but significant parts of the stand.

Source: Brown 1985.

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Carey, Andrew B. 1991. The biology of arboreal rodents in Douglas-fir forests. Gen.Tech. Rep. PNW-GTR-276. Portland,OR: U.S. Departmentof Agriculture, Forest Service, Pacific Northwest Research Station. 46 p. (Huff, Mark H.; Holthausen, Richard S.; Aubry, Keith B., tech. coords.; Biology and management of old-growth forests).

Arboreal rodents in Douglas-fir forests west of the Cascade crest in Oregon and Washington include (listed in decreasing order of dependence on trees) red tree vole (Phenacomys longicaudus), northern flying squirrel *(Glaucomys sabrinus),* Douglas squirrel *(Tamiasciurus* douglasii), dusky-footed woodrat *(Neotoma fuscipes),* bushy-tailedwoodrat *(Neotoma cinerea),* and Townsend's chipmunk *(Tamias townsendii).* The arboreal rodents constitute an ecological community-a group of species that interact and influence one another's pattern of abundance and use of resources. All but the Douglas' squirrel and Townsend's chipmunk are important prey of the spotted *owl (Strix occidentalis).* The arboreal squirrels are mycophagists and have important functions in ecosystem processes. Individual species exist in many habitats, but the arboreal rodent community reaches its highest diversity and abundance in old-growth forests. The rodents are not evenly distributed, however, across the Pacific Northwest; maximum diversity and abundance in the community occurs in mixed-conifer, old-growth forests that contain streams. Although the species differ in life histories and ecologies, all seem sensitive to timber harvesting because of both elimination of habitat and creation of barriers to dispersal.

Keywords: Bushy-tailed woodrat, Douglas' squirrel, dusky-footed woodrat, northern flying squirrel, old growth, red tree vole, Townsend's chipmunk, Oregon, Washington.

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