RED TREE VOLE

HABITAT AND MICROHABITAT UTILIZATION

IN DOUGLAS-FIR FORESTS OF NORTHERN CALIFORNIA

by

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A Report

Presented to

The California Department of Fish and Game

and

The U.S. Forest Service - Pacific Southwest Experiment Station

August, 1987

ABSTRACT

Red tree vole (<u>Arborimus</u> <u>longicaudus</u>) habitat and microhabitat use relative to availability was studied in young, mature, and old-growth Douglas-fir forests in Northern California between July and October, 1984 and June and September 1985. Seventy-nine of the 148 nest sites examined in this study contained evidence of inhabitation by red tree voles. An analysis of macrohabitat selection between seral stages indicated that the abundance of red tree vole nests was greatest in old-growth forests. Specifically, over half (45) of the red tree vole nests observed were located in two stands of Douglas-fir forest that were more mesic, due to their proximity with the Eel River, than the other seven stands examined in this study. Red tree vole nests were characterized by accumulations of resin ducts and red tree vole feces, and were composed primarily of small twigs. Nests were most frequently located on a branch directly adjacent to the trunk of the nest tree. Red tree vole nests were not found in any other tree species than Douglas-fir. Chi-square goodness of fit tests indicated that red tree vole nest trees had a greater frequency of conks, dead tops, and fire and damage scars than expected. Discriminant function analysis indicated that, for all seral stages combined, red tree vole nest sites could be distinguished from available, but unused, trees by four variables: distance to the nearest red tree vole nest tree, bole height, tree height, and tree diameter. Discriminant analysis of eleven structural habitat variables measured in 0.04ha square plots indicated that red tree vole habitat could be distinguished from available habitat, in all seral stages combined, by four variables: altitude, average percent canopy cover, the number of snags, and the number of stumps. Analysis of variance indicated that red tree vole habitat was characterized by shorter snags, larger diameter logs, and larger diameter trees, particularly Douglas-firs and redwoods, than were observed in available but unused habitat. Red tree vole habitat was also characterized by a smaller average percent cover of rock, a greater average percent cover of *Berberis nervosa* and of *Galium muricatum*, and a smaller average percent cover of herbaceous species, particularly deciduous herbaceous species, than was available habitat. It was suggested that the moist, cool conditions suitable for red tree vole istence in Northern California can be attributed to the dense, multilayered canopy of older, riparian Douglas-fir forests. It was recommended that management of Douglas-fir forests in Northern California for red tree voles on the macrohabitat level should include maintenance of Douglas-fir forests in mesic locations and micro-climates, i.e.: adjacent to rivers, streams, and ravines. Such management would not only ensure that the moisture requirements of this species are met, but would also provide suitable microhabitat for the existence of red tree voles in such forests.

ACKNOWLEDGEMENTS

Dr. Arlene T. Doyle has been most helpful with her advice and suggestions throughout the course of this project. I would like to thank her for all the informative discussions we have shared and for coordinating the cooperative agreement between the California Department of Fish and Game and the U.S. Forest Service.

After three years of intensive research, I sincerely thank and respect the members of my graduate committee, Dr. David W. Kitchen, Dr. Rick Golightly, and Dr. Tim Lawlor, for their suggestion that I narrow the scope of my proposed study. I am grateful to Gordon Gould, of the California Department of Fish and Game, for suggesting this topic in the first place, and for his support of the project through all its phases.

Cam and Katy Barrows were most helpful in providing facilities for our stay at the Coast Range Preserve. Their friendship and suggestions made the data collection portion of this project quite fun. I am grateful to the Nature Conservancy for permitting biological research to be conducted on the Northern California Coast Range Preserve and for providing housing facilities for researchers working at the preserve.

I would like to thank my four field assistants, David R. Hopper, Shawna L. Joyce, Dan W. Perritt, and Mark V. Tomaszewski, for all their efforts and enthusiasm. I am especially indebted to Dave for the safe and successful inspection of over one hundred and forty red tree vole and non-red tree vole nests, and to Dan, whose friendship and encouragement have seen me through to the successful completion of this study. He also kindly provided his artistic talents for the drafting of the study area maps. I am especially grateful to Pat O'Connor for her assistance in typing the extensive revisions of this thesis while my own time was occupied by my pursuit of a veterinary degree. The data collection would not have been possible without the stalwart constitution of a 1973 Volvo station wagon that carried us over hundreds of miles of dirt logging roads to gain access to the study areas.

This project was funded by Collection Agreement No. C-716 between the California Department of Fish and Game and the U.S. Forest Service Pacific Southwest Experiment Station. Humboldt State University provided computer time for data analysis and preparation of the final report and thesis.

The following people assisted with various aspects of this study: Bruce Bingham, Bill Block, Lenny Brennan, Chris Canaday, Pat Collins, Tom Evans, Vicky Meretsky, and Pete Steel.

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INTRODUCTION

The red tree vole (Arborimus longicaudus) is an arboreal microtine rodent that inhabits moist coniferous forests in the Pacific Northwest (Howell, 1926). The red tree vole feeds almost entirely on the needles of conifers such as Douglas-fir (Pseudotsuga menziesii), Grand fir (Abies grandis), or Sitka spruce (Picea sitchensis). A red tree vole discards the lateral resin ducts of the needle while it is consuming its meal of conifer needles (primarily Douglas-fir; Maser, 1966). These resin ducts accumulate within the nest to form a soft inner lining when fresh. As the resin ducts and fecal material accumulate and decay, they eventually compose a compacted base for the nest (Benson and Borell, 1931; and Maser, 1966). The red tree voles' specialized diet has been suggested as the explanation for the extended gestation period (up to 44 days), small litter size (2 or 3 young per litter), and the slow development of young (up to 35 days before weaning) observed in this species (Hamilton, 1962).

Numerous authors have described red tree vole nests, the behavior of captive voles, and the life history characteristics of this species (Benson and Borell, 1931; Howell, 1926; Jewett, 1920; and Maser, 1966). Red tree vole nest sites have been quantitatively described in young, mature, and old-growth Douglas-fir forests of Northern California (Vrieze, 1980; and Zentner, 1977).

It has been suggested that red tree voles find optimum habitat in old-growth and in mature forests (Franklin et. al., 1981). However, no research has been conducted to determine if red tree voles are actually selecting nest sites with specific attributes either within a given seral stage, or between different seral stages of Douglas-fir forest.

The primary purpose of this study was to determine, through a comparison of habitat and microhabitat usage relative to habitat availability, whether or not red tree voles have a preference for nest sites with particular characteristics (Johnson, 1980; and Partridge, 1978). Research satisfying this objective could provide much information relevant to the problem of how commercial Douglas-fir forests in the Pacific Northwest could be managed to produce optimal habitat conditions for red tree voles.

Red tree vole habitat selection was studied during the summer and early fall in nine stands of Douglas-fir forest, representing three age classes, in Northern California. The empirical tests of habitat selection were used to provide a quantitative analysis and description of red tree vole habitat and microhabitat utilization in three seral stages of Douglas-fir forest in Northern California. Specifically, the following questions were addressed by this study: 1) What seral stages are red tree voles most abundant in 2) What environmental characteristics are important to microhabitat use by red tree voles 3) Within a given seral stage, is the habitat use by red tree voles proportional to the available habitat 4) Is the microhabitat available to red tree vole significantly different between seral stages of Douglas-fir forest and 5) Between seral stages, do red tree vole nests have different characteristics, indicating that red tree voles require different microhabitats in different aged forests?

STUDY AREA

Nine stands of mixed evergreen forest, each approximately 20 hectares (ha) in size, were examined for the presence of red tree vole nests. Three replicate stands of mesic old-growth, mature, and young-growth forests were sampled. Vegetation features characterizing the three seral stages of old-growth, mature and young-growth have been described by Lang (1980). Two young growth stands ('Homestead' and 'Mud Springs') and one mature stand ('Harwood's Ninety') are located on land owned by the Harwood Lumber Mill in Branscomb, California (Secs. 13, 14, 23, 24; T21N, R16W) (Figure 1). Three old growth stands ('Alpine', 'Elder Creek', and 'Ten Mile'), two mature stands ('Fanny's Place' and 'White House'), and one young growth stand ('Barnes') are located on the Nature Conservancy's Northern California Coast Range Preserve (NCCRP) in Mendocino County, California (Secs. 15, 16, 20, 21, 27, 28, 29, 31, 32; T22N, R16W) (Figure 1). Johnson (1979) has described the topography, hydrology, climate, and vegetation of the Coast Range Preserve.

This location was originally chosen as a research site for the Old Growth Wildlife Habitat Program conducted by the U.S. Forest Service Pacific Southwest Experiment Station in Arcata, CA (Ruggierro and Carey, 1982; and Spies, 1983). These nine stands were selected for use in this study because they are representative of commercial Douglas-fir forests and because red tree vole nests have been observed in the area

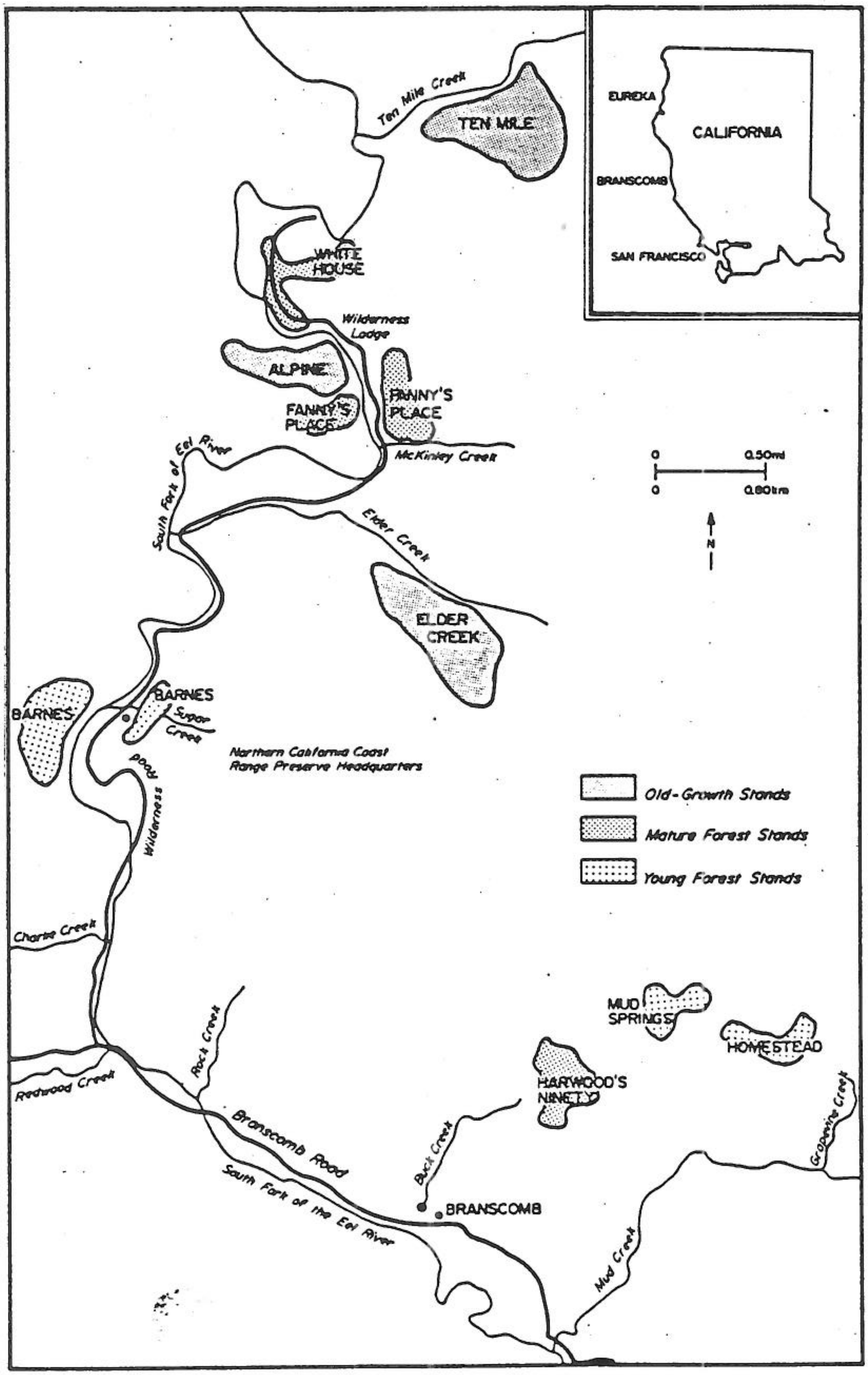

Figure 1. Map of the Study Area, with Regional Orientation Showing Geographic Locations of the Nine Study Sites relative to Branscomb, California.

(C. Barrows, pers. comm.). Bingham (1986) has described the study area in further detail.

Old Growth Stands

'Alpine' borders the west side of the Eel River directly across from Wilderness Lodge. The slopes adjacent to the river are moderate (30 - 59% slope) and densely (subjective visual estimation = SVE) populated with old growth redwoods (Sequoia sempervirens). Further from the river, the southeast facing slopes become steeper(60 - 100% slope), and the redwoods are replaced by old-growth Douglas-firs. Large tanoaks (Lithocarpus densiflora) and madrones (Arbutus menziesii) are also common (SVE) throughout the stand. Seven ravines intersect the transect strip in this stand.

'Elder Creek' is located on the south side of Elder Creek, approximately 2.25 Km upstream from the confluence of Elder Creek with the Eel River. No redwoods are present in this stand. It is characterized by dense thickets of salal (Gaultheria shallon) and evergreen huckleberry (Vaccinium ovatum). Steep shale slopes border the sides of the one ravine and two streams running through this stand. Spotted owls (Strix occidentalis) have nested in both 'Alpine' and 'Elder Creek' for several years (C. Barrows, pers. comm.).

'Ten Mile' is located approximately 0.5 Km southwest of the confluence of Ten Mile Creek with the Eel River. However, the study site was not directly adjacent to either Ten Mile Creek or the Eel River. This stand is characterized by steep (60 - 100% slope), north facing shale slopes. Five ravines and one stream crossed the transect. No redwoods are present in this stand, however, poison oak (Rhus diversiloba) is quite common (SVE).

Mature Stands

'Fanny's Place' is divided into two areas by the Eel River. The parcel on the east side of the river is approximately 15 ha in size. It is characterized by gentle (10 - 29% slope) west-facing grassy slopes. The eastern border of this area is sharply demarcated by a dense growth of manzanita (Arctostaphylos sp.). McKinley Creek and four ravines run through this portion of the stand. Scattered redwoods and old-growth Douglas-fir are present in this area. The portion of the stand on the west side of the Eel River is approximately 5 ha in size, and is characterized by moderately steep (60 - 100%), south-facing rocky slopes. A dirt road intersects the southwest corner of this portion of the stand. An abandoned meadow and a dirt road borders this area to the south. Although one ravine and a seep run through this portion of the stand it was generally more xeric than the area east of the river. No redwoods are present in the portion of the stand west of the river. However, a few scattered old-growth Douglas-fir are present.

'Harwood's Ninety' is located approximately 1.5 Km northeast of Branscomb, CA. A dirt logging road divides the stand into two areas. Both areas are bordered by manzanita. The southern portion of the area east of the road opens into a relatively flat (1 - 9% slope) area where chinkapin (Castanopsis chrysophylla) is well interspersed with the Douglas-fir. This stand is characterized by moderate (30 - 59%) slopes mixed with relatively open, flat areas (SVE). Seven ravines are located in this stand. No redwoods were observed in this stand.

'White House' is divided into two areas by Wilderness Road. The area east of the road is approximately 15 ha in size and is characterized by a moderate (30 - 59%) north-facing slope. The bottom of the slope is adjacent to an abandoned meadow. The top of the ridge is bordered by a dense growth of manzanita (SVE). One ravine intersected the transect in this section of the stand. The portion of the stand west of the road is adjacent to the Eel River and is approximately 5 ha in size. It is characterized by a moderate west-facing slope. One ravine intersected the transect in this portion of the stand. A few scattered redwoods and old-growth Douglas-fir are present in this area west of the road.

Young Stands

'Barnes' is divided into two areas by the Eel River. The portion east of the river is located directly behind the NCCRP headquarters. It is characterized by moderate west-facing slopes. Three ravines and Sugar Creek run through this portion of the stand. Shrubby undergrowth, including such species as Ceanothus incanus and Vaccinium ovatum, is quite dense (SVE) in areas of this stand. The area west of the river is characterized by steep (60 - 100%) east-facing slopes. Abandoned, rocky, dirt logging roads intersect this portion of the stand in numerous locations. Two ravines crossed the transect in this portion of the stand. Redwoods are common in the southern part of this parcel.

'Homestead' is located approximately 3 km northeast of Branscomb. Abandoned dirt logging roads intersect this stand in several localities. The slopes are gentle to moderate; the majority of the slopes face east (SVE). Five ravines intersected the transect line. No redwoods are present in this stand. The understory is relatively open (SVE).

'Mud Springs' is located approximately 2.5 Km northeast of Bransomb. This stand is divided into two portions by a dirt logging road. The understory of the smaller portion north of the logging road is relatively open (SVE). This area is characterized by gentle (10 - 29%), west-facing slopes. One ravine runs through this portion of the stand. The area on the south side of the road is approximately 15 ha in size. The southernmost portion of this portion of the stand is characterized by gentle (10 - 29%), south-facing shale slopes, and is covered by a dense understory of manzanita and poison oak (SVE). The majority (SVE) of this parcel, however, has gentle (10 - 29%), soil-covered slopes, and has the understory typical of a regenerating mixed evergreen forest (Sawyer, et al., 1977). Two ravines intersected the transect in this parcel. No redwoods are located in this stand.

METHODS

A total of 136 days were spent in the field, either collecting vegetation data or locating and/or identifying red tree vole nests. The three old-growth stands and one mature stand ('Fanny's Place') were sampled between 2 July 1984 and 19 October 1984. Two mature stands ('Harwood's Ninety' and 'White House') and the three young growth stands were sampled between 21 June 1985 and 6 September 1985.

Red Tree Vole Nest Location and Identification

Habitats available to and used by red tree voles were compared on the macrohabitat (between seral stages) and on the microhabitat (within a seral stage) levels. To obtain an estimate of red tree vole microhabitat use, each stand was examined for the presence of red tree vole nests over a three day period prior to measuring habitat plots in the stand. A 100-m wide transect strip, 1670-m in length, was searched for potential red tree vole nests. The center of this strip was a pre-existing transect located in each stand by the Old Growth Wildlife Habitat Research Project so as to run through habitat representative of a given seral stage.

Potential red tree vole nests were located by visually searching each tree with binoculars for nests. Both sides of the trees were examined by placing one observer along the center of the transect line and the other two observers on either side of the center line. The area up to 50-m away from the center line was searched for the presence of nests by these two observers.

Once a nest was located, the nest tree was flagged, its perpendicular distance (m) from the transect center line was measured with a metal tape, and its location was mapped relative to the transect line. The ground below the nest was searched for the presence of resin ducts and nest material. If resin ducts were found, then the nest was considered to be a confirmed red tree vole nest. If no resin ducts were found, the tree was subsequently climbed, using either climbing spurs or jumars, and the nest was examined for the presence of resin ducts. If resin ducts were found in the nest, the nest was considered to be a red tree vole nest (Benson and Borell, 1931; Howell, 1926; and Maser, 1966). If no resin ducts were found in the nest, the nest was assumed to have been constructed by an animal other than a red tree vole. Western gray squirrels (Sciurus griseus), Northern flying squirrels (Glaucomys sabrinus), and Douglas' squirrels (Tamiasciurus douglasi) all build nests externally similar to that of the red tree vole.

A description of the nest was recorded. The percent canopy cover in a 25-m^2 area above the nest was visually estimated in five percentage classes: 1-15%, 16-25%, 26-50%, 51-75%, 76-100%. The branches above the nest were visually inspected by the climber to determine if any nests had not been visible from the ground. A sample of the nest material was removed from the nest and examined for the presence of the following items: green or brown resin ducts; red tree vole or other species' feces; redwood and Douglas-fir bark shavings; lichen (Alectoria sarmentosa); moss (Dendroalsia abientina); green or brown Douglas-fir needles; Douglas-fir twigs or trimmings; tanoak, madrone, or oak (Quercus sp.) leaves; Douglas-fir cone scales; and animal hair.

The presence of resin ducts in a nest or on the ground below a nest indicated that red tree voles had either constructed the nest or had resided in the nest for a period of time. As the nest ages or is disturbed by weather or animals, clumps of resin ducts fall to the ground (Benson and Borell, 1931; Maser, 1966).

For the purposes of this study, it was not important that a nest be currently occupied by red tree voles, only that it had, at one time, been inhabited by this species. Thus, a dilapidated nest containing dry, brown, obviously old, resin ducts was considered to be a red tree vole nest because it indicated that red tree voles had inhabited the nest within the past few years. It was assumed that the amount of time required for a nest to decay (a matter of years) was on a much smaller scale than that required for the habitat surrounding the nest in an undisturbed forest to change, making the nest unsuitable for red tree voles (a matter of decades and centuries).

Habitat Variables

The spectrum of micro- and macrohabitats in each stand that could potentially be used by red tree voles was defined as the habitat available to the red tree vole (Brennan, 1984). The amounts and types of habitat structure available to and utilized by red tree voles in the nine stands of Douglas-fir forest were estimated by the following techniques.

The micro habitat around each red tree vole nest tree was characterized in a 0.04 ha (20-m on a side) square area centered around the nest tree ("red tree vole plots"). Microhabitat in each stand that was available but not used by red tree voles was estimated in thirty 0.04 ha plots randomly chosen within the transect strip ("available plots"). An area 30-m in radius from the randomly chosen plot center was examined for the presence of red tree vole nests. If a red tree vole nest was found within this area, a habitat plot was located around the red tree vole nest. The initial random plot was discarded and a replacement random plot was chosen. Eleven variables were measured within each 0.04 ha red tree vole and available plot (See Table 1 for variable descriptions and measurement techniques). These variables were used to characterize habitat differences between stand ages (i.e. the macro habitat of the red tree vole).

Micro and macro habitat variables were selected for use in this study on the basis of the following criteria:

1) Potential relevance to red tree vole microhabitat use, as determined by literature review (Howell, 1926; Maser, 1966; Zentner, 1977; and Vrieze, 1980),
2) Efficiency and accuracy of measurement with minimal disturbance to the habitat, and
3) Ease and accuracy of repeatablity (Doyle, 1985).

Trees, snags, and logs were also characterized within each 0.04 ha plot. The species of each tree, snag, or log was recorded. If the species of a log could not be determined, it was classified as 'unknown'. The diameter at breast height (dbh) of the trees and snags, and the maximum diameter of logs within the plot were estimated visually in five categories: 10-29cm, 30-59cm, 60-89cm, 90-119cm, and >= 120cm. The height of snags and the length of logs within the plot were measured to

Table 1. Description of Macro Habitat Variables Measured on 73 0.04 ha Red Tree Vole Plots and on 270 0.04 ha Randomly Sampled Plots of Available Habitat.

Variable	Description
Slope	Greatest percent slope through plot center measured with a relascope.
Aspect	Aspect of greatest slope through plot center. Measured in degrees with a compass.
Altitude	Elevation of plot in feet estimated from a topographic map. Values converted to meters for calculations.
Distance to water	Meters to nearest permanent source of water at least 1-m in width. Estimated from a topographic map.
Distance to ravine	Meters to nearest ravine up to 50-m away from plot center, measured with a metal tape. Distances greater than 50-m were recorded as 99.
Basal area	Basal area (m^2/ha) measured at plot center with a relascope.
Average canopy cover	Average percent canopy cover measured with a spherical densiometer 5-m from plot center along each of the four primary compass directions.
Tree number	Number of trees in the 0.04 ha plot.
Snag number	Number of snags in the 0.04 ha plot.
Log number	Number of logs in the 0.04 ha plot.
Stump number	Number of stumps in the 0.04 ha plot.

the nearest meter using a relascope and a metal tape respectively. Logs were classified into five decay classes as described by Franklin, et al. (1981).

Percent cover of evergreen and deciduous shrubs and herbs, and of six substrate types were estimated visually in four 4-m^2 subplots located 5-m from the center of the 0.04 ha plot along each of the four primary compass directions (Table 2). Plant species names follow Munz (1965).

Nest trees in red tree vole plots were characterized by the sixteen variables described in Table 3. In order to evaluate the potentially available but unused nest sites in a stand, the five trees closest to plot center in the randomly chosen plots ("test trees") were also characterized by the variables described in Table 3.

Red tree vole nests were examined visually with the aid of binoculars from the ground to determine the condition and structure of the nest. A nest was classified as 'old' if it did not have a well-defined shape, there was no sign of any recent activity (e.g.: green Douglas-fir needles on top of the nest), or it was obviously dilapidated (i.e., nest was flat in shape with pieces of the nest hanging down or fallen to the ground). A nest was considered 'fresh' if it was spherical in shape and had signs of recent activity.

The size of the primary material (generally twigs or sticks) composing the nest was classified as 'duff' (powdery, black material), 'small' (twigs $\leq$ 1 cm diameter), or 'large' (twigs > 1 cm diameter). The nests were examined for the presence of green Douglas-fir needles or trimmings on top of the nest, and for the presence of large deciduous leaves from such species as madrone or tanoak. The orientation and

Table 2. Description of Vegetation Variables Measured on 1372 4-m^2 Subplots. One Subplot was Placed 5-m from Plot Center Along Each of the Four Primary Compass Directions for Each of the 73 0.04 ha Red Tree Vole Plots and for Each of the 270 0.04 ha Available Plots.

Variable	Description
Substrate	Type of substrate present in subplot: exposed bare rock, exposed bare mineral soil, fine organic litter, coarse organic litter, moss, and lichen.
Substrate cover	Percent of subplot covered by a substrate type. Visually estimated in 5 percent cover classes: 1-15%, 16-25%, 26-50%, 51-75%, 76-100%.
Shrub species	Shrub species present in subplot.
Shrub cover	Percent of subplot covered by a shrub species. Visually estimated in 5 percent cover classes: 1-15%, 16-25%, 26-50%, 51-75%, 76-100%.
Herb species	Herbaceous species present in subplot.
Herb cover	Percent of subplot covered by an herb species. Visually estimated in 5 percent cover classes: 1-15%, 16-25%, 26-50%, 51-75%, 76-100%.
Deciduousness	Type of shrub or herb present in subplot: deciduous or evergreen.

Table 3. Description of Variables Used to Characterize Nest Trees in 73 0.04 ha Red Tree Vole Plots or the Test Trees in 270 0.04 ha Available Plots.

Variable	Description
Tree species	Species of nest tree or of five test trees.
Tree diameter	Diameter at breast height (cm) of nest tree or of five test trees. Measured with a cloth dbh tape.
Tree height	Height in meters of nest tree or of five test trees. Measured with a metric relascope.
Bole height	Height in meters to the lowest green branch on nest tree or on five test trees. Measured with a metric relascope or visually estimated if under 5-m.
Distance to nearest	Distance in meters to the tree nearest to the nest tree or to a test tree. Measured with a metal tape.
Distance to nest tree	Distance in meters to nearest nest tree from nest tree or from five test trees. Measured with a metal tape. Distances greater than 50-m were recorded as 99.
Distance to redwood	Distance in meters to the nearest redwood from nest tree or from test trees. Measured with a metal tape. Distances greater than 50-m were recorded as 99.
Moss	Percent cover of moss on nest or test tree trunks. Visually estimated in six percent cover classes: 0%, 1-15%, 16-25%, 26-50%, 51-75%, 76-100%.
Lightning	Presence or absence of lightning scars on nest tree or test tree trunk.
Fire scar	Presence or absence of fire scars on nest tree or test tree trunk.
Ladder	Presence or absence of "grouse ladder" (series of dead branches on trunk - often indicating an open-grown tree) on trunk of nest tree or test tree.

Table 3. Description of Variables Used to Characterize Nest Trees in 73 0.04 ha Red Tree Vole Plots or the Test Trees in 270 0.04 ha Available Plots (continued).

Variable	Description
Conk	Presence or absence of fungal conks on trunk of nest tree or test tree.
Dead top	Top of nest tree or test tree is alive or top is broken off or dead.
Cavity number	Number of cavities visible in trunk of nest tree or test tree.
Damage scar	Presence or absence of damage scars (other than lightning or fire scars) on trunk of nest tree or test tree.

Table 4. Description of Variables Used to Characterize Red Tree Vole Nests in 73 0.04 ha Red Tree Vole Plots.

Variable	Description
Nest orientation	Orientation of nest in tree. Measured in degrees with a compass from directly below the nest, with the observer's back next to the trunk of the nest tree.
Nest height	Height of nest in meters from the ground. Measured with a metric relascope.
Nest location	Location of nest on branch: adjacent to the trunk, in the middle of the branch, or at the end of the branch.
Nest condition	Condition of nest: old and dilapidated or well structured and fresh.
Needles	Presence or absence of green Douglas-fir needles on nest. Determined by visual examination of the nest from the ground through binoculars.
Leaves	Presence or absence of large leaves (e.g.: madrone or tanoak) incorporated in to the nest. Determined by visual examination of the nest from the ground through binoculars.
Stick size	Size of primary material composing the nest: duff, small, or large. Determined by visual examination of the nest from the ground through binoculars.
Resin ducts	Presence or absence of resin ducts on the ground below the nest.
Redwood shavings	Presence or absence of redwood bark shavings on ground below the nest.

height of the nest were measured. The nest's location on the branch (eg: adjacent to the trunk, in the middle of the branch, or of the tree or at the end of the branch) was recorded. The ground below the nest and around the nest tree was examined extensively for the presence of resin ducts and redwood bark shavings (Table 4).

Data Analysis

Macrohabitat Selection

A G test for goodness of fit (Sokal and Rohlf, 1969) was used to test the null hypothesis that there was no significant ($p > 0.05$) difference in the number of red tree vole nests found in each seral stage and that there was no significant difference in the number of red tree vole nests between stands within a given seral stage.

Microhabitat Selection

The following null hypotheses were evaluated using discriminant function analysis (DFA), a chi-square goodness of fit test, and a Brown-Forsythe one-way analysis of variance (ANOVA):

1) There was no significant difference between the available (but unused) and the used (inhabited by red tree voles) microhabitat groups within a given seral stage.
2) There was no significant difference between the available and the used microhabitat groups for all seral stages combined.
3) There was no significant difference between available microhabitats in the three different seral stages.

In this study, DFA was used to discriminate between available (but unused) and used habitat groups and also between different seral stages of Douglas-fir forest on the basis of the measured micro- and macrohabitat variables. DFA also provided an indication of how well the different habitat variables discriminate between the groups and of which variables were the most powerful discriminators (Klecka, 1981).

DFA was used to evaluate the above three null hypotheses with respect to the eleven habitat variables described in Table 1. DFA was also used to evaluate the null hypotheses 1-3 with respect to the following variables that were used to characterize the nest tree in red tree vole habitat plots or the test trees in the randomly chosen available habitat plots: dbh, height, bole height, distance to nearest tree, distance to nearest nest tree, and distance to nearest redwood. A two-way ANOVA was used to determine which variables had significant differences between the used and available habitat groups and between stands ages.

A chi-square goodness of fit test (Sokal and Rohlof, 1969) was used to test the following null hypothesis:

a) Null hypotheses 1 - 3 for the following variables: lightning scar, fire scar, damage scar, ladder, conk, live, tree species, and cavity number (see Table 3 for variable descriptions). Expected frequencies were based on the relative proportions of the available and red tree vole habitat plots.

b) Null hypotheses 1 - 3 for the variables characterizing the nest samples collected while examining potential red tree vole nests. Expected frequencies were based on the relative proportions of confirmed red tree vole nests and non-red tree vole nests examined during this study.

c) No significant difference between observed and expected frequencies of variables characterizing confirmed red tree vole nest samples between the three seral stanges.

d) No significant difference for all seral stages combined between the observed and expected frequencies of the following variables characterizing a confirmed red tree vole nest: nest location, nest condition, needles, leaves, stick size, resin ducts, and redwood bark shavings (see Table 4 for variable descriptions). Expected frequency values were based on a random distribution of the different characters for a given variable for the total number of red tree vole nests examined.

A Brown-Forsythe ANOVA that does not assume equal within group variances (Dixon, et. al., 1983) was used to test the following null hypotheses:

a) Null hypotheses 1 - 3 for percent moss cover of the nest /test trees, percent shrub cover, percent herb cover, and percent deciduousness; average tree, snag, and log dbh; snag height; and log length. The percent cover was evaluated for all shrub species, and of each of the five most common herb species. The average dbh was evaluated for all tree species combined and for each of the seven most common tree species.

b) No significant difference between percent cover of deciduous shrubs or deciduous herbs and percent cover of evergreen shrubs or evergreen herbs within a given seral stage and for all seral stages combined.

c) No significant difference in mean red tree vole nest orientation or mean red tree vole nest height between seral stages.

DFA and ANOVA were performed on Humboldt State University's CDC Cyber 170/760 computer using BMDP programs 7M and 7D (Dixon, et. al., 1983). Chi-square and G tests for goodness of fit were performed on a Hewlett Packard 15C calculator. All statistical tests were considered significant at the $p < 0.05$ level.

RESULTS

One hundred and forty-eight nest sites were examined for evidence of use by red tree voles. Resin ducts were found at 79 of these nest sites, either on the ground below the nest, on the nest tree, or in the nest itself. The 69 nests that did not contain evidence of inhabitation by red tree voles were assumed to have been constructed and/or occupied by such animals as Northern flying squirrels, Western gray squirrels, or Douglas' squirrels.

All the confirmed red tree vole nests examined in this study were located in Douglas-fir trees. Nests located in other tree species also were examined for the presence of resin ducts and red tree voles, but none contained any evidence of occupation by red tree voles.

A total of 73 0.04 ha habitat plots were done around the 79 red tree vole nests. Six of the red tree vole nests were located either in the same tree as another red tree vole nest or in a tree adjacent to another red tree vole nest tree, and so were included in the same habitat plot as another red tree vole nest.

Macrohabitat Analysis

Thirty-nine red tree vole nests were located in the three stands of old-growth Douglas-fir forest, 22 red tree vole nests were found in the three mature stands, and 18 red tree vole nests were located in the three stands of young-growth Douglas-fir forest. The number of red tree vole nests observed in each stand is presented in

Appendix A. The old-growth stands had a significantly greater number of red tree vole nests than expected from a random distribution of red tree vole nests between the three seral stages ($G = 9.025$, $p < 0.05$, 2 d.f.).

Within a given seral stage, Alpine had a significantly greater number of red tree vole nests than either of the other two old-growth stands ($G = 27.829$, $p < 0.05$, 2 d.f.). White House also had a significantly greater number of red tree vole nests than either of the other two mature stands ($G = 7.5597$, $p < 0.05$, 2 d.f.). There was no significant difference in the number of red tree vole nests between the three young-growth stands ($G = 2.911$, $p < 0.05$, 2 d.f.).

Microhabitat Analysis

Red Tree Vole Nest Characteristics

Frequencies of the variables characterizing nest samples collected while examining nest for evidence of red tree vole inhabitation are presented in Appendix B. For all seral stages combined, red tree vole nests contained a significantly greater frequency of rodent feces than did non-red tree vole nests than would have been expected based on the proportions of red tree vole nests and non-red tree vole nests in all stands combined. ($X^2 = 17.179$, $p < 0.05$, 1 d.f.). Similarly, red tree vole nests in mature and young-growth stands of Douglas-fir forest contained a significantly greater frequency of rodent feces than did non-red tree vole nests than would have been expected based on the proportions of red tree vole nests and non-red tree vole nests within a given stage (Mature: $X^2 = 7.699$, $p < 0.05$, 1 d.f.; Young: $X^2 = 12.835$, $p < 0.05$, 1 d.f.).

Douglas-fir bark shavings ($X^2 = 4.092$, $p < 0.05$, 1 d.f.), moss ($X^2 = 4.937$, $p < 0.05$, 1 d.f.), and animal hair ($X^2 = 11.754$, $p < 0.05$, 1 d.f.) were all found significantly more frequently in non-red tree vole nests than in red tree vole nests for all seral stages combined. These three variables were characteristic of Northern flying squirrel nests observed on the Coast Range Preserve (pers. observ.). Animal hair also was found significantly more frequently in non-red tree vole nests than in red-tree vole nests in mature ($X^2 = 7.369$, $p < 0.05$, 1 d.f.) and young-growth ($X^2 = 6.905$, $p < 0.05$, 1 d.f.) Douglas-fir stands.

Redwood bark shavings ($X^2 = 9.899$, $p < 0.05$, 2 d.f.) and lichen ($X^2 = 6.812$, $p < 0.05$, 2 d.f.) were found significantly more frequently in red tree vole nests in old-growth forests than in young-growth or mature forests. Douglas-fir bark shavings ($X^2 = 8.617$, $p < 0.05$, 2 d.f.), green Douglas-fir needles ($X^2 = 9.156$, $p < 0.05$, 2 d.f.), and Douglas-fir trimmings ($X^2 = 9.286$, $p < 0.05$, 2 d.f.) were found significantly more frequently in red tree vole nests in young Douglas-fir forests than in red tree vole nests in old-growth or mature stands.

Non-red tree vole nests in old-growth stands had a significantly higher frequency of rodent feces than did non-red tree vole nests in mature or young-growth stands of Douglas-fir forest ($X^2 = 8.636$, $p < 0.05$, 2 d.f.). However, these results also could be attributed to the small number of non-red tree vole nests containing rodent feces. Non-red tree vole nests in young stands of Douglas-fir forest had a significantly greater frequency of Douglas-fir bark shavings ($X^2 = 10.426$, $p < 0.05$, 2 d.f.), green needles ($X^2 = 6.6797$, $p < 0.05$, 2 d.f.), and trimmings ($X^2 = 6.492$, $p < 0.05$, 2 d.f.) than did nests in mature or old-growth stands.

Red tree vole nests were also characterized by the variables described in Table 4 (see Methods). Red tree vole nest height was significantly higher in old-growth stands than in mature or young-growth stands (Table 5). There was no significant difference in orientation of red tree vole nests between the three seral stages (Table 5).

Red tree vole nests were located significantly more often adjacent to the trunk of the nest tree ($\underline{n}$ = 68) than at the middle of the branch ($\underline{n}$ = 6) or at the end of the branch ($\underline{n}$ = 1; Goodness of fit $X^2 = 111.440$, $p < 0.05$, 2 d.f.). Nests located at the top of the tree were not included in this test. The number of red tree vole nests constructed primarily of small twigs ($\underline{n}$ = 66) was significantly greater than the number of nests composed of duff ($\underline{n}$ = 5) or of large twigs ($\underline{n}$ = 4; Goodness of fit $X^2 = 100.880$, $p < 0.05$, 2 d.f.). There was no significant difference in the number of old ($\underline{n}$ = 40) versus the number of fresh ($\underline{n}$ = 36) red tree vole nests (Goodness of fit $X^2 = 0.211$, $p > 0.05$, 1 d.f.).

The number of red tree vole nests with green Douglas-fir needles on top of the nest ($\underline{n}$ = 47) was significantly greater than expected based on a random distribution of the variable among red tree vole nests (Goodness of fit $X^2 = 4.813$, $p < 0.05$, 1 d.f.). The number of red tree vole nests without leaves incorporated into the nest ($\underline{n}$ = 61; Goodness of fit $X^2 = 29.453$, $p < 0.05$, 1 d.f.) or without redwood bark shavings below

Table 5. Brown-Forsythe ANOVA Tests for Red Tree Vole Nest Selection Between Three Seral Stages[a] of Douglas-fir Forest Examined in Mendocino County, California. Variables are Desribed in Table 4 (See Methods) * = $p < 0.05$).

	Old-Growth ($\underline{n}$ = 39)		Mature ($\underline{n}$ = 19)		Young-Growth ($\underline{n}$ = 18)[b]	
Variable	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error
NEST ORIENTATION (degrees)	162.4	15.48	200.1	22.29	169.4	23.83
NEST HEIGHT (meters)	19.4	1.13	15.5	1.38	13.4	0.997*

[a] See study area descriptions for descriptions of the three seral stages.
[b] The sample size in young-growth stands for Nest Orientation was 16; the sample size for Nest Height was 18.

the nest ($\underline{n}$ = 61; Goodness of Fit $X^2 = 23.956$, $p < 0.05$, 1 d.f.) was significantly greater than the number of red tree vole nests with leaves ($\underline{n}$ = 14) or with redwood bark shavings ($\underline{n}$ = 18). There was no significant difference between the number of red tree vole nests that had resin ducts on the ground below the nest ($\underline{n}$ = 42) and those that did not ($\underline{n}$ = 36; Goodness of Fit $X^2 = 0.462$, $p < 0.05$, 1 d.f.).

Red Tree Vole Nest Tree Characteristics

Observed frequencies of the variables used to characterized red tree vole nest trees and available test trees are presented in Appendix C. Red tree vole nest trees had significantly more fire scars ($X^2 = 81.445$, $p < 0.05$, 1 d.f.), conks ($X^2 = 97.306$. $p < 0.05$, 1 d.f.), dead tops ($X^2 = 25.660$ $p < 0.05$, 1 d.f.), and damage scars ($X^2 = 7.630$, $p < 0.05$, 1 d.f.) than did available test trees. In addition, red tree voles used Douglas-firs as nest trees significantly more frequently than the proportion of Douglas-fir test trees in available habitat plots for all seral stages combined ($X^2 = 179.74$, $p < 0.05$, 1 d.f.) and for within a given seral stage (Old-growth: $X^2 = 105.32$, $p < 0.05$, 1 d.f.; Mature: $X^2 = 32.5298$, $p < 0.05$, 1 d.f.; Young-growth: $X^2 = 54.932$, $p < 0.05$, 1. d.f.).

Within old-growth stands, the presence of fire scars ($X^2 = 29.622$, $p < 0.05$, 1 d.f.), conks ($X^2 = 39.865$, $p < 0.05$, 1 d.f.), dead tops ($X^2 = 11.531$, $p < 0.05$, 1 d.f.), and lack of cavities ($X^2 = 4.339$, $p < 0.05$, 1 d.f.) could potentially distinguish red tree vole nest trees from available test trees . The presence or absence of damage scars was not recorded in the three old-growth stands. In mature stands, the frequency of fire scars ($X^2 = 39.699$ $p < 0.05$, 1 d.f.), conks (X^2 =

43.398, $p < 0.05$, 1 d.f.), dead tops ($X^2 = 3.894$, $p < 0.05$, 1 d.f.), and damage scars ($X^2 = 31.413$, $p < 0.05$, 1 d.f.) was significantly higher in red tree vole nest trees than expected. In young stands, the absence of lightning scars and the presence of dead tops could potentially distinguish red tree vole nest trees from available test trees. However, the sample size for lightning scars was so small within any given seral stage that the significance of the chi-square test may not have any biological meaning for this variable.

In available habitat plots only, the presence of fire scars ($X^2 = 177.00$, $p < 0.05$, 2 d.f.), conks ($X^2 = 28.455$, $p < 0.05$, 2 d.f.), and cavities ($X^2 = 30.312$, $p < 0.05$, 2 d.f.) could potentially distinguish test trees in old-growth stands from test trees in mature or young-growth stands. Test trees in mature stands had a significantly greater frequency of dead tops than did those in old or young-growth stands ($X^2 = 9.294$, $p < 0.05$, 2 d.f.). Test trees in young stands had a significantly higher frequency of grouse ladders than did those in mature or old-growth stands ($X^2 = 103.58$, $p < 0.05$, 2 d.f.).

A two-way ANOVA between seral stages and between red tree vole nest tree and available test tree sites indicated that six variables (tree diameter, tree height, bole height, distance to nearest tree, distance to nearest nest tree, and distance to nearest redwood) used to characterize the nest/test trees could potentially distinguish between seral stages (Table 6). Correlation coefficients of these variables are presented in Appendix D.

The two-way ANOVA also indicated that five variables (tree diameter, tree height, bole height, distance to nearest tree, and distance to nearest nest tree) could potentially distinguish between red tree vole nest trees and test trees in available habitat (Table 6). Of the five variables, stepwise discriminant analysis indicated that for all seral stages combined, red tree vole nest trees could be distinguished from available but unused test trees on the basis of distance to nest tree, bole height, tree height, and tree diameter (Table 7). For all seral stages combined, red tree vole nest trees were characterized as closer to other red tree vole nest trees than were available test trees (Tables 6 and 7). The average bole height, tree height, and tree diameter were greater for red tree vole nest trees than for available test trees for all seral stages combined (Tables 6 and 7). In old-growth stands, discriminant analysis indicated that red tree vole nest trees could be distinguished from available test trees by the same four variables (tree diameter, distance to nest tree, tree height, and bole height) that differentiated between nest and test trees for all seral stages combined (Tables 6 and 8). In mature stands, red tree vole nest trees were closer to other nest trees than were available test trees. However, the average distance to the nearest tree was farther for red tree vole nest trees than for available test trees. Discriminant analysis also indicated that tree diameter could potentially separate red tree vole nest trees from available test trees in both mature and young-growth stands as well as in old-growth stands. The average diameter of red tree vole nest trees was greater than that of available test trees in all three stand ages (Tables 6 and 8). In young-growth stands, red tree vole nest trees also were distinguished from available test trees on the basis of their closer proximity to other red tree vole nest trees than available test trees (Tables 6 and 8).

Table 6. Physical Characteristics of the Variables Used to Characterize 79 Red Tree Vole Nest Trees and 1350 Available Test Trees in Three Seral Stages[a] of Douglas-fir Forest in Mendocino County, California. (ns = $p > 0.05$, * = $p < 0.05$).

	Red Tree Vole Nest Trees						Available Test Trees								
	Old-Growth (n = 35)		Mature (n = 22)		Young-Growth (n = 18)		Old-Growth (n = 450)		Mature (n = 450)		Young-Growth (n = 450)				
Variable	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	p[b]	p[c]	p[d]
Tree Diameter (cm)	115.9	3.29	109.6	8.84	48.4	5.00	39.6	1.58	29.8	1.13	25.4	0.73	*	*	*
Tree Height (m)	54.5	2.04	48.6	3.28	24.2	2.14	21.9	0.73	19.2	0.51	23.2	0.34	*	*	*
Bole Height (m)	15.6	0.87	11.6	1.20	9.1	1.01	7.4	0.32	6.1	0.24	4.8	0.18	*	*	*
Distance to Nearest Tree (m)	2.5	0.21	3.7	0.56	2.0	0.21	2.4	0.07	1.8	0.06	1.6	0.05	*	*	*
Distance to Nest Tree (m)	53.3	6.07	63.8	8.02	61.1	9.78	84.5	1.23	92.8	0.84	93.9	0.78	*	*	ns
Distance to Redwood (m)	63.0	5.94	85.6	6.47	94.1	4.94	89.9	1.22	93.5	0.91	71.7	1.93	*	ns	*

[a] See study area descriptions for descriptions of the three seral stages.
[b] Two-way ANOVA significance level for between seral stages, df = 2, 1, 2; 1423.
[c] Two-way ANOVA significance level for between red tree vole and available groups, df = 2, 1, 2; 1423.
[d] Two-way ANOVA significance level for interaction between seral stages and red tree vole and available groups, df = 2, 1, 2; 1423.

Table 7. Summary of Stepwise Discriminant Analysis Used to Differentiate Between Red Tree Vole Nest Trees and Available Test Trees. Values Represent Standardized Coefficients for Canonical Variables Included in the Discriminant Function. Absolute Magnitude of the Coefficients Indicates Relative Contribution of the Canonical Variables to the Discriminant Function. Sign of the Coefficient Indicates Direction of the Contribution. Variable Means and Standard Errors are Presented in Table 6 (* = $p < 0.05$).

Variable or Character	Discriminant Function
Tree Diameter	-0.69062
Tree Height	-0.34571
Bole Height	0.25051
Distance to Nest Tree	0.44039
Percent Correctly Classified	91.3%
Eigenvalue	0.4146
Canonical correlation	0.5414
Approximate F (degrees of freedom)	147.587 (4, 1424)*

Table 8. Summary of Stepwise Discriminant Analysis Used to Differentiate Between Red Tree Vole Nest Trees and Available Test Trees Within a Given Seral Stage of Douglas-fir Forest in Mendocino County, California. Values Represent Standardized Coefficients for Canonical Variables Included in the Discriminant Function. Absolute Magnitude of the Coefficients Indicates Relative Contribution of the Canonical Variables to the Discriminant Function. Sign of the Coefficient Indicates Direction of the Contribution. Variable Means and Standard Errors are Presented in Table 6 (* = p < 0.05).

	Old-Growth	Mature	Young-Growth
Variable or Character	Discriminant Function	Discriminant Function	Discriminant Function
Tree Diameter	-0.6702	-0.8451	-0.6353
Distance to Nest Tree	0.3794	0.31295	0.7869
Tree Height	-0.5082	-	-
Bole Height	0.3774	-	-
Distance to Nearest Tree	-	-0.2408	-
Percent Correctly Classified	89.0%	93.9%	86.3%
Eigenvalue	0.5069	0.5559	0.2066
Canonical correlation	0.57999	0.5977	0.4138
Approximate F (degrees of freedom)	61.336 (4,484)*	86.713 (3,468)*	48.032 (2,465)*

Table 9. Summary of Stepwise Discriminant Analysis Used to Differentiate Between Available Test Trees in Three Seral Stages of Douglas-fir Forest in Mendocino County, California. Values Represent Standardized Coefficients for Canonical Variables Included in the Discriminant Function. Absolute Magnitude of the Coefficients Indicates Relative Contribution of the Canonical Variables to the Discriminant Function. Sign of the Coefficient Indicates Direction of the Contribution. Variable Means and Standard Errors are Presented in Table 6 (* = $p < 0.05$).

Variable or Character	Discriminant Function I	Discriminant Function II
Tree Diameter	-0.0287	0.9079
Tree Height	0.5293	0.8224
Distance to Nearest Tree	0.4059	0.4522
Distance to Nest Tree	-0.3543	-0.3843
Distance to Redwood	-0.6223	-0.5274
Percent Correctly Classified	51.2%	51.2%
Eigenvalue	0.2175	0.0642
Canonical correlation	0.4227	0.2456
Approximate F (degrees of freedom)	37.134 (10, 2686)*	

In available habitat only, discriminant function analysis separated between the three seral stages on the basis of the following five variables: tree diameter, tree height, distance to nearest tree, distance to nest tree, and distnace to redwood (Tables 6 and 9). Average test tree diameter and distance to the nearest tree were greater in old-growth stands than in mature stands and greater in mature stands than in young-growth stands (Tables 6 and 9). Test trees in old-growth stands were closer to red tree vole nest trees than were test trees in mature stands, while those in mature stands were closer to nest trees than were test trees in young-growth stands. However, available test trees in young-growth stands were closer to redwoods and were taller than test trees in old-growth stands. The average test tree height was taller and the average distance to redwood was closer in old-growth stands than in mature stands of available habitat (Tables 6 and 9).

A Brown-Forsythe ANOVA indicated that, for all seral stages combined, the percent cover of moss on test tree trunks in available habitat ($\overline{X}$ = 20.9%, n = 1348) was significantly greater than on red tree vole nest tree trunks ($\overline{X}$ = 6.9%, n = 79; F = 350.35, $p < 0.05$, 1 d.f.). Within a given seral stage, the percent cover of moss on test tree trunks in available habitat (old growth: $\overline{X}$ = 31.8%, n = 448; mature: $\overline{X}$ = 21.7%, n = 450; young-growth: $\overline{X}$ = 9.2%, n = 450) was significantly greater than the percent cover of moss on red tree vole nest tree trunks (old growth: $\overline{X}$ = 7.6%, n = 39; mature: $\overline{X}$ = 8.0%, n = 22; young-growth: $\overline{X}$ = 4.0%, n = 18) (old-growth: F = 296.71; mature: F = 135.49; young-growth: F = 21.57, $p < 0.05$, 1 d.f.). For available habitat only, test trees in old growth stands had a significantly greater percent cover of moss on their trunks than did test trees in mature or young-growth stands ($F = 107.07$, $p < 0.05$, 2d.f.).

Habitat Characteristics

A two-way ANOVA between seral stages and between red tree vole and available habitat indicated that of the eleven variables used to characterize macrohabitat ten variables (slope; aspect; altitude; distance to water; distance to ravine; basal area; and tree, snag, log, and stump number) could potentially distinguish between seral stages and two variables (average canopy cover and stump number) could potentially separate red tree vole habitat from available but unused habitat (Table 10). Product moment correlation coefficients of the eleven macrohabitat variables are presented in Appendix E. Distance to water and altitude were the only two variables with a correlation coefficient greater than 0.4.

For all seral stages combined, the following four variables were selected by stepwise discriminant analysis as being most effective in distinguishing between red tree vole habitat and available habitat (Table 10 and 11).

Red tree vole habitat was characterized by greater percent canopy cover, greater number of stumps, lower altitude, and fewer snags than available but unused habitat in all seral stages combined (Table 10 and 11).

In old-growth stands, discriminant analysis indicated that red tree vole habitat was closer to ravines, had less steep slopes, and was lower in altitude than available habitat (Tables 10 and 12). Red tree vole habitat in mature stands was characterized as having more logs, being closer to water, and farther from ravines than available habitat

Table 10. Red Tree Vole and Available Macrohabitat Characteristics of Three Seral Stages[a] of Douglas-fir Forest in Mendocino County, California. (ns = p > 0.05, * = p _0.05).

	Red Tree Vole Macrohabitat						Available Macrohabitat								
	Old-Growth (n = 35)		Mature (n = 22)		Young-Growth (n = 18)		Old-Growth (n = 90)		Mature (n = 90)		Young-Growth (n = 90)				
Variable	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	p[b]	p[c]	p[d]
Slope (%)	51.8	3.31	47.9	5.29	46.8	4.26	58.9	1.85	50.0	1.84	43.6	1.84	*	ns	ns
Aspect (°)	154.6	24.85	203.6	21.84	229.4	19.09	115.8	13.09	193.2	10.33	205.4	10.44	*	ns	ns
Altitude (m)	500.0	7.21	478.4	22.53	672.3	17.01	539.5	6.58	544.6	12.69	637.1	9.46	*	ns	*
Distance to Water (m)	252.6	16.96	198.4	26.77	611.8	61.56	296.1	15.06	287.3	13.27	534.3	25.27	*	ns	*
Distance to Ravine (m)	34.7	5.29	87.8	6.48	76.8	8.88	59.3	4.15	70.7	4.05	73.9	3.87	*	ns	*
Basal Area (m^2/ha)	41.9	1.83	41.7	2.79	35.5	2.47	38.6	1.31	43.7	1.34	35.2	1.56	*	ns	ns
Average Canopy Cover (%)	93.4	0.65	95.5	0.98	96.6	0.92	92.6	0.699	94.1	0.56	93.0	0.89	ns	*	ns
Tree Number	18.2	1.28	19.9	2.37	29.4	2.39	17.3	0.79	24.1	1.28	29.9	1.44	*	ns	ns
Snag Number	0.83	0.15	1.36	0.41	0.81	0.28	1.03	0.15	2.07	0.24	1.14	0.16	*	ns	ns
Log Number	4.6	0.38	7.6	2.24	16.4	2.99	4.7	0.42	6.2	0.54	12.9	0.94	*	ns	ns
Stump Number	0.60	0.14	1.27	0.32	4.56	0.92	0.69	0.09	1.51	0.21	2.49	0.27	*	*	*

[a] See study area descriptions for descriptions of the three seral stages.
[b] Two-way ANOVA significance level for between seral stages, df = 2, 1, 2; 337.
[c] Two-way ANOVA significance level for between red tree vole and available groups, df = 2, 1, 2; 337.
[d] Two-way ANOVA significance level for interaction between seral stages and red tree vole and available groups, df = 2, 1, 2; 337.

Table 11. Summary of Stepwise Discriminat Analysis Used to Differentiate Between Red Tree Vole and Available Habitat for All Three Seral Stages of Douglas-fir Forest in Mendocino County, California. Values Represent Standardized Coefficients for Canonical Variables Included in the Discriminant Function. Absolute Magnitude of the Coefficients Indicates Relative Contribution of the Canonical Variables to the Discriminant Function. Sign of the Coefficient Indicates Direction of the Contribution. Variable Means and Standard Errors are Presented in Table 10 (* = $p < 0.05$).

Variable or Character	Discriminant Function
Average Canopy Cover	-0.4439
Snag Number	0.5829
Stump Number	-0.5254
Altitude	0.8807
Percent Correctly Classified	62.4%
Eigenvalue	0.0675
Canonical correlation	0.2514
Approximate F (degrees of freedom)	5.700 (4, 338)*

(Tables 10 and 12). In young-growth stands, red tree vole habitat could be distinguished from available habitat on the basis of a greater number of stumps in red tree vole habitat (Tables 10 and 12).

Available habitat in old-growth stands was characterized as being closer to ravines, having steeper slopes, and having fewer trees and logs than available habitat in mature and young-growth stands (Tables 10 and 13). Available habitat was also characterized by the following: basal area was greatest in mature stands and least in young-growth stands. The number of snags also was greatest in mature stands, but least in old-growth stands. Mature stands were the seral stage closest to water, while young-growth stands were the seral stage furthest from water (Tables 10 and 13).

<u>Tree, Snag, and Log Characteristics</u>

For all seral stages combined (Table 14) and for old-growth stands (Table 15), snags were significantly taller in available habitat than in red tree vole habitat. In young-growth stands, snag dbh was significantly greater in available habitat than in red tree vole habitat (Table 15). There was no significant difference between seral stages for either snag dbh or snag height in available habitat (Table 16).

For all seral stages combined (Table 14) and for old-growth stands (Table 15), there was no significant difference in maximum log diameter between available and red tree vole habitat. In mature stands, maximum log diameter was significantly greater in red tree vole habitat than in available habitat (Table 15). In young-growth stands, maximum log diameter was significantly larger in available habitat than in red

Table 12. Summary of Stepwise Discriminant Analysis Used to Differentiate Between Red Tree Vole and Available Habitat Within a Given Seral Stage of Douglas-fir Forest in Mendocino County, California. Values Represent Standardized Coefficients for Canonical Variables Included in the Discriminant Function. Absolute Magnitude of the Coefficients Indicates Relative Contribution of the Canonical Variables to the Discriminant Function. Sign of the Coefficient Indicates Direction of the Contribution. Variable Means and Standard Errors are Presented in Table 10 (* = $p < 0.05$).

	Old-Growth	Mature	Young-Growth
Variable or Character	Discriminant Function	Discriminant Function	Discriminant Function
Distance to Water	-	0.9060	-
Distance to Ravine	0.5555	-0.5758	-
Log Number	-	-0.5633	-
Stump Number	-	-	-0.9999
Slope	0.4563	-	-
Altitude	0.6238	-	-
Percent Correctly Classified	70.4%	67.9%	71.7%
Eigenvalue	0.1932	0.1711	0.0733
Canonical correlation	0.4024	0.3822	0.2614
Approximate F (degrees of freedom)	7.794 (3, 121)*	6.160 (3, 108)*	7.628 (1, 104)*

Table 13. Summary of Stepwise Discriminant Analysis Used to Differentiate Between Available Habitat in Three Seral Stages of Douglas-fir Forest in Mendocino County, California. Values Represent Standardized Coefficients for Canonical Variables Included in the Discriminant Function. Absolute Magnitude of the Coefficients Indicates Relative Contribution of the Canonical Variables to the Discriminant Function. Sign of the Coefficient Indicates Direction of the Contribution. Variable Means and Standard Errors are Presented in Table 10 (* = $p < 0.05$).

Variable or Character	Discriminant Function I	Discriminant Function II
Slope	0.1916	0.4015
Aspect	-0.3514	-0.5648
Distance to Water	-0.5090	0.40298
Distance to Ravine	-0.2020	0.2647
Basal Area	0.2841	-0.3044
Tree Number	-0.5281	-0.1691
Snag Number	0.1011	-0.4121
Log Number	-0.6127	0.1521
Percent Correctly Classified	71.5%	71.5%
Eigenvalue	1.2855	0.2305
Canonical correlation	0.74997	0.4328
Approximate F (degrees of freedom)	22.002 (16, 520)*	

Table 14. Brown-Forsythe ANOVA Tests for Snag, Log, and Tree Characteristics Between Red Tree Vole and Available Habitat Plots in All Seral Stages[a] of Douglas-fir Forest Examined in Mendocino County, California. (* = $p < 0.05$).

	Red Tree Vole Habitat			Available Habitat		
Variable	n	Mean	Standard Error	n	Mean	Standard Error
Snag Diameter (cm-class)	72	26.1	1.917	380	25.5	0.792
Snag Height (m)	72	4.9	0.369	380	6.2	0.25*
Maximum Log Diameter (cm-class)	586	30.2	0.871	2145	29.2	0.422
Log Length (m)	586	4.5	0.147	2145	4.1	0.066*
<u>Average Tree Dbh</u>:						
All Species	1547	33.0	0.704	6420	28.2	0.230*
ARME[b]	264	26.9	0.950	1481	26.8	0.381
PSME[b]	326	62.9	2.382	1087	39.7	0.934*
QUCH[b]	162	24.7	0.946	652	25.5	0.549
QUWI[b]	13	19.5	0.000	288	20.99	0.377*
SESE[b]	17	57.8	10.416	137	31.1	2.081*
UMCA[b]	31	19.5	0.000	118	22.5	0.828*
LIDE[b]	724	24.1	0.394	2582	25.7	0.246*

[a] See study area description for descriptions of the three seral stages.
[b] The following mnemonics were used for the tree species: ARME = *Arbutus menziesii*, PSME = *Pseudotsuga menziesii*, QUCH = *Quercus chrysolepis*, QUWI = *Quercus wislizenii*, SESE = *Sequoia sempervirens*, UMCA = *Umbellularia californica*, LIDE = *Lithocarpus densiflora*.

Table 15. Brown-Forsythe ANOVA Tests for Snag, Log, and Tree Characteristics Between Red Tree Vole and Available Habitat Plots Within a Given Seral Stage[a] of Douglas-fir Forest Examined in Mendocino County, California. (* = $p < 0.05$).

	Old-Growth				Mature				Young-Growth			
	Red Tree Vole		Available		Red Tree Vole		Available		Red Tree Vole		Available	
Variable	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error
Snag Diameter (cm-class)	31.4	3.989	27.9	1.782	23.8	2.233	23.5	0.943	19.5	0	27.2	1.75*
Snag Height	3.6	0.331	5.6	0.4888*	6.6	0.607	6.9	0.398	3.8	0.914	5.4	0.372
Maximum Log Diameter (cm-class)	37.1	2.020	33.2	1.161	30.2	1.680	25.9	0.653*	25.9	0.975	29.3	0.564*
Log Length (m)	5.95	0.368	5.3	0.188	3.9	0.204	4.6	0.125*	4.1	0.185	3.5	0.076*
<u>Average Tree Dbh</u>:												
All Species	36.4	1.252	33.7	0.640	35.3	1.501	27.9	0.382*	26.4	0.622	25.2	0.243
ARME[b]	29.9	1.929	31.4	1.024	23.9	1.211	26.2	0.572	27.6	1.786	24.97	0.536
FSME[b]	95.5	3.824	68.6	2.724*	73.97	4.624	38.1	1.362*	32.2	1.465	27.2	0.678*
QUCH[b]	25.1	3.675	27.5	1.351	24.9	1.234	25.3	0.729	24.2	1.501	24.2	1.011
QUWI[b]	-	-	-	-	19.5	0.000	20.998	0.378*	-	-	-	-
SESE[b]	59.1	13.251	85.1	14.598	70.6	22.293	-	-	19.5	0.000	26.4	1.191*
UMCA[b]	19.5	0.000	22.6	1.324*	19.5	0.000	23.1	1.658*	19.5	0.000	21.6	1.200
LIDE[b]	24.4	0.520	26.4	0.462*	25.4	1.291	27.1	0.605	23.1	0.652	24.8	0.327*

[a] See study area description for descriptions of the three seral stages.
[b] The following mnemonics were used for the tree species: ARME = <u>Arbutus menziesii</u>, FSME = <u>Pseudotsuga menziesii</u>, QUCH = <u>Quercus chrysolepis</u>, QUWI = <u>Quercus wislizenii</u>, SESE = <u>Sequoia sempervirens</u>, UMCA = <u>Umbellularia californica</u>, LIDE = <u>Lithocarpus densiflora</u>.

Table 16. Brown-Forsythe ANOVA Tests for Snag, Log, and Tree Characteristics in Available Habitat Between Three Seral Stages[a] of Douglas-fir Forest Examined in Mendocino County, California. ($* = p < 0.05$)

	Old-Growth			Mature			Young-Growth		
Variable	n	Mean	Standard Error	n	Mean	Standard Error	n	Mean	Standard Error
Snag Diameter (cm-class)	91	27.9	1.782	186	23.5	0.943	103	27.2	1.75
Snag Height (m)	91	5.6	0.488	186	6.9	0.398	103	5.4	0.371
Maximum Log Diameter (cm-class)	430	33.2	1.161	556	25.9	0.653	1159	29.3	0.564*
Log Length (m)	430	5.3	0.188	556	4.6	0.125	1159	3.5	0.076*
<u>Average Tree Diameter</u>:									
All Tree	1555	33.7	0.640	2179	27.9	0.382	2686	25.2	0.243*
ARME[b]	306	31.4	1.024	565	26.2	0.572	610	24.97	0.536*
PSME[b]	213	68.6	2.724	442	38.1	1.364	482	27.2	0.608*
QUCH[b]	136	27.5	1.351	360	25.3	0.729	156	24.2	1.011
QUWI[b]	0	-	-	287	20.99	0.378	1	19.5	0.000*
SESE[b]	11	85.1	14.598	0	-	-	126	26.4	1.191*
UMCA[b]	40	22.6	1.324	43	23.1	1.658	35	21.6	1.200
LIDE[b]	837	26.4	0.462	445	27.1	0.605	1300	24.8	0.327*

[a] See study area description for descriptions of the three seral stages.
[b] The following mnemonics were used for the tree species: ARME = *Arbutus menziesii*, PSME = *Pseudotsuga menziesii*, QUCH = *Quercus chrysolepis*, . QUWI = *Quercus wislizenii*, SESE = *Sequoia sempervirens*, UMCA = *Umbellularia californica*, LIDE = *Lithocarpus densiflora*.

tree vole habitat. In available habitat, maximum log diameter was significantly greater in old-growth stands than in mature or young-growth stands (Table 16).

For all seral stages combined (Table 14) and for mature and young-growth stands (Table 15), log length was significantly greater in red tree vole habitat than in available habitat. There was no significant difference in log length between red tree vole and available habitat for old-growth forests. However, for available habitat, logs were significantly longer in old-growth forests than in mature and young-growth stands (Table 26).

Average dbh of all tree species combined was significantly higher in red tree vole habitat than in available habitat for all seral stages combined (Table 14) and for mature stands (Table 15). For all seral stages combined, the average dbh of Douglas-fir and redwood was significantly higher in red tree vole habitat than in available habitat (Table 14). The average dbh of interior live oak (*Quercus wislizenii*), California bay (*Umbellularia californica*), and tanoak trees was significantly smaller in red tree vole habitat than in available habitat.

Within all three seral stages, the average dbh of Douglas-fir was significantly greater in red tree vole habitat than in available habitat (Table 15). Within old-growth stands, the average dbh of California bay and tanoak was significantly smaller in red tree vole habitat than in available habitat. Within mature stands, the average dbh of interior live oak and California bay was significantly smaller in red tree vole habitat than in available habitat. In young-growth stands, the average dbh of redwood and tanoak was significantly less in red tree vole habitat than in available habitat (Table 15).

In available habitat, the average dbh of all tree species combined and of madrone, Douglas-fir, redwood, and tanoak was significantly larger in old-growth stands than in mature or young-growth stands (Table 16). The average dbh of interior live oaks was significantly higher in mature stands than in young-growth stands for available habitat.

Shrub, Herb, and Substrate Characteristics

For all seral stages combined, there was a significantly greater percent cover of only one substrate, rock, in available habitat than in red tree vole habitat (Appendix F). Within old and young-growth stands, the percent cover of rock was also significantly greater in available habitat than in red tree vole habitat (Appendix G). The percent cover of fine litter was significantly greater in red tree vole habitat than in available habitat in old-growth stands, and significantly less in red tree vole habitat than in available habitat in mature stands.

In available habitat, the percent cover of fine litter was significantly greater in mature stands than in the other two seral stages (Table 17). The percent cover of moss was significantly greater in old-growth stands than in mature or young-growth stands. The percent cover of soil was significantly greater in young-growth stands than in mature or old-growth stands.

There was no significant difference in the percent cover of evergreen or deciduous shrubs between red tree vole and available habitat for all seral stages combined (Appendix F) and for old-growth stands (Appendix G). In mature stands, red tree vole habitat had a

Table 17. Brown-Forsythe ANOVA Tests for Average Percent Cover of Substrate, Shrubs, Herbs, and Deciduous and Evergreen Shrubs and Herbs in Available Habitat Between Three Seral Stages[a] of Douglas-fir Forest Examined in Mendocino County, California. (* = $p < 0.05$).

	Old-Growth			Mature			Young-Growth		
Variable	n	Mean	Standard Error	n	Mean	Standard Error	n	Mean	Standard Error
<u>Average Percent Cover of Substrate</u>:									
Rock	156	16.1	1.206	146	15.4	1.346	103	15.7	1.825
Soil	173	13.6	0.851	215	11.8	0.704	176	15.7	1.254*
Fine Litter	360	70.1	1.233	360	79.1	0.927	360	75.4	1.062*
Coarse Litter	182	14.7	0.908	153	14.4	1.079	253	16.2	0.871
Moss	333	24.0	1.196	302	16.4	0.969	216	14.1	0.876*
<u>Average Percent Cover of Shrubs</u>:									
All Species	904	17.1	0.608	834	10.8	0.332	780	14.1	0.503*
LIDE[b]	268	21.7	1.278	155	15.5	1.241	259	17.2	1.023*
PSME[b]	101	14.7	1.66	116	10.9	0.752	106	14.5	1.499*
QUCH[b]	115	10.7	0.694	180	9.5	0.459	100	10.5	0.540
RHDI[b]	146	20.2	1.636	96	8.1	0.125	76	11.2	0.867*
LOHI[b]	60	8.4	0.280	89	8.5	0.362	60	10.5	1.394
BENE[b]	84	12.6	0.894	1	88.0	0.000	3	8.0	0.000*
<u>Average Percent Cover of Herbs</u>:									
All Species	805	10.2	0.282	461	11.3	0.584	412	11.4	0.571
GAMU[c]	118	8.5	0.223	34	9.8	0.740	20	8.6	0.600
GRAS[c]	57	9.1	0.454	90	19.0	2.502	58	12.7	1.32*
IRSP[c]	148	11.1	0.752	46	9.0	0.504	53	8.7	0.385*
POMU[c]	71	10.6	0.823	37	9.6	0.684	18	12.7	1.419
VAPL[c]	103	8.4	0.200	34	8.4	0.353	35	9.9	1.599
<u>All Shrub Species</u>:									
Deciduous	330	14.8	0.813	262	8.6	0.337	201	11.2	0.675*
Evergreen	574	18.4	0.832	571	11.8	0.454	579	15.1	0.630*
<u>All Herb Species</u>:									
Deciduous	260	11.9	0.842	221	9.9	0.541	392	8.6	0.130*
Evergreen	356	12.1	0.602	147	8.8	0.250	96	9.1	0.359*

[a] See study area descriptions for descriptions of the three seral stages.

[b] The following mnemonics were used for the shrub species: LIDE = <u>Lithocarpus densiflora</u>, PSME = <u>Pseudotsuga menziesii</u>, QUCH = <u>Q[illegible]s chrysolepis</u>, RHDI = <u>Rhus diversiloba</u>, LOHI = <u>Lonicera hispidula</u>, BENE = <u>Berberis nervosa</u>.

[c] The following mnemonics were used for the herb species: GAMU = <u>Galium muricatum</u>, GRAS = grass (species unidentified), IRSP = <u>Iris</u> sp., POMU = <u>Polystichum munitum</u>, VAPL = <u>Vancouveria planipetala</u>.

significantly greater percent cover of evergreen shrubs than did available habitat (Appendix G). In young stands, the percent cover of both deciduous and evergreen shrubs was significantly greater in available habitat than in red tree vole habitat.

In available habitat only, old-growth stands had a significantly greater percent cover of both deciduous and evergreen shrubs than did mature or young-growth stands (Table 17). The percent cover of evergreen shrubs was significantly greater than the percent cover of deciduous shrubs for all seral stages combined and within each seral stage (Table 18).

Dwarf Oregon grape (Berberis nervosa) was the only shrub species that had a significantly greater percent cover in red tree vole habitat than in available habitat for all seral stages combined (Appendix F) and for old-growth stands (Appendix G). There was no significant difference in percent cover of any other shrub species between red tree vole habitat and available habitat for all seral stages combined (Appendix F) or for old-growth stands (Appendix G). Within mature stands, the percent cover of all shrub species combined was significantly greater in red tree vole habitat than in available habitat (Appendix G). In young-growth stands, the percent cover of all shrub species combined and the percent cover of poison oak was significantly greater in available habitat than in red tree vole habitat.

In available habitat, the percent cover of all shrub species combined and of tanoak, poison oak, and dwarf Oregon grape was significantly greater in old-growth stands than in mature or young-growth stands (Table 17). The percent cover of Douglas-fir was significantly greater in old and young-growth stands than in mature

Table 18. Brown-Forsythe ANOVA Tests Between Average Percent Cover of Deciduous and Evergreen Shrubs, and Average Percent Cover of Deciduous and Evergreen Herbs for All Three Seral Stages[a] and Within a Given Seral Stage of Douglas-fir Forest Examined in Mendocino County, California (* = $p < 0.05$).

	Deciduous			Evergreen		
Variable	n	Mean	Standard Error	n	Mean	Standard Error
<u>All Seral Stages</u>:						
Shrubs	793	11.8	0.406	1724	15.1	0.385*
Herbs	873	9.9	0.295	599	10.8	0.373
<u>Old Growth</u>:						
Shrubs	330	14.8	0.813	574	18.4	0.832*
Herbs	392	8.6	0.130	356	12.1	0.602*
<u>Mature</u>:						
Shrubs	262	8.6	0.337	571	11.8	0.454*
Herbs	221	9.9	0.541	147	8.8	0.250
<u>Young</u>:						
Shrubs	201	11.2	0.675	579	15.1	0.630*
Herbs	260	11.9	0.842	96	9.1	0.359*

[a] See study area descriptions for descriptions of the three seral stages.

stands. A complete list of tree and shrub species observed in the three seral stages is presented in Appendix H.

The percent cover of deciduous herbs was significantly higher in red tree vole habitat than in available habitat for all seral stages combined (Appendix F) and for young-growth stands (Appendix G). There was no significant difference in the percent cover of evergreen herbs between red tree vole and available habitat for all seral stages combined (Appendix F) or within any given seral stage (Appendix G).

In available habitat, the percent cover of both evergreen and deciduous herbs was significantly greater in old-growth stands than in mature or young-growth stands (Table 17). There was no significant difference between the percent cover of deciduous herbs and the percent cover of evergreen herbs for all seral stages combined and for mature stands (Table 18). In old-growth stands, the percent cover of evergreen herbs was significantly greater than that of deciduous herbs. However, in young-growth stands, the percent cover of deciduous herbs was significantly greater than that of evergreen herbs.

For all seral stages combined, the percent cover of all herbaceous species combined was significantly greater in available habitat than in red tree vole habitat (Appendix F). However, the percent cover of bedstraw (*Galium muricatum*) was significantly greater in red tree vole habitat than in available habitat. In old-growth stands, the percent cover of grass (species unidentified) and of iris (*Iris* sp.) was significantly greater in red tree vole habitat than in available habitat (Appendix G). There was no significant difference in the percent cover of any herb species between red tree vole and available habitat in mature stands. In young-growth stands, the percent cover of all herb species combined and of grass and sword fern (Polystichum munitum) was significantly greater in available habitat than in red tree vole habitat.

For available habitat only, the percent cover of grass was significantly greater in mature stands than in old or young-growth stands (Table 17). The percent cover of iris was significantly greater in old-growth than in mature or young-growth stands. A complete list of herbaceous species observed in the three seral stages is presented in Appendix I.

DISCUSSION

The abundance of red tree vole nests observed in this study was greatest in old-growth stands of Douglas-fir forest, thus, apparently leading to the conclusion that old-growth Douglas-fir forests provide more suitable habitat for red tree voles than do mature or young-growth forests. An important aspect of the mesic old-growth forest canopy is that it serves as a climatic buffer, providing a microclimate with high humidity, low windspeed, reduced daily maximum temperature, and reduced daily temperature range within the forest (Lang 1980; and Franklin, et, al., 1981). Cool air drainage, high transpiration by deciduous vegetation, and low evaporative demand in shaded ravines also contribute to the maintenance of moist, cool riparian microclimates (Lang 1980).

A moist microclimate, eg, old growth canopy ("fog drip"), may be an important factor influencing habitat utilization by the red tree vole. Hamilton (1962) indicated that the humid coastal fog belt was critical to fulfilling the water requirements of the red tree vole both by providing water to be licked from the needles and by maintaining fresh foliage for consumption. Under captive conditions, red tree voles suffered weight loss and mortality if the food supply (Douglas-fir needles) was not kept sufficiently moist, whereas captive red tree vole survival was good if the Douglas-fir needles were moistened frequently (Bensen and Borell, 1931; and Hamilton, 1962).

In this study, conditions providing sufficient moisture to meet the requirements of the red tree vole were found primarily in the two stands in closest proximity to the Eel River (Alpine and White House), and were reflected by the fact that more than half (57%) of the total number of red tree vole nests observed in this study were found in these two stands. Of the nine study stands, only Alpine and White House were directly exposed to the early morning and evening fogs following the course of the Eel River during the summer months (pers. obs.), which would result in a microclimate with increased humidity (Lang, 1980). In mature Douglas-fir stands, proximity to water was the most important variable distinguishing red tree vole habitat from available habitat, a factor again reflecting a microclimate with increased humidity.

Microhabitat Use

Red Tree Vole Nest Characteristics

All 79 red tree vole nests observed in this study were located exclusively in Douglas-fir trees. When evaluating the results of this study with respect to habitat management for red tree voles, the fact that red tree vole nests have been observed in other conifers (eg. grand fir (*Abies grandis*) or Sitka spruce (*Picea sitchensis*) in more northern portions of their range should be considered (Anderson, 1981; Benson and Borell, 1931; Maser, 1966; and Vrieze, 1980). However, these conifer species were not present in the Douglas-fir forests examined in this study (pers. obs.). According to Johnson (1980), usage can be considered selective if components are used disproportionately to their availability. Thus, in this study, red tree voles can be considered to have been selective in their choice of nest trees, using Douglas-firs in much greater proportion than the availability of this species in the study area. The significantly greater use of Douglas-fir trees as nest sites can be attributed to the restricted diet of the red tree vole. As discussed previously, Douglas-fir needles comprise the principle component of the diet of this species (Howell, 1926; and Benson and Borell, 1931).

Red tree vole nests observed in this study were characterized by accumulations of resin ducts and red tree vole feces. The skeletal structure of the nests was composed primarily of small twigs. The majority (91%) of red tree vole nests were located adjacent to the trunk of the nest tree, at the fork of two or more branches. The nests observed in this study were similar to those that have been described in detail by Howell (1926), Maser (1966), and Zentner (1977). In this study, nests constructed solely by red tree voles were observed, as well as those constructed by other species but inhabited by red tree voles (as indicated by the presence of Douglas-fir bark trimmings, moss, or long black and white animal hair, along with the presence of resin ducts). One red tree vole nest was found in a mud constructed, abandoned bird's nest. Red tree vole nests containing mud balls also were observed by Benson and Borell (1931), who suggested that these were built on top of old robins' nests.

Maser (1966) has observed terrestrial red tree vole nests and red tree voles have been captured in pit-fall traps (Corn and Bury, 1984). Although no terrestrial red tree vole nests were found during the course of this study, terrestrial activity by this species was indicated on the Coast Range Preserve by the capture of red tree voles in pit-fall traps set out as part of the Old-Growth Wildlife Habitat Program (C. Barrows, pers. comm.).

Between seral stages, red tree vole nests were constructed from materials availabile in the Douglas-fir stand. For example, redwood bark shavings and lichen (Alectoria sarmentosa) were common components of nests in Alpine, an old-growth stand, but were rarely observed in red tree vole nests in the other stands examined throughout the course of this study. Lichen hanging from Douglas-fir branches and redwoods were both prevalent throughout Alpine, but less available in the other eight stands. Douglas-fir bark shavings, Douglas-fir trimmings, and green needles characterized both red tree vole and non-red tree vole nests in young-growth stands, indicating that red tree voles in young-growth stands may have been inhabiting nests originally constructed by other species such as Northern flying squirrels or Western grey squirrels. Howell (1926), Maser (1966), and Zenter (1977) also observed red tree voles inhabiting nests constructed by other species.

Red tree vole nests in old-growth stands were located higher in a tree than those in mature or young-growth stands. This can be attributed to the height of the Douglas-firs available within a given stand. Both the bole height and the total tree height of the available trees were taller in old-growth stands than in mature or young-growth stands. Vrieze (1980) found that red tree vole nest height was correlated with bole height and that the differences in nest height between study areas was due to differences in bole height of the nest trees on his study areas.

In this study, the average red tree vole nest height was approximately 4.0 m above the bole height in all three seral stages. Vrieze (1980) observed that red tree vole nests tended to be in the lower portion of the crown, averaging 3.7 m above the lowest living branch. Vrieze (1980) attributed red tree vole nest location to the abundance of protective cover and the maximization of horizontal foraging capacity.

Red tree vole nests observed in this study were located, on average, on the south side of the tree for each seral stage (Table 5). Orientation of the nest on the south side of the tree would facilitate warming and heat retention of the nest during inclement weather, as well as drying the nest after heavy winter rains. Zentner (1977) has shown that the red tree vole nest provides effective insulation from adverse weather conditions. By comparing the rate of heat loss in the nest chamber to the rate at the outer surface of the nest, Zentner (1977) observed that small red tree vole nests were capable of reducing the rate of heat loss by 62% while medium and large red tree vole nests reduced the rate of heat loss by as much as 87%.

Red Tree Vole Nest Tree Characteristics

In this study, red tree vole nest trees were significantly taller and had a larger diameter than expected on the basis of availability. Selection of large, old-growth trees potentially maximized food availability for the red tree vole, since the food resource (Douglas-fir needles) is concentrated on fewer individuals than in young-growth stands (Franklin, et. al. 1981). Such a situation would be advantageous to the red tree vole, due to its restricted diet and specialized, arboreal lifestyle.

Red tree vole nest trees were characterized by having a greater frequency of conks, dead tops, and fire and damage scars than available trees (Appendix C). These characteristics are representative of older trees, thus reinforcing the selection of large, older trees as nest sites by red tree voles. However, within old-growth stands, available trees also were characterized by the presence of fire scars, conks, and cavities. Thus, the condition of the nest trees in old-growth stands is probably reflective of the condition of the available trees, particularly the Douglas-firs, rather than any selectivity for this type of tree by red tree voles within this seral stage .

Available trees had a greater frequency of moss covering their trunks than did red tree vole nest trees. The lack of moss on nest trees can be attributed to the fact that all the nest trees were Douglas-firs, a species which rarely has moss growing on its trunk. However, the majority of available trees were tanoaks, which commonly (> 75%) have moss (particularly Dendroalsia abientina) growing profusely on their trunks (pers. obs.).

Red tree vole nest trees also were nearer to other nest trees than were potentially available but unused trees. Zentner (1977) and Benson and Borell (1931) have suggested that red tree voles may be found in "colonies". However, Vrieze (1980) conducted a nearest neighbor analysis and found that the dispersion of red tree vole nests was not significantly different from a random pattern. In this study, red tree vole nests were not colonial in the strict sense of the word. Although nests were observed in the same general area of the forest, they were not closely grouped. Much of the "grouping" observed in this study can be attributed to higher densities of nests in preferred habitat. The majority of nests were located in the two stands adjacent to the Eel River which had moister, cooler microclimates that the more non-riparian stands, as discussed previously.

Habitat Characteristics

Habitat characteristics found to be important in use of an area by red tree voles in this study included low altitude, high percent canopy cover, high stump density, low snag density, shorter snags, and larger diameter logs and trees. Red tree vole habitat also was characterized vegetatively by large Douglas-fir and redwood trees, the presence of dwarf Oregon grape (*Berberis nervosa*) and *Galium muricatum*, lower average percent cover of herbaceous species, particularly deciduous herbs, and lower average percent cover of rock.

The microhabitat available to red tree voles differed between seral stages. Variability between stand age in such factors as percent canopy cover can all be attributed to the successional stage of the forests. For example, available habitat in old-growth stands was characterized by fewer but larger trees, logs, snags, and stumps, and a higher percent shrub cover than in mature or young-growth stands. All of these are features expected in old-growth stands (Franklin, et. al., 1981). Stand location can account for variability in such factors as slope, aspect, or altitude. Ideally, in a habitat comparison study such as this one, stand locations would be standardized as much as possible. However, when comparing forests of different ages, in which a stand age is determined by its logging or fire history, a variety of locations for different stand ages cannot be avoided (eg: old-growth stands would probably be in the least accessible areas). Thus, environmental features such as slope or altitude should be considered descriptive characteristics rather than used to discriminate available habitat in one seral stage from that in another seral stage.

However, within a given seral stage, such features may aid in determining if red tree vole habitat use was in proportion to the available habitat. In old-growth stands, red tree vole nests were located in areas close to ravines, shallow slope, and low in altitude. Red tree vole habitat in old-growth stands was characterized vegetatively by the presence of grass and iris, and by fine litter as the primary substrate cover. In mature stands, red tree vole habitat was closer to water, further from ravines, and had more logs than did available habitat. Red tree vole habitat in mature stands could also be distinguished from available habitat on the basis of higher percent shrub cover and lower percent cover of fine litter. In young stands, red tree vole habitat was characterized by high stump density and low percent herb and shrub cover.

Recommendations for Red Tree Vole Habitat Management

Management of Douglas-fir forests in Northern California for red tree vole habitat should include consideration of a given forest's location and its successional stage. On the basis of this study, older Douglas-fir forests in mesic locations or micro-climates, such as riparian or ravine sites, appear to provide the most suitable habitat for red tree voles. Older forests probably provide red tree voles with a more suitable microclimate than younger Douglas-fir forests due to the climatic buffering capabilities of older forests.

Within a given seral stage, factors such as location with respect to ravines, and shrub and herb cover should also be considered when evaluating Douglas-fir forests for suitability as red tree vole habitat. It is recommended that management of red tree vole habitat in Northern California should entail the maintenance of Douglas-fir forests in mesic, cool locations or microclimates not only to ensure that the moisture requirements of this species are satisfied, but also to provide suitable microhabitat for inhabitation by red tree voles.

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APPENDIX A. Number of Red Tree Vole Nests Observed in Old-Growth, Mature, and Young-Growth Stands[a] of Douglas-fir Forest in Mendocino County, California.

Seral Stage Stand[b]	# Red Tree Vole Nests
Old-Growth	
Alpine	29
Elder Creek	4
Ten Mile	6
Total Old-Growth:	39
Mature	
Fanny's Place	2
Harwood's Ninety	4
White House	16
Total Mature:	22
Young-Growth	
Barnes'	2
Homestead	10
Mud Springs	6
Total Young-Growth:	18

[a] See Figure 1 for stand locations.
[b] See study area descriptions for descriptions of individual stands.

APPENDIX K. Observed Frequencies of Variables Used to Characterize Nest Samples Collected While Examininig a Nest for Evidence of Inhabitation by Red Tree Voles.

Variable	Red Tree Vole Nests[a]				Non-Red Tree Vole Nests			
	Old-Growth[b] (n = 35)	Mature[b] (n = 22)	Young-Growth[b] (n = 18)	Total (n = 75)	Old-Growth[b] (n = 19)	Mature[b] (n = 29)	Young-Growth[b] (n = 21)	Total (n = 69)
Feces	20	13	11	44	7	4	0	11
Redwood bark shavings	15	1	2	18	6	6	1	13
Douglas-fir bark shavings	3	3	8	14	1	10	14	25
Lichen	19	6	2	27	14	15	6	35
Moss	14	7	3	24	11	18	10	39
Green Douglas-fir needles	7	7	13	27	5	12	17	34
Brown Douglas-fir needles	22	12	6	40	14	21	11	46
Douglas-fir trimmings	8	5	10	23	3	4	10	17
Douglas-fir twigs	19	9	5	33	10	21	6	37
Leaves	4	1	2	7	2	1	2	5
Douglas-fir cone scales	4	0	0	4	3	2	3	8
Animal hair	8	1	1	10	6	13	11	30

[a] Four nest samples contained only resin ducts, and thus were not included in this part of the analysis.
[b] See study area descriptions for descriptions of seral stages.

Appendix C. Observed Frequencies of Variables Characterizing Red Tree Vole Nests Trees and Available Test Trees in Three Seral Stages[a] of Douglas-fir Forest Examined in Mendocino County, California.

	Red Tree Vole Nests Trees				Available Test Trees			
Variable	Old-Growth (n = 39)	Mature (n = 22)	Young-Growth (n = 18)	Total (n = 79)	Old-Growth (n = 450)	Mature (n = 450)	Young-Growth (n = 450)	Total (n = 1350)
Tree Species (Douglas-fir only)	39	22	18	79	76	131	81	288
Lightning	0	0	0	1	0	2	1	3
Fire Scar	38	12	0	50	171	40	19	230
Ladder	2	8	7	17	38	117	193	348
Conk	12	4	0	16	19	3	0	22
Dead Top	1	2	4	7	0	10	7	17
Cavity Number[b]	5	1	1	7	144	68	90	302
Damage Scar[c]	-	9	8	17	-	64	84	148

[a] See study area description for descriptions of the three seral stages.
[b] The sample size for cavity number for available test trees in young-growth stands was 449.
[c] Sample size for damage scar were: Mature - red tree vole nest trees: n = 17; available test trees: n = 275. Young - red tree vole nest trees: n = 16; available test trees: n = 300.

Appendix D. Product Moment Correlations of the Six Nest/Test Tree Variables Used in the Stepwise Discriminant Analysis.

Variable	Tree Diameter	Tree Height	Bole Height	Distance to Nearest Tree	Distance to Nest Tree	Distance to Redwo
Tree Diameter	-					
Tree Height	0.871	-				
Bole Height	0.611	0.717	-			
Distance to Nearest Tree	0.223	0.203	0.066	-		
Distance to Nest Tree	-0.249	-0.219	-0.219	-0.109	-	
Distance to Redwood	-0.073	-0.011	0.015	0.073	0.077	-

Appendix L. Product Moment Correlations of the Eleven Habitat Variables Used in the Stepwise Discriminant Analysis.

Variable	Slope	Aspect	Altitude	Distance to Water	Distance to Ravine	Basal Area	Average Canopy Cover	Tree Number	Snag Number	Log Number	S[illegible]p Number
Slope	–										
Aspect	-0.043	–									
Altitude	-0.2698	0.069	–								
Distance to Water	-0.202	0.075	0.702	–							
Distance to Ravine	0.035	-0.045	0.137	0.095	–						
Basal Area	0.032	-0.062	-0.129	-0.147	0.061	–					
Average Canopy Cover	0.061	0.127	-0.0395	-0.018	0.038	0.244	–				
Tree Number	-0.132	0.045	0.273	0.2996	0.237	0.261	0.276	–			
Snag Number	0.006	0.065	-0.066	-0.078	0.0598	0.243	0.095	0.186	–		
Log Number	-0.298	0.1499	0.297	0.257	-0.022	-0.142	-0.057	0.035	-0.011		
Stump Number	-0.159	0.102	0.365	0.335	0.159	0.017	-0.085	0.239	0.129	0.324	–

APPENDIX F. Brown-Forsythe ANOVA Tests for Average Percent Cover of Substrate, Shrubs, Herbs, and Deciduous and Evergreen Shrubs and Herbs in Red Tree Vole and Available Habitat Plots in All Three Seral Stages[a] of Douglas-fir Forest Examined in Mendocino County, California. Variables Are Defined in Table 2. (* = $p < 0.05$)

	Red Tree Vole Habitat			Available Habitat		
Variable	n	Mean	Standard Error	n	Mean	Standard Error
Substrate Average Percent Cover:						
Rock	88	12.2	1.02	405	15.7	0.815*
Soil	140	14.4	1.250	564	13.6	0.545
Fine Litter	292	75.2	1.177	1080	74.9	0.634
Coarse Litter	162	15.6	1.034	588	15.2	0.546
Moss	232	18.6	1.212	851	18.8	0.638
Average Percent Cover of Shrubs:						
All Species	646	14.8	0.606	2518	14.1	0.294
LIDE[b]	205	18.6	1.267	682	18.6	0.701
PSME[b]	55	11.3	1.778	323	13.2	0.769
QUCH[b]	87	10.9	0.834	395	10.1	0.322
RHDI[b]	80	13.6	1.415	318	14.4	0.836
LOHI[b]	61	8.2	0.197	209	9.0	0.439
BENE[b]	56	20.4	2.357	88	13.3	1.213*
Average Percent Cover of Herbs:						
All Species	559	9.9	0.294	1678	10.8	0.253*
GAMU[c]	65	10.8	0.812	172	8.8	0.225*
GRAS[c]	58	13.3	1.864	205	14.4	1.201
IRSP[c]	82	9.2	0.396	247	10.2	0.472
POMU[c]	41	12.7	1.622	126	10.6	0.547
VAPL[c]	47	8.0	0.000	172	8.7	0.353
All Shrub Species:						
Deciduous	236	13.0	0.806	793	11.8	0.406
Evergreen	410	15.9	0.832	1724	15.1	0.385
All Herb Species:						
Deciduous	301	9.0	0.223	873	9.9	0.295*
Evergreen	200	10.2	0.503	599	10.8	0.373

[a] See study area descriptions for descriptions of the three seral stages.

[b] The following mnemonics were used for the shrub species: LIDE = *Lithocarpus densiflora*, PSME = *Pseudotsuga menziesii*, QUCH = *Quercus chrysolepis*, RHDI = *Rhus diversiloba*, LOHI = *Lonicera hispidula*, BENE = *Berberis nervosa*.

[c] The following mnemonics were used for the herb species: GAMU = *Galium muricatum*, GRAS = grass (species unidentified), IRSP = *Iris* sp., POMU = *Polystichum munitum*, VAPL = *Vancouveria planipetala*.

APPENDIX G. Brown-Forsythe ANOVA Tests for Average Percent Cover of Substrate, Shrubs, Herbs, and Deciduous and Evergreen Shrubs and Herbs in Red Tree Vole and Available Habitat Plots Within a Given Seral Stage[a] of Douglas-fir Forest Examined in Mendocino County, California. (* = $p < 0.05$).

	Old-Growth				Mature				Young-Growth			
	Red Tree Vole		Available		Red Tree Vole		Available		Red Tree Vole		Available	
Variable	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error
<u>Substrate Average Percent Cover</u>:												
Rock	11.2	1.108	16.1	1.206*	16.5	2.575	15.4	1.346	8.5	0.522	15.7	1.825*
Soil	11.7	1.095	13.6	0.851	12.6	1.363	11.8	0.704	20.5	3.884	15.7	1.254
Fine Litter	76.2	1.599	70.1	1.233*	73.5	2.203	79.1	0.927*	75.5	2.749	75.4	1.062
Course Litter	16.2	1.697	14.7	0.908	14.0	1.594	14.4	1.079	16.6	2.196	16.2	0.871
Moss	19.98	1.848	24.0	1.196	18.8	1.882	16.5	0.969	13.8	2.695	14.	0.876
<u>Average Percent Cover of Shrubs</u>:												
All Species	17.9	1.061	17.1	0.608	12.7	0.874	10.8	0.332*	11.2	0.660	14.1	0.503*
LIDE[b]	19.9	1.866	21.7	1.278	19.2	3.029	15.5	1.241	14.6	1.331	17.2	1.023
PSME[b]	10.6	2.147	14.7	1.661	12.7	3.66	10.9	0.752	9.7	1.714	14.5	1.499
QUCH[b]	11.1	3.056	10.7	0.694	11.3	0.824	9.5	0.459	9.0	1.000	10.5	0.540
RHDI[b]	16.0	2.063	20.2	1.636	12.8	2.745	8.1	0.125	8.0	0.000	11.2	0.867*
LOHI[b]	8.0	0.000	8.4	0.280	8.0	0.000	8.5	0.362	8.8	0.800	10.5	1.394
BENE[b]	20.4	2.357	12.6	0.894*	–	–	–	–	–	–	–	–
<u>Average Percent Cover of Herbs</u>:												
All Species	9.5	0.372	10.2	0.282	10.7	0.557	11.3	0.584	8.6	0.346	11.4	0.571*
GAMU[c]	10.2	1.018	8.5	0.223	11.6	1.357	9.8	0.740	8.0	0.000	8.6	0.600
GRAS[c]	8.0	0.000	9.1	0.454*	17.1	3.033	19.0	2.502	8.0	0.000	12.7	1.320*
IRSP[c]	8.8	0.424	11.1	0.752*	10.4	1.101	9.0	0.504	8.9	0.857	8.7	0.385
POMU[c]	14.3	2.613	10.6	0.823	11.2	1.933	9.6	0.684	8.0	0.000	12.7	1.419*
VAPL[c]	8.0	0.000	8.4	0.200	8.0	0.000	8.4	0.353	8.0	0.000	9.9	1.599
<u>All Shrub Species</u>:												
Deciduous	17.1	1.442	14.8	0.813	9.8	0.911	8.6	0.337	8.4	0.364	11.2	0.675*
Evergreen	18.3	1.458	18.4	0.832	14.5	1.288	11.8	0.454*	12.5	0.892	15.1	0.630*
<u>All Herb Species</u>:												
Deciduous	8.7	0.301	8.6	0.130	9.3	0.360	9.9	0.541	9.0	0.692	11.9	0.842*
Evergreen	10.5	0.751	12.1	0.602	10.1	0.750	8.8	0.250	8.5	0.500	9.1	0.359

[a] See study area descriptions for descriptions of the three seral stages.

[b] The following mnemonics were used for the shrub species: LIDE = <u>Lithocarpus densiflora</u>, PSME = <u>Pseudotsuga menziesii</u>, QUCH = <u>Quercus chrysolepis</u>, RHDI = <u>Rhus diversiloba</u>, LOHI = <u>Lonicera hispidula</u>, BENE = <u>Berberis nervosa</u>.

[c] The following mnemonics were used for the herb species: GAMU = <u>Galium muricatum</u>, GRAS = grass (species unidentified), IRSP = <u>Iris</u> sp., POMU = <u>Polystichum munitum</u>, VAPL = <u>Vancouveria planipetala</u>.

APPENDIX H. Tree and Shrub Species Observed in 73 0.04 ha Red Tree Vole Plots and 270 0.04 ha Randomly Chosen Available Plots in Three Seral Stages of Douglas-fir Forest in Mendocino County, California.

	Seral Stage		
Species	Old-Growth	Mature	Young-Growth
Acer macrophyllum	x	x	x
Alnus sp.	x		x
Arctostaphylos canescens			x
Arctostaphylos columbiana			x
Arctostaphylos manzanita		x	x
Arbutus menziesii	x	x	x
Baccharis pilularis			x
Berberis nervosa	x	x	x
Castanopsis chrysophylla	x	x	x
Ceanothus incanus		x	x
Ceanothus velutinus			x
Cornus nuttalli	x	x	x
Corylus cornuta	x	x	x
Gaultheria shallon	x		x
Heteromeles arbutifolia			x
Holodiscus discolor	x	x	
Lithocarpus densiflora	x	x	x
Lonicera hispidula	x	x	x
Pseudotsuga menziesii	x	x	x
Quercus chrysolepis	x	x	x
Quercus garryana		x	
Quercus kelloggii		x	
Quercus wislizenii	x	x	x
Rhamnus californica		x	x
Rhus diversiloba	x	x	x
Ribes sp.	x	x	x
Rosa gymnocarpa	x	x	x
Rubus leucodermis		x	x
Rubus parviflorus		x	
Sequoia sempervirens	x	x	x
Taxus brevifolia	x		x
Umbellularia californica	x	x	x
Vaccinium ovatum	x	x	x

APPENDIX I. Herbaceous Species Observed in 1372 4-m^2 Subplots[a] in Three Seral Stages of Douglas-fir Forest in Mendocino County, California.

Species	Seral Stage		
	Old-Growth	Mature	Young-Growth
Achlys tryphylla	x		x
Adenocaulon bicolor	x	x	
Apocynum androsaemifolium	x	x	x
Campanula prenanthoides		x	x
Carex sp.		x	
Chimaphila menziesii	x	x	x
Chimaphila umbellata	x		x
Corallorhiza maculata		x	
Dryopteris arguta	x	x	x
Fragaria californica		x	x
Galium californicum	x	x	x
Galium muricatum	x	x	x
Galium triflorum	x	x	x
Goodyera oblongifolia	x	x	
Grass (sp. unidentified)	x	x	x
Heuchera micrantha	x	x	x
Hieracium albiflorum	x	x	x
Iris sp.	x	x	x
Lathyrus sp. or *Vicia* sp.		x	x
Lilium rubescens	x		
Lotus humistratus			x
Madia madioides	x	x	x
Osmorhiza chilensis		x	x
Oxalis oregana	x	x	
Pedicularis densiflora			x
Pityrogramma triangularis		x	x
Polygala californica	x	x	x
Polystichum munitum	x	x	x
Pteridium aquilinum	x	x	x
Pyrola picta	x	x	x
Smilacina racemosa	x	x	x
Stachys rigida		x	x
Trientalis latifolia	x	x	x
Trillium ovatum			x
Vancouveria planipetala	x	x	x
Viola glabella	x	x	x
Viola sempervirens	x		x
Whipplea modesta	x	x	x
Woodwardia fimbriata	x		
Xerophyllum tenax	x	x	x

[a] One subplot was placed 5-m from plot center along each of the four primary compass directions in each of the 73 0.04 ha red tree vole habitat plots and each of the randomly chosen available habitat plots.