AN ABSTRACT OF THE THESIS OF

James Kerr Swingle for the degree of Master of Science in Wildlife Science presented on November 29, 2005.
Title: Daily Activity Patterns, Survival, and Movements of Red Tree Voles (*Arborimus longicaudus*) in Western Oregon.

Abstract approved: Redacted for privacy

Eric D. Forsman

We radiocollared a sample of 61 red tree voles in Douglas County, Oregon and monitored their movements to determine daily, seasonal, and sexual differences in behavior and home range attributes. We also collected information on nest attributes, survival, and dispersal of the radiocollared voles. Individual voles were monitored for periods ranging from 8–307 days ($\bar{X} \pm SE = 75.4 \pm 8.2$). Of the 52 voles used in the analysis of home range size, 20 (6 males, 14 females) occupied a single nest and adjacent foraging trees that had interconnecting branch pathways with the nest tree. The other 32 voles (16 males, 16 females) occupied ranges that included 2–6 nest trees that were spaced 4–131 m apart and 7 of these voles (6 males, 1 female) frequently moved between nest trees throughout the sampling period. Estimates of mean home range size were 1,378 ± 333 m^2 for the 100% Minimum Convex Polygon method and 1,599 ± 327 m^2 for a new method that we referred to as the Crown Area Polygon. Little of the variation in home range size was explained by the sex or age of voles or by forest age. Two

radiocollared juveniles that dispersed from their natal nests moved straight-line distances of 50 and 75 m, respectively, before settling in new nests.

Voles were most active 2–4 hrs after sunset with decreasing levels of activity throughout the night. During the day, voles were usually located in the relative security of their nests. Compared to males, females occupied larger and fewer nests and made fewer movements between nest trees. We did not detect use of ground nests by the radiocollared voles, although we did infrequently confirm that voles traveled on the ground to move between nests trees without interconnecting branch pathways.

Annual survivorship was low ($\bar{X}$ = 0.13, 95% *CI* = 0.06–0.20) and did not differ between sex or age classes. Most mortality was due to predation with 15 of 25 confirmed cases attributed to weasels (*Mustela* spp.). Weasels preyed upon significantly more females than males (12:3, respectively).

Comparisons of nests located by visual searches from the ground versus nests located by following radiocollared voles indicated that many active nests could not be seen from the ground, and that nests located by visual searches were biased towards large nests. This may explain why most historic collections of tree voles captured by naturalists who visually searched for nests were biased towards females, which tend to occupy larger nests than males. Our data also suggested that the strong male bias in samples from pitfall traps could be due to more frequent movements of males between nest trees. Our results also indicated that a management approach based only on the protection of active nests detected during ground-based surveys will result in destruction of large numbers of nests not detectable from the ground. Our results also indicated that, in some areas, there are relatively high densities of tree voles in young forests. In areas where old forests have been largely eliminated, young forests may play a critical role in the persistence of tree voles. Thus, we think there is much to learn about the relative suitability of young and old forests as habitat for tree voles.

Daily Activity Patterns, Survival, and Movements of Red Tree Voles (*Arborimus longicaudus*) in Western Oregon

by

James Kerr Swingle

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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James Kerr Swingle, Author

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History (USNM); John Rozdilsky and Jeff Bradley at the Thomas Burke Memorial Washington State Museum, University of Washington (UWBM); and Paula Holahan at the University of Wisconsin Zoology Museum (UWZM).

At the Roseburg BLM office, I was fortunate to have Joe Lint as an office mate. He was a mentor and a friend, and helped me to understand the complex interplay between science and management. Tom Snetsinger, Pete Loschl, and Chris McCafferty listened and offered helpful insights during the analysis of the data. Peggy Kavanagh was a voice of reason throughout the journey, especially when she reviewed the manuscript. I thank Jason Mowdy, Nicole Magguli and Heather Wise for volunteering to help with the field work. Janice Reid at the FS Pacific Northwest Research Station Field Office in Roseburg gave me invaluable guidance and insight in all aspects of the project. She was so enthusiastic that she even volunteered in her free time to help track voles. I also became quite fond of her dog "Kosmos", despite his tendency to swill my tequila and get a little too closely involved with the field work.

The field work was an epic 7-day-a-week 15-month adventure. I could not have pulled it off without some incredibly dedicated and capable field assistants. Megann Aitken-Voth, Scott Graham and Amy Price helped me get the project going during the early months when we were all learning on the job. Then Nicholas Hatch and Michael McDonald joined the crew, and really put the "epic" in the adventure. They lived on a diet of tortillas, day-old bagels, and Nutella and seemed to be able to work 24 hours a day. It was common for them to work all night and then sleep in the van beside the road so they could be there to help with tree climbing on the following day. They also did the majority of the tedious continuous monitoring sessions. Working with these young, enthusiastic, tree climbing biologists was one of the most enjoyable and rewarding things I have ever done. They are the reason that I wrote this thesis using "we" instead of "I".

I was recently described by a friend as a hyperactive 6-year-old after telling her of spending the day "voling" and tree climbing with Eric Forsman. Since she also knows "Doc", I asked her how old she thought he was if I was only 6. She replied that Doc was much more mature than I and that he was at least an 8-year-old. I want to thank that 8-year-old for the opportunity to work on a difficult but interesting study subject and for showing me how to be a modern day scientist with deep roots that reach back to the old time naturalists who were intrigued by tree voles: Aurelius Todd, Vernon Bailey, Alex Walker, Stanley Jewett, Walter Taylor, Alfred Shelton, Joseph Mailliard, Seth Benson, A. Brazier Howell, Percy Clifton, William Hamilton III, Don Roberts, Murray Johnson, Chris Maser, Wayne Hammer and Doug Bake.

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DEDICATION

This is dedicated to the memory of Kay Dee Campbell for her energy and passion for life, especially when things were not quite right in her world. And to my mother who taught me to be independent, the gift of sharing, and reverence of life.

"Nature first, then theory. Or, better, Nature and theory closely intertwined while you throw all your intellectual capital at the subject. Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow. If they don't, the love and pleasure will have been enough."

E. O. Wilson, Naturalist 1994

DAILY ACTIVITY PATTERNS, SURVIVAL, AND MOVEMENTS OF RED TREE VOLES (*ARBORIMUS LONGICAUDUS*) IN WESTERN OREGON.

INTRODUCTION

Red tree voles (*Arborimus longicaudus*) are small nocturnal mammals that are endemic to the coniferous forests of western Oregon and the coastal region of northern California (Taylor 1915; Benson and Borell 1931). They are among the most unique and highly specialized microtine rodents in the world in that they live in the forest canopy and feed primarily on the needles and twigs of coniferous trees. In most of their range they occur primarily in forests of Douglas-fir (*Pseudotsuga menziesii*) but they also live in forests of Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and grand fir (*Abies grandis*—True 1890; Taylor 1915; Walker 1928; Benson and Borell 1931). The diet of the tree vole is probably less varied than any other North American mammal (Hamilton 1962), and individual voles seem to develop a preference for feeding on the needles of the species on which they are raised (Walker 1930). When foraging, they chew off cuttings of fresh growth from the tip of a branch and carry them back to the nest where they stockpile the cuttings on top of the nest or pull them inside the tunnels of the nest (Taylor 1915). Occupied or recently occupied nests can usually be identified by the presence of fresh cuttings piled on top of the nest and green resin ducts and green fecal pellets inside the nest (Howell 1926).

When eating Douglas-fir needles, tree voles have highly specialized feeding behavior (Benson and Borell 1931). They clip off 1 needle at a time and remove the filamentous resin ducts along the edges of the needle before eating the central portion or "midrib" of the needle. The resin ducts are filled with terpenes and other volatile compounds, and apparently are less palatable than the midrib (Cates 1989). Removal of the resin ducts is done in a rapid, mechanical manner. The vole holds the needle in its front feet and passes the needle through its mouth like an ear of corn, rapidly nibbling off the outside edge of the needle with the incisors (Howell 1926; Clifton 1960). Then, the vole quickly flips the needle end-for-end and rolls it over before repeating the process on the opposite side of the needle. The resin ducts are discarded and the vole rapidly eats the midrib "...as one would eat a stalk of celery" (Benson and Borell 1931:229). The process of clipping off a needle, removing the resin ducts, and eating the rest of the needle takes about 10 seconds (Clifton 1960). Based on a study of captive voles, Clifton (1960) estimated that voles ate 50–75% of their body mass of Douglas-fir needles per day.

Tree vole nests are constructed of resin ducts, needles, and small twigs that remain from their meals (Todd 1891; Clifton 1960; Maser 1966; Gillesberg and Carey 1991; Meiselman and Doyle 1996). Variable amounts of lichen are sometimes found in the nests as well (Taylor 1915; Gillesberg and Carey 1991). Sleeping chambers are lined with green resin ducts and fecal chambers are filled with fecal pellets (Taylor 1915; Brown 1964). Old nests often include considerable amounts of fecal pellets and soil-like material that is the product of decaying feces and vegetation that accumulates over multiple generations (Taylor 1915; Maser 1966). Nests range in size from very small ephemeral structures about the size of a grapefruit, to large old maternal nests that may be nearly as large as a bushel basket and completely encircle the trunk of the tree (Taylor 1915; Howell 1926; Verts and Carraway 1998). Some authors (Taylor 1915; Clifton 1960; Maser 1966) have stated that females tend to build larger nests than males. Nests are often placed on a branch whorl against a tree trunk, but in old trees with large limbs, many nests are built out on limbs some distance from the trunk (Taylor 1915; Howell 1926; Benson and Borell 1931). A few ground nests (Howell 1926; Maser et al. 1989; Thompson and Diller 2002) and nests in tree cavities have also been observed (Walker 1928; Maser 1966; Gillesberg and Carey 1991; M. L. Johnson field notes on file at University of Washington Burke Museum, UWBM), but little is known about the relative frequency of these types of nest.

There are 2 species of tree voles. The red tree vole (*A. longicaudus*) occurs in western Oregon from the Columbia River south to approximately the Klamath River in northern California (Johnson and George 1991; Murray 1995; Bellinger et al. 2005). The Sonoma tree vole (*A. pomo*) occurs in the coastal forests of northern California from the Klamath River south to Sonoma County (Johnson and George 1991; Murray 1995). Further study is needed to better elucidate the taxonomic relationships between *A. longicaudus* and *A. pomo* and to determine the degree to which they overlap geographically (Bellinger et al. 2005). Historically, the red tree vole was divided into 2 subspecies, the dusky tree vole (*A. longicaudus silvicola*) in northwest Oregon (Howell 1921; Booth 1950) and the red tree vole (*A. l. longicaudus*) in the rest of Oregon and extreme northwestern California (Maser and Storm 1970). The validity of this subspecific split is still unclear (Johnson and George 1991; Bellinger et al. 2005), although a recent study by Miller et al. (2006) did indicate a genetic discontinuity between tree voles in northern and southern Oregon.

Because of their unique life history, tree voles have long intrigued naturalists. They have often been captured alive and bred in captivity, and as a result there is considerable information on the details of their feeding behavior, mating behavior, gestation period, growth rates, and climbing behavior (Benson and Borell 1931; Clifton 1960; Hamilton 1962; Maser 1966; Coriell 1974). In contrast, little is known about their population ecology, long-term population trends, spatial use patterns, or dispersal (Howell 1926; Bailey 1936; Maser et al. 1981; Verts and Carraway 1998) because they are virtually impossible to sample using conventional mark-recapture methods. Tree voles are often referred to as uncommon and patchily distributed (Howell 1926; Maser 1998). However, V. O. Bailey (1914 field notes on file at the Smithsonian Institution Manuscript Collection) stated that "...the treetop mouse is not a rare species but probably the most inaccessible of our small mammals". Higher capture frequencies of tree voles in pitfall traps in old forests have led many to suggest that tree voles are most abundant in old forests (Corn and Bury 1986; Aubry et al. 1991; Gillesberg and Carey 1991; Huff et al. 1992; Gomez and Anthony 1998; Martin 1998). Although some authors have speculated that young forests do not provide suitable habitat for tree voles (Carey 1989, 1991; Aubry et al. 1991), many tree voles have been captured in young forests (Jewett 1920; Howell 1926; Clifton 1960; Maser 1966; M. L. Johnson field notes on file at UWBM). Recent surveys by the Bureau of Land Management and U. S. Forest Service have also located large numbers of tree vole nests in young forests, although generally lower numbers than in old forests (USDA Forest Service and USDI Bureau of Land Management Survey and Manage Program Interagency Species Management System, ISMS, unpubl. data). These inconsistencies make it obvious that there is a need for better data on the distribution, abundance, and habitat associations of tree voles.

Although many have tried, tree voles are difficult or impossible to study using conventional small mammal trapping methods (McLellan 1894; Bailey 1915, 1936; Howell 1926; Walker 1930; Gillesberg and Carey 1991). They have occasionally been captured in pitfall traps (Corn and Bury 1986, 1991; Raphael 1988; Gilbert and Allwine 1991; Ralph et al. 1991; Gomez and Anthony 1998; Manning and Maguire 1999; Martin and McComb 2002), live traps (Borrecco 1973; Swingle et al. 2004), or snap traps placed on nests (Wight 1925; W. C. Russell field notes on file at University of California, Berkeley, Museum of Vertebrate Zoology, MVZ). Most tree vole specimens in museums have been captured by climbing trees and chasing tree voles out of their nests (Bailey 1915; Taylor 1915; Benson and Borell 1931; Clifton 1960; Maser 1966; Johnson and George 1991) or by loggers who grabbed disorientated voles after nest trees were cut down (Todd 1891; Bailey 1915; Walker 1930; D. Bake pers. comm.). By climbing to every visible nest and removing any tree vole that he found, Maser (1966:203) data indicated that there were 0.97 adult tree voles per hectare in a 12.4 ha stand of 29–50-year-old Douglas-fir and Oregon white oak (*Quercus garryana*) in western Oregon.

Occasional captures of male tree voles in ground nests and a preponderance of females captured in tree nests, has led some to suggest that male tree voles reside largely in ground nests (Howell 1926; Anthony 1928; Cahalane 1947), or that tree voles spend more time in ground nests during the hot summer months (Ingles 1947; Maser 1966). It has also been suggested that roads or forest fragmentation may block dispersal by tree voles, thereby leading to isolated subpopulations that may be prone to local extinction (Aubry et al. 1991; Thomas et al. 1993; Adam and Hayes 1998). None of this speculation has been well documented, and nothing is known about the daily or seasonal movements of tree voles.

In July 2002–September 2003, we conducted a study in which we used radiotelemetry to observe the movements of tree voles. Our objectives were to describe daily and seasonal activity patterns, relative use of different types of nests by males and females, survival rates, and home range areas of males and females in young forests (≤55 years old) and old forests (≥110 years old). In this report we describe the results of our study and discuss management implications of our findings. We also collected information on predation, nest site attributes, and differences in detectability of nests located via visual searches from the ground versus nests located via radiotelemetry.

STUDY AREAS

The study was conducted in 3 different study areas in Douglas County, Oregon (Fig. 1), each of which contained about equal amounts of young and old forest. The Yellow Creek Study Area was located in the Oregon Coast Range 32 km north of Roseburg, on lands administered by the Roseburg District of the Bureau of Land Management (43° 29' 48" N, 123° 24' 53" W). Elevation at Yellow Creek ranged from 430–610 meters. The Taft Creek Study Area was located in the Little River drainage on the west slope of the Cascade Mountains 45 km east of Roseburg, on lands administered by the Umpqua National Forest (43° 12' 36" N, 122° 48' 15" W). Elevation at Taft Creek ranged from

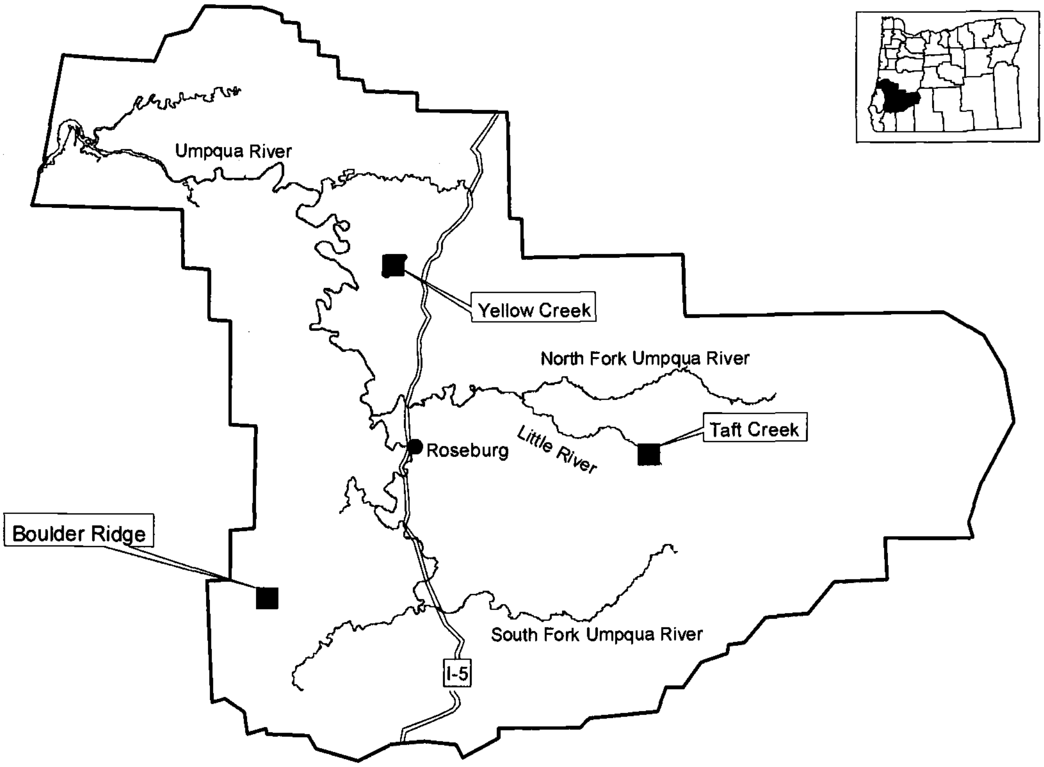

Fig. 1.—Radiotelemetry study areas in Douglas County, Oregon, July 2002–September 2003. Yellow Creek and Boulder Ridge Study Areas were on lands administered by the Roseburg District of the Bureau of Land Management. The Taft Creek Study Area was on the North Umpqua District of the Umpqua National Forest.

480–670 m. The Boulder Ridge Study Area was located 38 km southwest of Roseburg, on lands administered by the Roseburg District of the Bureau of Land Management (42° 57' 48" N, 123° 40' 50" W). Elevation at Boulder Ridge was 610 meters. Only 1 vole was radiocollared at Boulder Ridge, and this site was dropped due to logistical considerations after the radiotransmitter expired.

Vegetation at Yellow Creek included a mixture of 22–39-year-old forests regenerating on old clear-cuts, intermixed with areas of mature and old-growth forest that were 110–225 years old. Species composition was predominantly Douglas-fir with variable amounts of grand fir, incense-cedar (*Calocedrus decurrens*), western hemlock, bigleaf maple (*Acer macrophyllum*), golden chinquapin (*Castanopsis chrysophylla*), western redcedar (*Thuja plicata*), and Pacific madrone (*Arbutus menziesii*).

Vegetation at Taft Creek included a mosaic of 37–55-year-old forests, 250-year-old forests, and mixed stands of both age classes on old partial cuts. Species composition was predominantly Douglas-fir, with variable amounts of grand fir, incense-cedar, western hemlock, western redcedar and Pacific yew (*Taxus brevifolia*). At both study sites, riparian areas typically included a mixture of conifers and deciduous species such as red alder (*Alnus rubra*) and bigleaf maple.

Although they were some distance apart, the Yellow Creek and Boulder Ridge Study Areas were both in the Umpqua Interior Foothills Ecoregion that consists of narrow interior valleys, terraces, and foothills (Pater et al. 1998). This region is characterized by cool, wet winters and hot, dry summers. Annual precipitation ranges from 75–130 cm, which occurs mostly as rain during October–April (Pater et al. 1998). The Taft Creek Study Area was in the Umpqua Cascades Ecoregion which is characterized by mountains that are highly dissected by medium-to-high-gradient streams. The Umpqua Cascades Ecoregion has a mesic temperature regime characterized by cool wet winters and warm, dry summers, with mean annual precipitation ranging from 50–200 cm (Pater et al. 1998).

METHODS

LOCATING NESTS AND CAPTURING VOLES

To locate voles and attach radiocollars, we visually searched for tree vole nests in the forest canopy while walking or driving through the forest. Upon sighting a suspected nest from the ground, we climbed the tree with climbing spurs or free climbed on branches to reach the nest. If a nest was thought to be an active tree vole nest, we attempted to chase the vole out of the nest by gently probing the nest with a stiff wire rod (2 mm diameter) or by searching the tunnels and chambers of the nest with our fingers. This usually caused voles to leave the nest, at which point they typically jumped from the tree, ran down or up the bole of the tree, or out onto a limb. When they did this, we captured them by grabbing them by hand. Voles that jumped from the nest tree were usually captured by assistants on the ground, who positioned themselves so they could catch the falling voles in dip nets or by hand, or grab them as they hit the ground and tried to run away. In very bushy nest trees or very large old-growth nest trees, we sometimes positioned an additional climber directly below the nest to catch voles that jumped from the nest. This was necessary to keep voles from landing on limbs below the nest and escaping before a climber could get to the vole. Regardless of whether we used the wire probe or our fingers to chase voles from nests, we were careful not to damage nests, as we did not want to influence vole behavior by destroying their nests. The wire probe was especially useful for this task, because it did very little damage.

Upon capture, voles were fitted with a radiocollar (Models BD-2C & BD-2NC, Holohil Systems, Ltd., Woodlawn, Ontario). We used 3 different sizes of radiocollars (0.6, 1.0, and 1.5 g) depending on the body mass of the vole, such that transmitter size did not exceed 5% of body mass. We attached radiocollars by using the stainless steel wire antenna to form a loop around the neck of the vole (Fig. 2). The antenna was run through a brass sleeve, then through a short piece of Tygon tubing ($\approx$ 25 mm), then back through a hole in the body of the transmitter, then back through the brass sleeve, and half-way back through the tubing before exiting through a small hole in the middle of the tubing. This created a loop with the end of the antenna sticking out through a hole in the tubing on the dorsal side of the loop (Fig. 2). The loop was then slipped over the head of the vole and adjusted for a snug fit around the neck before being locked in place by crimping the brass sleeve with needle-nose pliers. Then, we used the pliers to bend the protruding section of antenna wire to lay flat along the back of the vole.

We estimated the age, sex, and reproductive condition of each vole at capture based on multiple external clues. Voles were labeled as adults or subadults based on mass, pelage color, and outward evidence of reproductive condition (Clifton 1960; Hamilton 1962; Maser and Storm 1970). Sex was determined based on the distance between the urogenital opening and the anus (anogenital distance) and visible evidence of mammae or testes. We categorized females as "lactating" (mammae visible and prominently distended), "post-lactating" (mammae conspicuous but flaccid), or "non-lactating" (mammae inconspicuous). Male reproductive condition was determined by examination of the testes to note if they were descended or not. We collected a tissue sample from each animal by clipping off a 4–6-mm-long section from the tip of the tail and preserving it in a sterile Nalgene cryogenic vial containing 1 ml of tissue storage buffer (100 mM Tris HCL pH 8, 100 mM EDTA, 10 mM NaCl, and 0.5% SDS). Voles were then released at the base of the tree from which they were captured. The entire handling sequence from capture to release took about 20 minutes. Tissue samples were sent to S. M. Haig at the U. S. Geological Survey, Forest and Rangeland Ecosystem Science Center in Corvallis, Oregon for studies of the taxonomy and population structure of tree voles (Bellinger et al. 2005; Miller et al. 2006).

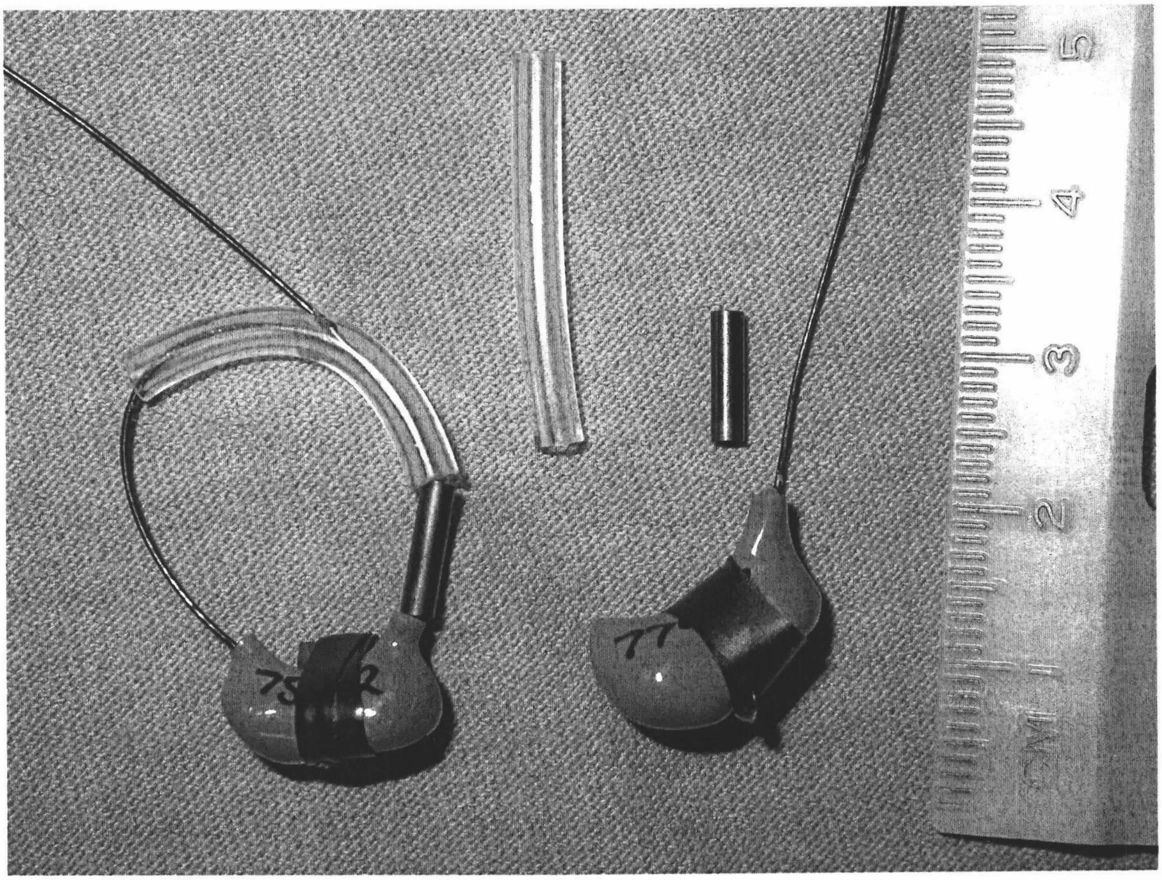

Fig. 2.—Radiocollar transmitters used to monitor movements of red tree voles in Douglas County, Oregon, July 2002–September 2003. Photograph illustrates transmitter, brass crimp, and Tygon tubing used to make the radiocollar (right) and the assembled radiocollar ready to slip over the head of the vole (left). After the neck loop was cinched down for a snug fit, the brass sleeve was crimped with needle-nose pliers, and the trailing end of the antenna was bent to lay flat along the back of the vole. Both radiocollars have electricians tape securing a magnet that temporarily deactivates the transmitter.

RADIOTRACKING

We used hand-held H-antennas (Model RA-2AK, Telonics, Inc., Mesa, Arizona) and portable hand-held radio receivers (Model R-1000, Communications Specialists, Orange, California) to relocate radiocollared voles. For nocturnal relocations, the normal procedure was to triangulate on the radiotransmitter signal until the vole was located in a specific tree. Then we estimated the height of the vole in the tree by a series of triangulations taken from multiple locations around the tree. If we could not isolate the signal to a specific tree, we tried to isolate the signal to the smallest possible group of trees. Of 2,537 relocations obtained during the study, 2,166 were determined to the nearest tree, 312 were narrowed down to a cluster of trees within a 10 m radius, and 59 locations were discarded because we could not get an accurate location.

We used 2 sampling methods to monitor radiocollared voles. One method was to record a single location for each vole every-other-night. To ensure that observations were evenly distributed throughout the night, we used systematic sampling schedule in which we collected observations on individual animals during a different 2-hr time period each night. The other method was to randomly select a vole (random sampling with replacement) and monitor it continuously for a 1-hr period. This method was used on 1–4 nights or days each week, with a maximum of 1 vole monitored on the same day or night. Continuous monitoring was accomplished by sitting or standing quietly in the forest near the vole, listening for changes in signal strength, and periodically triangulating on the vole to determine if it changed locations. During continuous monitoring sessions we recorded whether the vole used more than 1 tree during the period and whether the vole was active during the period, as indicated by changes in transmitter signal strength, vole location, or both. All voles were monitored until they died, or until the radiotransmitter either failed or was removed by the vole or a predator.

ACCURACY OF RADIOTELEMETRY LOCATIONS

Of the 88 transmitters we put on 61 voles, we subsequently recovered 71. Of these, 50% had the antenna chewed off at the point where the antenna exited the Tygon tubing on the back of the neck. However, we could detect little difference in signal strength or directionality of transmitters with shortened antennas, so we do not think this influenced our ability to locate voles. Most of locations (77%) were in the same tree as the ground-based triangulation, when we then climbed trees to determine the exact location of the vole. Mean telemetry error was 1.50 m ± 0.02 ($n = 129$, *range* = 0–21.0 m). Linear regression of telemetry error on height of radiocollared voles in trees suggested a marginal increase in telemetry error as the height of the vole increased ($R^2 = 0.14$, $P = 0.09$).

DIEL ACTIVITY PATTERNS

While triangulating to locate voles and while conducting 1-hr continuous monitoring sessions, we used fluctuations in signal strength to estimate the level of activity of the vole during the observation period. The level of activity was scored as 1–3, where a score of 1 indicated no movement, 2 indicated occasional movement, and 3 indicated frequent movement during the period of observation. In a few cases where we suspected that our presence may have caused voles to move, we excluded the data from the analysis. Data collected during the period between sunset and sunrise were divided into eight 2-hr intervals in order to evaluate differences in the level of activity at different times of the night. We combined data collected during diurnal hours into a single sample for comparison with the 2-hr nocturnal time intervals. Differences in mean activity scores in the 2-hr intervals and the diurnal interval were evaluated with one-way analysis of variance (ANOVA).

We also used an approximation of the Fishers exact test (Ramsey and Schafer 2002) to test the hypothesis that voles were equally active during diurnal and nocturnal periods. For this test, we constructed a 2 x 2 table of counts with rows consisting of diurnal or nocturnal periods and columns consisting of binary counts of the number of occasions when voles were either inactive or active. For this test we considered voles as inactive if the activity score = 1 and active if the activity score = 2 or 3.

In cases during nocturnal monitoring when a vole was found in a different tree than the one it had been occupying during previous locations, we conducted a follow-up visit the next day to determine if the vole was still in the new tree or had moved back to the previously used nest tree. This often involved climbing 1-or-more trees with the radiotelemetry equipment until we confirmed a new nest, discovered the body of a cached vole, or located the radiocollar. Nearly all nests used by radiocollared voles were confirmed on 1-or-more occasions by climbing the nest tree, locating the nest, and using the receiver to confirm that the vole was in the nest. We did this by removing the coaxial antenna cable and placing the receiver close to the nest. If the receiver picked up the signal without the antenna, then we knew that the vole was in the nest. Incidental to radiomonitoring voles, we also tested a Hughes Probeye Palm Infrared Imager (Western Sensor Company, Hayden, Idaho) to determine if it was useful for detecting thermal images of voles while they were in their nests or in the forest canopy. These tests were conducted under a variety of field conditions and distances from nests during winter 2002–2003.

NEST SITE ATTRIBUTES

For every nest tree that we located and climbed, we recorded the tree species, diameter at breast height (DBH), nest height above ground, height to first live limb, Universal Transverse Mercator (UTM) coordinates, and estimated activity status of the nest (Table 1). At nests that were determined to be tree vole nests, we collected additional information on the physical characteristics of the site and nest tree. These included tree diameter at nest height (DNH), type of nest support (Table 1), nest dimensions (length, width, depth), distance from bole to nest, nest aspect relative to bole, horizontal crown spread (length, width), and amount of physical contact between limbs of the nest tree and adjacent trees. Measurements were obtained with a metric tape except for total tree height, which was measured with a laser (Impulse LR, Laser Technology, Inc., Centennial, Colorado). Slope aspect and percent slope were measured at the base of the nest tree using a compass and clinometer. We estimated mean canopy closure based on measurements taken with a spherical densiometer (Model C, Forest Densiometers, Bartlesville, Okalahoma) at 4 points that were 5 m from the nest tree in each cardinal direction.

We estimated age of tree vole nests based on the presence and approximate age of nest material (Table 1). Active tree vole nests contained fresh green Douglas-fir cuttings, fecal pellets, and resin ducts. Older, inactive nests contained desiccated cuttings, brown–black fecal pellets, and/or tan resin ducts. Occupancy was only assumed if we actually found voles in the nest.

Table 1.—Codes used to classify activity status and nest support of nests of red tree voles and other species in Douglas County, Oregon, June 2002–September 2003.

Code	Description of code
Activity status	
VC	Tree vole present and nest contains fresh green cuttings and resin ducts.
VN	Tree vole present but no fresh green cuttings present.
VR	Very fresh cuttings and resin ducts but no vole present.
MR	Desiccated green resin ducts and cuttings, but no vole present.
OR	Old green resin ducts, no fresh cuttings or evidence of very recent use.
MO	Brown or tan resin ducts or old intact feces.
VO	Decayed resin ducts, feces, and/or twigs with bark chewed off.
AO	Active or recently active nest of species other than tree vole.
IO	Inactive, old nest of species other than tree vole.
UN	Non-nest or very old decayed nest, debris, moss, and/or lichen.
Nest support	
Branch whorl	Whorl of closely-spaced limbs radiating out from bole at the same height.
Palmate branch cluster	Fan-like growth of multiple branches originating from single point on bole.
Forked branch cluster	Single limb with multiple branches originating from single point on limb.
Single limb	Nest located on a single limb without forked branch cluster.
Forked trunk	Fork or bowl-shaped structure created by ≥2 trunks.
Broken top	Deformed or broken top with ≥1 leaders and abnormal branch growth.
Cavity	Hole in tree bole.
Dwarfmistletoe growth	Dense cluster of aberrant limbs caused by dwarfmistletoe infection.

To test the hypothesis that nest aspect relative to the tree bole differed from random we used Rayleigh's uniformity test (Batschelet 1981) in program Oriana (2004). To test the hypothesis that nests tended to be on the downhill side of the nest tree, we used the V-test in program Oriana (Batschelet 1981). The range of possible values in the latter analysis was from 0° (no difference between observed and expected, nest on downhill side of tree) to 180° (nest on uphill side of tree).

To estimate the amount of physical contact or "connectivity" between the nest tree and adjacent Douglas-firs we counted the number of Douglas-firs that had limbs that were in contact with the nest tree, and we estimated the relative abundance of interconnecting limbs on a geometric scale (0, 2, 4, 8, 16, 32, 64, 128, 256, and 512), with 0 being none and 512 indicating tree canopies that were largely intertwined. Our objective in recording these data was to quantify the number of potential pathways that voles could use to travel between nest trees and adjacent Douglas-firs.

NEST DETECTABILITY

To test the hypothesis that tree vole nests could be reliably identified by visually inspecting them from the ground, we used the sample of all nests that were first detected from the ground and subsequently examined by climbing. After detecting a nest and before climbing the tree, we examined the nest with binoculars and visually searched for resin ducts under the tree. Based on this evidence we recorded an activity code to indicate which species we thought built the nest, and whether or not we thought the nest was recently occupied (Table 1). Then, we climbed the tree and determined which species actually built the nest based on a variety of physical clues, including the types of material used to construct the nest, presence or absence of resin ducts and fecal pellets, or visual confirmation of the occupant. By comparing the ground-based estimate of activity status with the activity status determined at the nest, we were able to estimate the percentage of nests that were correctly identified based on visual examination from the ground.

To estimate the percentage of nests that could be detected from the ground we used the sample of nests occupied by radiocollared voles. Each time that we located a radiocollared vole in a previously undetected nest, we visually searched for the nest from the ground, and assigned the nest to 1 of 3 categories (easily visible, moderately visible, or not visible). We used these data to estimate the minimum percentage of occupied nests that might be missed during a thorough visual search from the ground. Each nest was only used once for this analysis. We used a *t*-test to test the hypothesis that nests located from the ground were larger than nests detected from radiotelemetry. We expected that nests located from the ground would be biased towards larger nests because large nests would be easier to see than small nests. Volume of nests was estimated in cm^3 by multiplying the length x width x depth of the nest. Nest length and width was measured at right angles across the top of the nest.

HOME RANGE ANALYSIS

Although it was usually possible to determine in which tree a vole was, we could not reliably tell where in the tree the vole was by triangulating from the ground, especially at night. For example, it was difficult to determine if the vole was in its nest or out on a limb, several meters from its nest. This created problems for estimation of home range areas with convex polygons or kernel estimators, particularly when all locations for a vole were in 1 or

2 nests. Because of these factors, we developed an alternative method of home range estimation based on the horizontal crown spread of trees used by voles, which we referred to as the Crown Area Polygon (CAP). With this method, the home range was considered to be the area within a rounded polygon connecting the outer edges of the crowns of the trees in which the vole was located (Fig. 3). With this method we assumed that voles foraged to the outer ends of the limbs in trees in which they were located, which is probably a reasonable assumption considering that branch cuttings in vole nests usually consist of fresh new growth from the outer ends of limbs (Taylor 1915; Howell 1926).

To estimate individual vole home range area, we used a compass and laser to determine the distance and direction between all trees used by each vole. We imported these data into Program ARCVIEW 3.2 (ESRI, Inc., Redlands, California) and used the DISTANCE AND AZIMUTH TOOL extension (Jenness Enterprise, www.jennessent.com) to determine the coordinates of each location. We used a metric tape to determine the mean crown diameter of each tree used by each vole (the average of two measurements of crown width, measured at right angles in the field). The area within the CAP was then estimated in ARCVIEW based on the coordinates and crown areas of trees in which the vole was located (Fig. 3).

In addition to the CAP estimates of home ranges, we also calculated 100% Minimum Convex Polygon (MCP—Hayne 1949) estimates of home ranges for most voles in the ANIMAL MOVEMENT extension (Hooge and Eichenlaub 1997) of ARCVIEW, so that we could compare our estimates with results from other studies in which the MCP method was used to estimate home range of voles (Fig. 3).

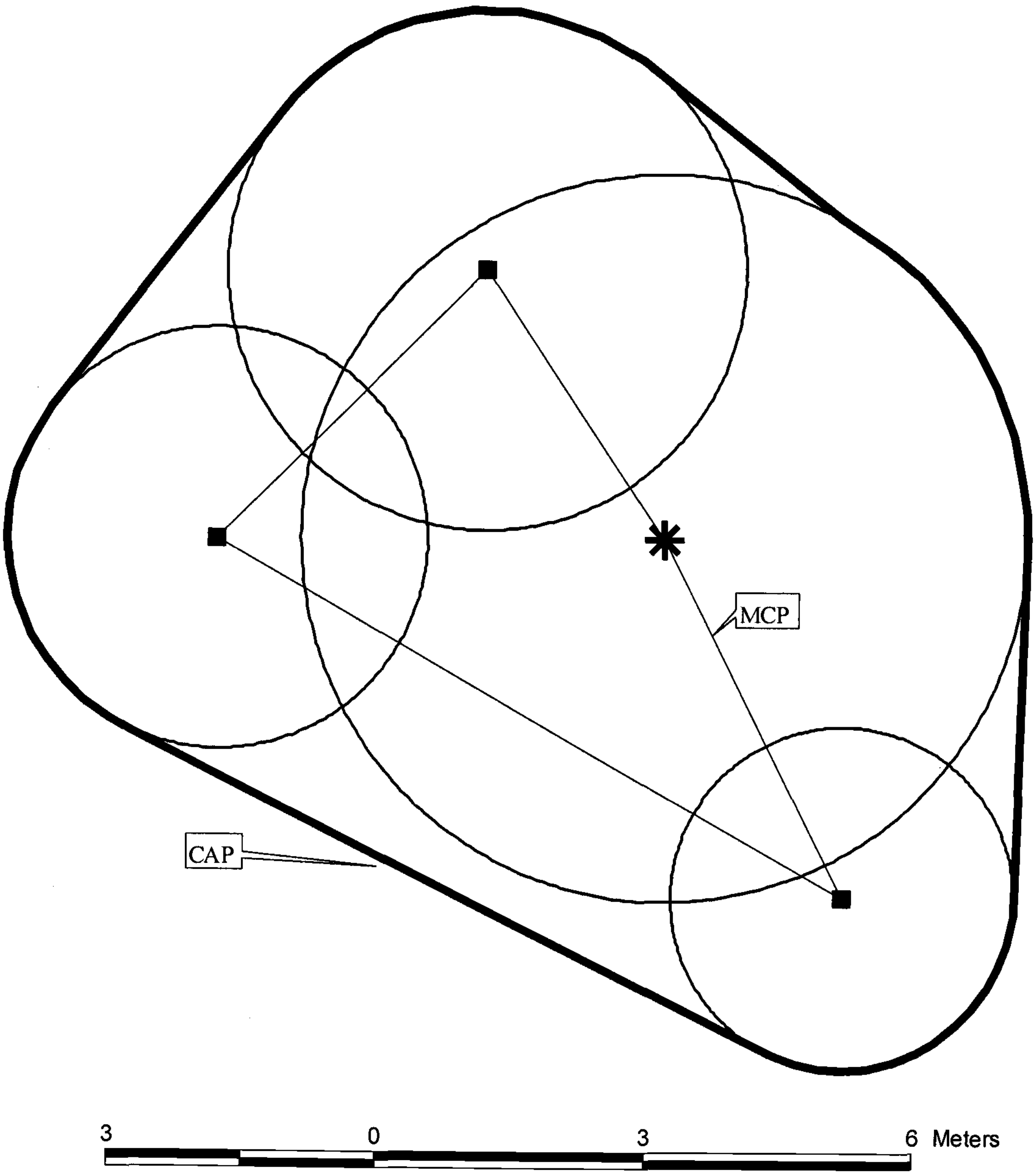

Fig. 3.—Home range of adult female red tree vole GRF02 in Douglas County, Oregon, 26 August–24 October 2002, illustrating the 2 methods used to estimate ranges. The 100% Minimum Convex Polygon (MCP) and Crown Area Polygon (CAP) ranges are indicated by thin and thick lines, respectively. Star (nest tree) and solid dots (foraging trees) indicate boles of trees used by the vole. Circles indicate the estimated crown area of each tree in which the vole was located.

We used multimodel regression analysis to evaluate the effects of sex, vole age, study area, number of days in the sample period, and forest age on estimates of CAP home range size (Burnham and Anderson 2002). For this analysis we excluded the single home range estimate from the Boulder Ridge Study Area, because a sample of 1 was too small to evaluate differences among areas. The analysis was conducted with a set of 14 *a priori* models (Table 2). We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank models and we used Akaike weights to evaluate model likelihood (Akaike 1973; Burnham and Anderson 2002). For this information-theoretic analysis, any model within 2 AIC_c units of the best model was considered competitive with the best model (Burnham and Anderson 2002). To evaluate the relative importance of each parameter across all models, we summed Akaike weights across models for each parameter (Burnham and Anderson 2002). We estimated the amount of variance explained by the best model as the difference in residual variance between the intercept-only (no-effects) model and the top model using the estimates of residual variance computed with program SPSS (2002). Because home range estimates tended to be skewed towards smaller ranges, we log-transformed the data to improve normality before conducting analyses. However, we present the untransformed estimates in tables and figures.

Table 2.—*A priori* models used to examine the effects of sex, vole age, study area, forest age, and number of days in the sample period on home range estimates of red tree voles on the Yellow Creek and Little River Study Areas, Oregon, July 2002–September 2003.

Model structure[a]	Model description
days + sex + age + area + forest	Additive effects of days, sex, vole age, study area, forest age
days + sex + age + forest	Additive effects of days, sex, vole age, forest age
sex + age + area + forest	Additive effects of sex, vole age, study area, forest age
days + sex + age	Additive effects of days, sex, vole age
days + area + forest	Additive effects of days, study area, forest age
days + forest	Additive effects of days, forest age
days + sex	Additive effects of sex, days
sex + age	Additive effects of sex, vole age
days + age	Additive effects of days, vole age
forest	Effect of forest age
days	Effect of days
age	Effect of vole age
sex	Effect of sex
no-effects model	No days, sex, vole age, study area, forest age effects

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[a] Covariates indicate structure for number of days in sample period (days), sex and age of voles, study area (area), and forest age class (forest).

BODY MASS

We used one-way ANOVA to compare mean mass of voles captured at the different study areas. We used *t*-tests to examine differences in mean mass of males and females at first capture, mean mass of breeding and non-breeding females, and mean mass of males with testes descended and not descended. Approximate age of juveniles located in nests was estimated based on body mass (Clifton 1960; Hamilton 1962).

SEXUAL DIFFERENCES IN MOVEMENTS, NEST FIDELITY AND NEST SIZE

We used 3 methods to compare nest tree fidelity and movements of males and females. In the 1st analysis we used a *t*-test to compare the total number of nests used per individual, regardless of the length of sampling period. In the 2nd analysis we used a *t*-test on the log transformed data to examine sexual differences in the mean minimum distance moved (MMDM) per day, where MMDM was the sum of the distances between all sequential locations divided by the number of days in the sample period. In the 3rd analysis we coded each relocation as a 0 if the vole was located in the same tree as the previous relocation or 1 if it was at a different location. Then we compiled a 2 x 2 table of the data, subdivided by sex and computed the log odds ratio of the likelihood of movement between successive relocations of males and females.

We used multimodel regression analysis to evaluate the effects of sex, vole age, study area, and forest age on the mean number of nests used per month by radiocollared voles. This analysis was conducted with a set of 9 *a priori* models (Table 3). Methods used to select the best model and estimate the variance explained by the best model were the same as for the analysis of home range size, described earlier.

To test the hypothesis that nest size did not differ between the sexes or between levels of nest detectability from the ground, we used one-way ANOVA to compare means of the log-transformed estimates of volume of nests occupied by males and females and between the different categories of nest detectability.

Table 3.—*A priori* models used to examine the effects of sex, vole age, study area, and forest age on the mean number of nest trees used per month by red tree voles on the Yellow Creek and Little River Study Areas, Douglas County, Oregon, July 2002–September 2003.

Model structure[a]	Model description
sex + age + area + forest	Additive effects of sex, vole age, study area, forest age
age + area + forest	Additive effects of vole age, study area, forest age
sex + age + area	Additive effects of sex, vole age, study area
age + area	Additive effects of vole age, study area
sex + forest	Additive effects of sex, forest age
forest	Effect of forest age
age	Effect of vole age
sex	Effect of sex
no-effects model	No effects of sex, vole age, study area, or forest age

[a] Covariates indicate structure for sex and age of voles, study area (area) and forest age class (forest).

SURVIVAL

We used the Kaplan-Meier product limit estimator (Kaplan and Meier 1958) with a staggered entry design (Pollock et al. 1989) to estimate bi-weekly survival rates of radiocollared voles. To evaluate the effects of vole age, sex, mass at first capture, and time since initial capture on bi-weekly survival, we examined a set of 12 *a priori* models (Table 4) in Program MARK (White and Burnham 1999) and used the AIC_c model selection process to determine which model(s) best fit the data. As in earlier analyses, we considered any model within 2 AIC_c units of the best model as a reasonably good fit to the data.

We used $\alpha = 0.05$ as the level for significance in statistical tests. All means and standard errors are expressed as $\overline{X} \pm SE$.

Table 4.—*A priori* models used to examine the effects of sex, vole age, forest age, vole mass at first capture, and time on bi-weekly survival of radiocollared red tree voles in Douglas County, Oregon, July 2002–September 2003.

Model structure[a]	Model description
sex * age * forest	Interactive effects of sex, vole age, forest age
sex * age	Interactive effects of sex, vole age
sex * forest	Interactive effects of sex, forest age
age * forest	Interactive effects of age, forest age
t + mass	Additive effects of time and vole mass
sex	Effect of sex
age	Effect of vole age
forest	Effect of forest age
mass	Effect of vole mass
t	Variable time effect
T	Linear time effect
no-effects model	No effects of sex, vole age, time, area, or forest age

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[a] Covariates indicate model structure for variable time effects (t), liner time effects (T), forest age (forest), and vole sex, age and mass at first capture.

RESULTS

NEST AND NEST TREE ATTRIBUTES

We climbed 924 trees a total of 1,273 times to check suspected nest structures that were visible from the ground or to locate radiocollared voles. We inspected 1,151 arboreal structures, including 878 that were found during ground surveys and 273 that were found while we were climbing to locate radiocollared voles or to examine nests that were visible from the ground. Of the 878 arboreal structures located during ground surveys and examined by tree climbing, 159 (18%) were occupied or recently occupied vole nests, 367 (42%) were old, inactive vole nests, 163 (19%) were nests of species other than tree voles, and 189 (21%) were dwarfmistletoe clumps or natural accumulations of debris. Of the 163 nests of other species, 48 were occupied or recently occupied. Animals observed at the latter nests included 11 northern flying squirrels (*Glaucomys sabrinus*), 6 dusky-footed woodrats (*Neotoma fuscipes*), 1 Douglas squirrel (*Tamiasciurus douglasii*), and 4 deer mice (*Peromyscus maniculatus*). We also captured 1 adult western red-backed vole (*Clethrionomys californicus*) in a nest that was 10.8 m above ground and that had evidence of recent occupancy by a tree vole, including green resin ducts and fresh Douglas-fir cuttings.

Five tree vole nests were also occupied by single clouded salamanders (*Aneides ferreus*), including 1 in a tree cavity. Two of these nests were simultaneously co-occupied by tree voles (Fig. 4), and 3 still contained clouded salamanders when we reexamined them 60, 104, and 115 days later, respectively. Average height of nests occupied by clouded salamanders was 11.0 m ± 2.2 (range = 9.0–20.1).

Fig. 4.—Adult clouded salamander (*Aneides ferreus*) that cohabitated the nest of adult male tree vole GRM08 at the Yellow Creek Study Area. The salamander was located in the "soil" created by the composted mixture of tree vole fecal pellets, Douglas-fir needle resin ducts, unconsumed Douglas-fir cuttings, and lichen.

Of 324 active vole nests examined by tree climbing, 159 were located from ground-based surveys, 44 were found by radiotracking voles to nests that were not visible from the ground, 45 were found when we rechecked previously inactive nests and found that they had been reoccupied, and 76 were spotted while climbing trees. Of the 324 active vole nests examined, 173 (53%) were in young forest (22–55 years old) and 151 (47%) were in old forest (110–250 years old). Mean DBH, height to first live limb, nest height, and tree height were similar between active and inactive nests within forest age classes (Table 5; all P-values > 0.05), but all mean estimates of nest height, DBH, height to first live limb and tree height were greater in old forests than in young forest (Table 5; all P-values < 0.05). Of 324 active nests, 322 (99.4%) were in live trees and 2 (0.6%) were in dead trees. Of the nests in live trees, 9 (2.8%) were located below the live crown, 181 (56.2%) were in the lower third of the live crown, 93 (28.9%) were in the middle third of the live crown, and 39 (12.1%) were in the upper third of the crown. In young forest, most nests were in the upper 2/3rds of the live crown, whereas most nests in old forest were in the lower third of the live crown (Table 6). Both nests in dead trees were in Douglas-fir snags, include one in the broken top of a decay class III snag and one in a side cavity of a decay class II snag (snag decay class scale = I–V; Franklin et al. 1981). The voles in both snags apparently obtained food by crossing over into adjacent Douglas-firs on live limbs that were in contact with the snags.

Table 5.—Mean (± *SE*, range) measurements of trees in which active and inactive red tree vole nests were located in Douglas County, Oregon, July 2002–September 2003. Measurements were calculated separately for nests in young forest (22–55 years old) and old forest (>110 years old).

	Active nests	Inactive nests
Young forest	*n* = 173	*n* = 50
Diameter at breast height (cm)	38.2 ± 0.9 (10–78)	38.5 ± 1.1 (14–61)
Height to first live limb (m)	8.1 ± 0.3 (0.2–20.2)	6.9 ± 0.3 (0.2–18.5)
Nest height (m)	13.6 ± 0.4 (3.7–28.4)	11.7 ± 0.5 (3.2–22.6)
Tree height (m)	22.7 ± 0.5 (9.7–46.7)	22.5 ± 1.1 (10.7–32.3)
Old forest	*n* = 151	*n* = 197
Diameter at breast height (cm)	92.5 ± 2.5 (10–78)	90.4 ± 0.9 (17–169)
Height to first live limb (m)	15.3 ± 0.5 (3.8–39.2)	16.2 ± 0.3 (0.3–37.6)
Nest height (m)	22.0 ± 0.7 (5.7–53.5)	21.2 ± 0.4 (4.0–68.0)
Tree height (m)	48.4 ± 1.1 (13.5–76.0)	47.5 ± 1.1 (23.7–77.0)

Table 6.—Percentage of active and inactive red tree vole nests relative to position in live crown of the nest tree, Douglas County, Oregon, July 2002–September 2003. Sample sizes are in parentheses.

	Young forest		Old forest		Total	
Position in live crown	Active (173)	Inactive (50)	Active (151)	Inactive (197)	Active (324)	Inactive (247)
Below 1st live limb	4	2	1	1	3	1
Lower third	42	24	74	48	56	43
Middle third	38	12	19	11	29	11
Upper third	16	62	6	40	12	45

Of the 324 active vole nests that we confirmed by climbing trees, 303 were in Douglas-fir, 9 were in grand fir, 4 were in western hemlock, 4 were in bigleaf maple (Fig. 5), 3 were in Pacific yew (Fig. 6) and 1 was in a golden chinquapin (Table 7). All 21 nests in trees other than Douglas-fir were in trees that were in direct contact with branches of adjacent Douglas-firs and contained Douglas-fir cuttings and resin ducts, indicating that the voles were obtaining their food by crossing over into adjacent Douglas-fir. All nests that were occupied by voles contained a stockpile of fresh green Douglas-fir cuttings, but 5 also included 1–2 fresh cuttings of western hemlock, grand fir, or western redcedar.

Types of nest support differed between young forests and old forests. In young forests, 65% of nests were built on branch whorls or forked trunks, 33% were built on broken tops, single limbs, or palmate branch clusters, and no nests were found in cavities or in crevices behind bark (Table 8). In old forests, 84% of nests were built on palmate branch clusters or single limbs, and 4% of nests were located in cavities or in crevices behind bark that was sloughing off the bole (Table 8; Fig. 7). Of 13 cavity nests located, 9 were first detected from ground-based surveys and 4 were located while climbing trees.

Fig. 5.—Red tree vole nest built in an abandoned squirrel nest in a bigleaf maple tree. One Douglas-fir cutting was pulled into the side entrance and green Douglas-fir resin ducts were spilling out of the entry hole. The cutting was collected by the vole from nearby Douglas-firs that had interconnecting branch pathways with the maple. The nest contained a small amount of tree vole fecal pellets, resin ducts, and cuttings indicating that it was used only for a short time.

Fig. 6.—Maternal nest of tree vole TCF09 was located in top of the Pacific yew tree at the center of the picture. Stockpiled cuttings of Douglas-fir on this nest were obtained by crossing over on branches to a nearby Douglas-fir.

Table 7.—Mean attributes ($\bar{X}$ ± *SE*, range, *n*) of active red tree vole nest trees in Douglas County, Oregon, July 2002–September 2003. Estimates of nest height, diameter at nest height, and distance from bole are based on a sample of 324 active nests located in 292 trees.

Tree species	DBH (cm)	Height to first live limb (m)	Nest height (m)	Tree height (m)	Diameter at nest height (cm)	Distance from bole (cm)
Douglas-fir	61.9 ± 2.3	11.9 ± 0.4	18.0 ± 0.5	34.2 ± 1.1	39.4 ± 1.5	35.3 ± 4.8
	(10–168)	(0.2–39.2)	(3.7–53.5)	(9.7–76.0)	(4–121)	(0–560)
	274	272[a]	303[b]	274	303[b]	303[b]
Grand fir	51.8 ± 6.4	6.8 ± 0.5	14.6 ± 2.2	25.4 ± 3.9	36.0 ± 5.0	15.0 ± 15.0
	(32–75)	(5.2–9.1)	(5.7–25.4)	(14.2–39.4)	(20–56)	(0–135)
	8	8	9[c]	8	9[c]	9[c]
Western hemlock	55.3 ± 2.5	6.8 ± 2.3	13.6 ± 3.6	29.6 ± 2.6	34.3 ± 8.4	87.8 ± 87.8
	(51–62)	(2.8–13.4)	(5.1–21.2)	(23.6–36.2)	(18–54)	(0–351)
	4	4	4	4	4	4
Bigleaf maple	33.5 ± 3.5	1.5 ± 0.2	9.3 ± 0.7	19.9 ± 14.0	23.0 ± 2.4	30.3 ± 21.2
	(30–37)	(1.1–1.8)	(7.7–10.9)	(13.7–26.0)	(20–30)	(0–90)
	2	2	4[d]	2	4[d]	4[d]
Pacific yew	31.3 ± 2.6	2.9 ± 0.5	7.1 ± 1.7	11.8 ± 1.1	14.0 ± 4.2	183.3 ± 183.3
	(27–36)	(2.2–3.8)	(4.3–10.1)	(9.8–13.6)	(8–22)	(0–550)
	3	3	3	3	3	3

Table 7.—Continued.

Tree species	DBH (cm)	Height to first live limb (m)	Nest height (m)	Tree height (m)	Diameter at nest height (cm)	Distance from bole (cm)
Golden chinquapin	53	4.0	19.8	24.4	15	0
	1	1	1	1	1	1
All trees in old forest	91.3 ± 3.1	16.0 ± 0.6	22.0 ± 0.7	48.0 ± 1.4	59.4 ± 2.0	55.6 ± 8.5
	(17–168)	(4.7–39.2)	(5.7–53.5)	(13.5–76.0)	(4–121)	(0–560)
	131	130[e]	151[f]	131	151[f]	151[f]
All trees in young forest	38.3 ± 1.0	8.1 ± 0.4	13.6 ± 0.4	22.9 ± 0.5	20.7 ± 0.7	20.1 ± 5.3
	(10–78)	(0.2–20.2)	(3.7–28.4)	(9.7–46.7)	(6–54)	(0–550)
	161	160[e]	173[g]	161	173[g]	173[g]
All trees combined	61.0 ± 2.2	11.5 ± 0.4	17.1 ± 0.5	33.6 ± 1.0	37.2 ± 1.6	29.4 ± 5.0
	(10–168)	(0.2–39.2)	(3.7–53.5)	(9.7–76.0)	(4–121)	(0–560)
	292	290[a]	324[h]	292	324[h]	324[h]

[a] Sample excluded 2 nests in dead trees.

[b] 27 trees contained 2 nests and 1 tree contained 3 nests.

[c] 1 tree contained 2 nests.

[d] 1 tree contained 3 nests.

[e] Sample excluded 1 nest in a dead tree.

[f] 18 trees contained 2 nests and 1 tree contained 3 nests.

[g] 10 trees contained 2 nests and 1 tree contained 3 nests.

[h] 28 trees contained 2 nests and 2 trees contained 3 nests.

Table 8.—Percentage of active red tree vole nests constructed on different types of support structures, subdivided by tree species and forest age, Douglas County, Oregon, July 2002–September 2003. Sample sizes are in parentheses.

Nest tree species (*n*)	Behind bark	Branch whorl	Cavity[a]	Forked branch	Forked trunk	Dwarf-mistletoe	Palmate branch cluster	Broken top	Single branch
Grand fir (9)	11	22	11	0	11	0	11	11	22
Bigleaf maple (4)	0	0	0	0	50	0	0	0	50
Golden chinquapin (1)	0	0	0	0	100	0	0	0	0
Douglas-fir (303)	0	24	2	1	15	<1	24	7	27
Pacific yew (3)	0	0	0	0	67	0	0	0	33
Western hemlock (4)	0	0	0	0	25	0	25	25	25
Young forest (173)	0	37	0	2	28	<1	9	12	12
Old forest (151)	<1	7	4	0	3	0	40	2	44
Totals (324)	<1	23	2	1	16	<1	23	7	27

[a] Included 2 nests in dead trees and 2 nests in live trees.

Fig. 7.—Adult female tree vole BRF01 was radiotracked to this nest behind sloughing bark in the dead top of a grand fir. To collect food this vole had to descend the bole about 6 m before crossing over into an adjacent Douglas-fir on a live limb.

The majority of the 324 active nests (73%) in both forest age classes were built against the trunk of the tree, but old forests had more nests (44%) that were built out on limbs away from the trunk than did young forest (12%). The mean position of nests with respect to the tree bole was not random (Fig. 8), 71% of nests occurred on the south or southwest side of the bole ($\overline{X} = 205°$, 95% $CI = 190–220°$, $r = 0.32$, Rayleigh z-test = 27.8, $P < 0.001$, $n = 272$). Placement of nests relative to the downhill side of the tree bole differed from expected, indicating that nests were not consistently placed on the downhill side of the bole ($\overline{X} = 70°$, $CI = 64–77°$, $r = 0.64$, V-test = 4.953, $P < 0.001$, $n = 272$; Fig. 9).

Of the arboreal nests examined, at least 35% were originally built by other species and then occupied by tree voles. Some of these nests contained layers of different nest material, indicating that multiple species built upon the nest of the previous occupant. Nests that were most commonly taken over by tree voles were constructed by squirrels or woodrats, but we also found 3 voles that had built on top of bird nests.

Of the trees that contained active vole nests, 83% of 151 trees were in old forest, and 99% of 173 trees in young forest had limbs that were in contact with the limbs or trunk of at least 1 adjacent live Douglas-fir. Mean estimates of the number of Douglas-fir in contact with nest trees was higher in young forest than in old forest (4.7 ± 0.2 versus 1.7 ± 0.2, respectively; $t = 12.2$, $d.f. = 220$, $P < 0.001$). Mean estimates of limb connectivity between nest trees and adjacent Douglas-firs also averaged higher in young than in old forest (157.4 ± 9.1 versus 63.8 ± 13.0, respectively; $t = 5.3$, $d.f. = 220$, $P < 0.001$)

Based on data from 65 nests occupied by radiocollared voles, we found that estimated mean canopy closure at nest sites in young forest (86.3 % ± 0.5, range = 65.9–92.5%, $n = 44$) was slightly higher than at nest sites in old forest (78.2 % ± 1.5, range = 53.2–91.4%, $n = 21$, $t = 7.5$, *d.f.* = 64, $P < 0.001$).

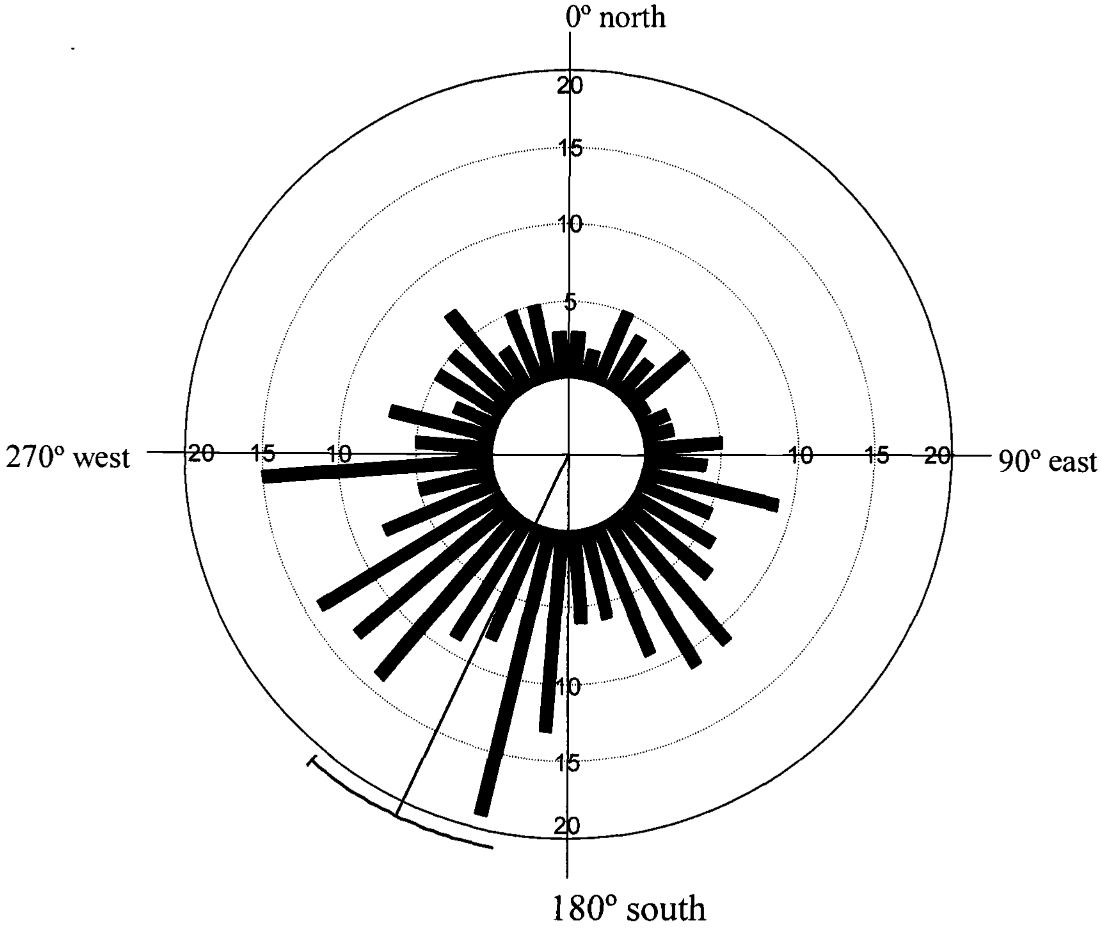

Fig. 8.—Nest aspect in relationship to the bole for 272 active red tree vole nests in Douglas County, Oregon, July 2002–September 2003. Excludes 52 active nests that encircled the bole or that were in the center of a forked trunk or broken top. The data were subdivided into forty 9° arcs. The length of each bar represents the number of observations in each 9° arc. The mean vector (205°) is shown as a thin black line extending from the center and the arc at the terminal end of the main vector represents the 95% confidence interval (*CI* = 190–220°).

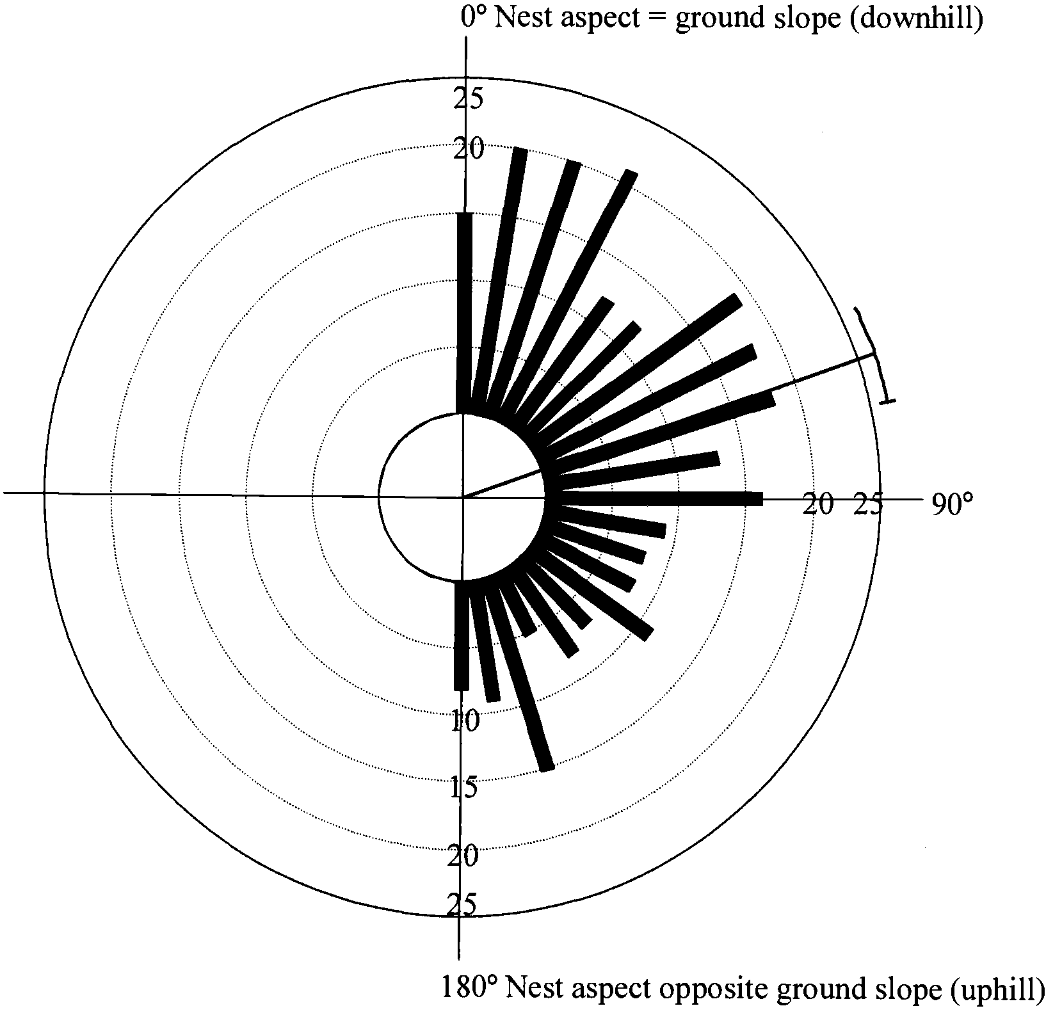

Fig. 9.—Position of red tree vole nests in relationship to the downhill side of the nest tree based on a sample of 272 active nests in Douglas County, Oregon, July 2002–September 2003. Excludes 52 active nests that encircled the bole or that were in the center of a forked trunk or broken top. The data were subdivided into 20 categories with the length of the bars indicating the number of nests in each group. Measurements ranged from 0° (nest aspect = ground aspect) to 180° (nest aspect was opposite the ground aspect). The mean vector (70°) is shown as a thin black line extending from the center and the arc at the terminal end of the mean vector represents the 95% confidence interval (*CI* = 64–77°).

NEST DETECTABILITY AND NEST VOLUME

Our ground-based estimates of nest activity status were correct for 66% of active vole nests, 52% of old unoccupied vole nests, and 56% of nests built by other species (Table 9). Of the nests that we thought were nests of other species based on visual examination from the ground (categories AO and IO in Table 9), 11–15% were occupied or recently occupied tree vole nests (Table 9). Examination of 56 nests that were not seen from the ground in initial surveys and subsequently located by radiotracking voles, revealed that 55% were not visible from the ground, 24% were moderately visible from the ground, and 21% were conspicuous from many locations on the ground (Table 10). There was no difference in the proportions of nests that were not visible from the ground in older versus young forests ($\chi^2 = 0.67$, $P = 0.80$; Table 10).

Mean volume of nests occupied by radiocollared voles did not differ between study areas ($F = 0.816$, *d.f.* = 2, 132, $P = 0.487$), so we combined the data from all areas to compare nest size of males and females. Estimated volume of nests occupied by females was 1.8 (95% $CI = 1.0$–3.0) times larger than nests occupied by males ($t = 2.132$, *d.f.* = 134, $P = 0.035$; Table 11; Figs. 10 and 11). Occupied nests that were visible from the ground were significantly larger than occupied nests that were not visible from the ground ($t = 3.466$, *d.f.* = 134, $P = 0.007$; Table 11). Nests of females that were not visible from the ground were 2.49 times smaller than nests of females that were visible from the ground (Table 11).

Table 9.—Activity status of 878 arboreal nests based on visual examination from the ground versus physical examination at the nest, Douglas County, Oregon, July 2002–September 2003. The percentage of cases in which both methods were in agreement is indicated on the diagonal axis.

Nest activity verified at nest[a]	Nest activity estimate based on visual examination from ground[a]							
	VR	MR	OR	MO	VO	AO	IO	UN
VR	**66**	26	0	11	9	15	11	16
MR	15	**26**	15	13	5	6	2	11
OR	2	2	**57**	3	2	2	1	1
MO	8	17	0	**17**	6	4	3	12
VO	4	11	14	31	**52**	2	15	34
AO	4	9	0	5	2	**56**	11	3
IO	0	5	14	17	21	15	**56**	11
UN	1	4	0	3	3	0	1	**12**

[a] Activity codes were: VR = occupied or recently occupied tree vole nest with fresh green resin ducts and cuttings; MR = moderately recent tree vole nest with desiccated green resin ducts and cuttings; OR = older tree vole nest with faded green resin ducts and older tree vole fecal pellets but no fresh cuttings or evidence of recent use; MO = moderately old tree vole nest with brown or tan resin ducts or old intact tree vole fecal pellets; VO = very old tree vole nest with decayed resin ducts and fecal pellets; AO = occupied or recently occupied nest of species other than tree vole; IO = old, inactive nest of species other than tree vole; UN = debris clump, or species and activity status unknown.

Table 10.—Percentage of red tree vole nests that were highly visible, moderately visible, or not visible from the ground in Douglas County, Oregon, July 2002–September 2003. Estimates were based on nests of radiocollared voles only. Sample sizes are in parentheses.

	Highly visible	Moderately visible	Not visible
Old forest (11)	27	9	64
Young forest (45)	29	22	49
Total (56)	21	24	55

Table 11.—Estimated volume (cm^3) of nests of male and female tree voles in Douglas County, Oregon, July 2002–September 2003. Data were subdivided by sex and by nests that were visible from the ground versus those that were not visible from the ground.

Category	*n*	$\bar{X} \pm SE$	Range	95% *CI*
Females				
Visible	38	85,573 ± 12,433	560–405,000	61,204–109,942
Not visible	37	31,029 ± 9,366	432–251,160	12,672–75,331
All nests	75	58,665 ± 8,382	432–405,000	42,235–75,094
Males				
Visible	23	47,428 ± 12,527	792–203,889	22,875–84,631
Not visible	38	35,040 ± 11,740	504–357,445	12,030–58,051
All nests	61	39,711 ± 8,674	504–357,445	22,709–90,459
All Voles				
Visible	61	71,190 ± 9,315	560–405,000	52,932–89,448
Not visible	75	33,061 ± 7,485	432–357,445	18,391–47,732

Fig. 10.—Example of a moderately large (97,944 cm^3) maternal nest (77 x 53 x 24 cm) used by adult female red tree vole GRF03. This nest was built near the top of a Douglas-fir that had a broken top, with multiple limbs growing upwards from below the break. Ruler = 15 cm.

Fig. 11.—Small nest (9 x 14 x 9 cm) used by adult male red tree vole GRM15. This nest, which was not visible from any point on the ground, was built in a fork of a 39-year-old Douglas-fir. Pencil = 13 cm.

ADULT MASS AND PELAGE COLOR

At first capture, adult females were significantly heavier (32.3 g ± 0.4, $n = 27$) than adult males (27.0 g ± 0.5, $n = 21$; $t = 8.0$, $d.f. = 46$, $P < 0.001$). There was no study area difference in mean mass of either sex at first capture ($F = 1.65$, $d.f. = 2, 48$, $P = 0.18$). On average, adults were 2.36 g heavier (95% $CI = 0.63$–4.10; $t = 2.71$, $d.f. = 76$, $P = 0.008$) between the first capture and subsequent recaptures ($\bar{X} \pm SE = 98.2$ days ± 9.8). Mean mass of adult females with evidence of pregnancy or recent reproduction (33.5 g ± 0.5) was only slightly greater than mean mass of females with no evidence of pregnancy or recent reproduction (31.7 g ± 0.8 ; $t = 1.98$, $d.f. = 48$, $P = 0.053$; Fig. 12). Mean mass of males with inguinal testes (27.2 g ± 0.5) did not differ from mean mass of males with descended testes (26.8 g ± 1.0; $t = 0.34$, $d.f. = 23$, $P = 0.740$).

Of 39 voles captured on the Yellow Creek Study Area, 3 males and 3 females were melanistic individuals characterized by uniformly black pelage (Fig. 13). This was unexpected, as there is only 1 previous report of melanistic tree voles (Hayes 1996). Two of the melanistic voles were captured in nests that were 600 m apart on the north end of the study area, and 4 were captured in nests that were 230–285 m apart ($\bar{X} \pm SE = 255$ m ± 16) on the southern end of the study area, 4.7 km SW of the other nests. All voles captured at the Taft Creek Study Area had typical reddish pelage.

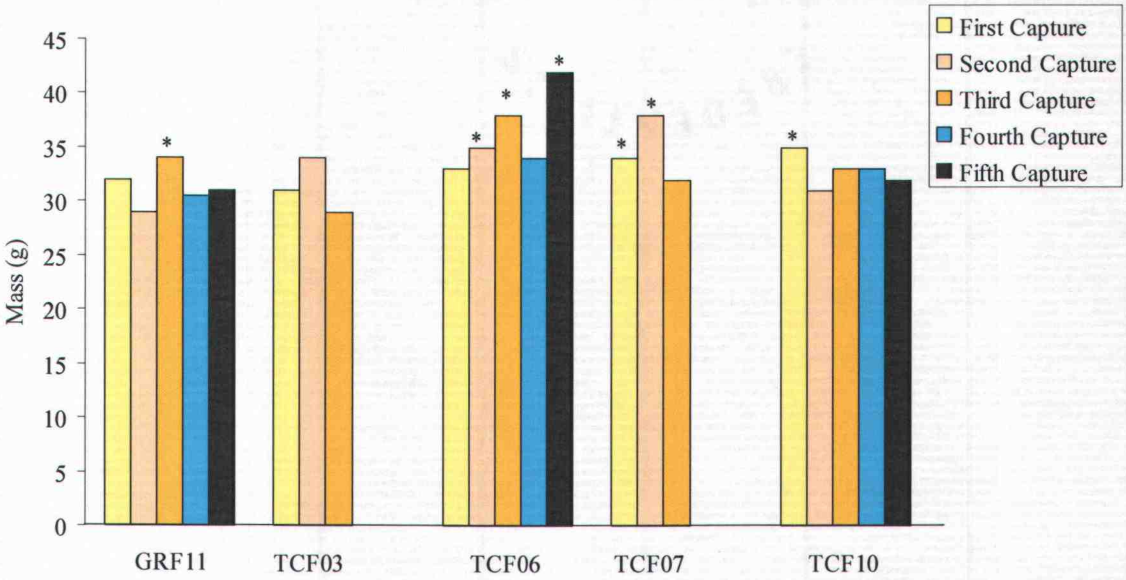

Fig. 12.—Changes in body mass of 5 adult female tree voles captured ≥3 times each in Douglas County, Oregon, July 2002–September 2003. Astrices above columns indicate capture occasions when there was visible evidence of lactation. Codes below columns indicate individual voles.

Fig. 13.—Typical pelage (bottom) and melanistic pelage (top) of adult tree voles in the Yellow Creek Study Area, Douglas County, Oregon. Six of 39 tree voles captured in this area were melanistic.

DIEL ACTIVITY PATTERNS

Both methods that we used to estimate vole activity levels indicated that voles were most active at night and were generally inactive during the day (Fig. 14). On the longest nights of the year, activity during the last few hours before sunrise declined to levels that were similar to diurnal activity scores (time intervals 7–8 in Fig. 14A). Activity scores recorded while we were triangulating on voles indicated that the relative odds that a vole would be active was 3.0 times greater at night than during the day (95% $CI = 2.4–3.9$, $Z = 8.53$, $P < 0.001$). Data from 192 continuous monitoring sessions at night indicated that voles were inactive in 19 sessions (10%), moderately active in 55 sessions (29%), and highly active in 118 sessions (61%). In contrast, in 21 continuous monitoring sessions during the day, voles were inactive in 9 sessions (43%), moderately active in 12 sessions (57%), and highly active in no sessions. Of 173 intervals in which voles were active at night, 41 (24%) involved movements between trees (range = 2–4 trees), 16 (9%) involved horizontal or vertical movement in the nest tree, and 116 (67%) were cases in which we could not tell if voles were in their nests or moving about in the nest tree.

During continuous monitoring, virtually all of the diurnal activity seemed to take place inside the nest. However, on 2 occasions when we climbed to nests during the day we saw voles that briefly left the nest to feed and groom on top of the nest or on a branch that supported the nest. While radiotracking during summer, we also located 2 voles that appeared to be sleeping on branches in trees in which we did not locate any nests. Both voles were subsequently located in nests that they had used previously.

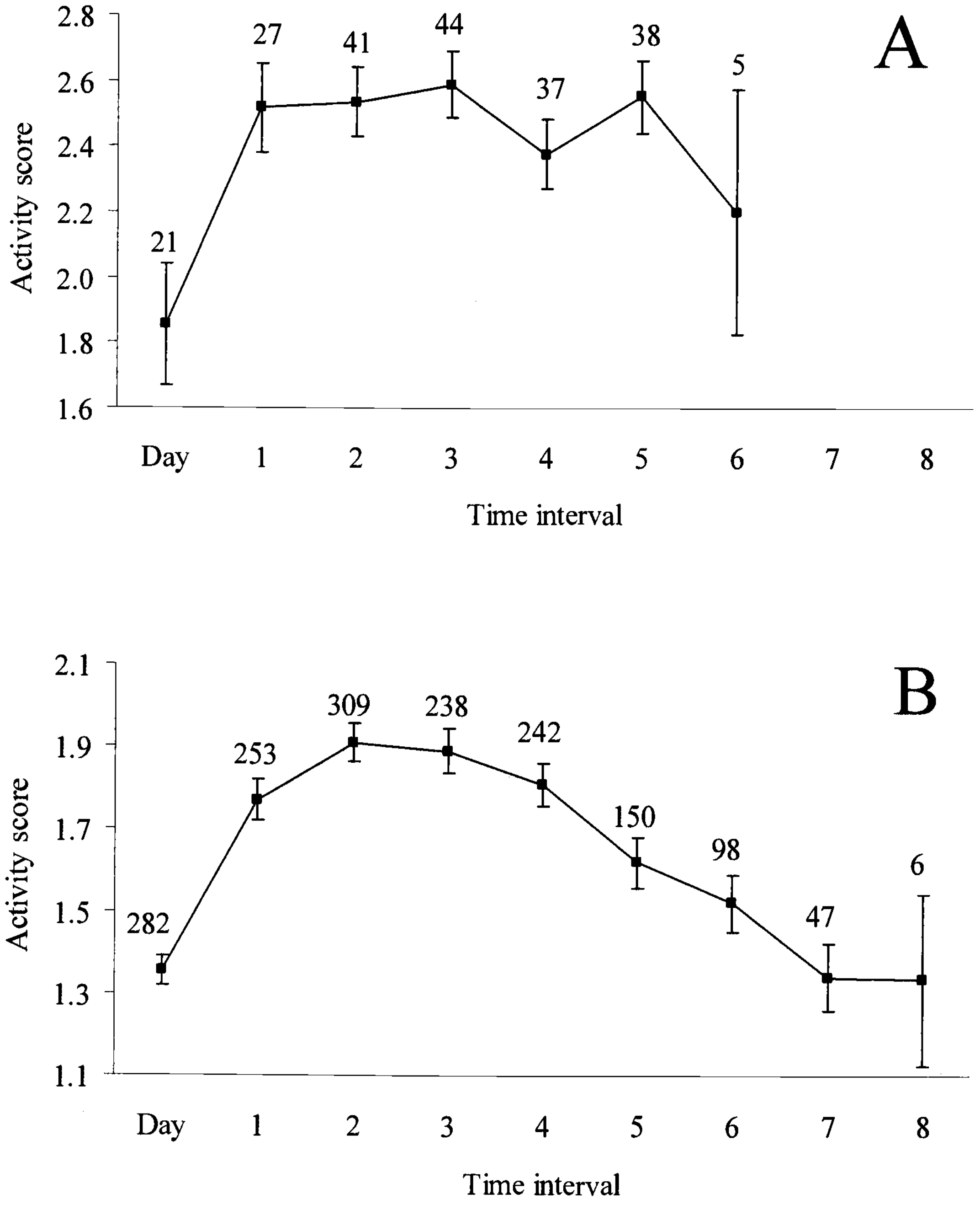

Fig. 14.—Mean activity scores (± *SE*) and number of observations of radiocollared red tree voles during diurnal hours (interval D) and during 2-hr intervals starting at sunset (intervals 1–8) in Douglas County, Oregon, July 2002–September 2003. Estimates are shown separately for data collected during 213 continuous 1-hr monitoring sessions (A) and during 1,625 occasions while we were triangulating on voles (B). Means indicate average of activity scores recorded in the field (low = 1, moderate = 2, high = 3).

HOME RANGE AND MOVEMENTS

Home Range Estimates.—Of 61 voles that we radiocollared, 5 adults and 4 juveniles were not included in the analysis of home range because no activity was detected before they disappeared, they lost their transmitters, or they were predated shortly after they were radiocollared. Of the 52 voles used in the analysis, 30 were females and 22 were males (Table 12).

Table 12.—Sex and age of 52 radiocollared red tree voles used in analyses of home range in Douglas County, Oregon, July 2002–September 2003, subdivided by forest age in which the voles occurred. Young forest = 22–55 years old. Old forest ≥110 years old.

	Adults		Subadults		
Stand age	Males	Females	Males	Females	Total
Young Forest	9	23	3	3[a]	38
Old forest	8	3	2[a]	1	14

[a] One subadult was radiocollared as a juvenile in the natal nest.

On average, we located individual voles 4.2 ± 0.1 times per week and radiotracked them for 75.4 days ± 8.2 (range = 8–307 days). Of the 52 voles used in the analysis, 32 were radiocollared 1 time only. The other 20 were recaptured and recollared on 1 ($n = 15$), 2 ($n = 3$), or 3 ($n = 2$) occasions to replace transmitters that failed or were about to fail. Two voles that were recollared 3 times and 1 vole that was recollared twice were also recaptured at the end of the study to remove their radiocollars. Of the voles captured, 82% continued to use their original nest after they were captured, and 90% were found in the original nest at least once after they were radiocollared (Table 13). This led us to believe that our capture technique did not greatly disrupt the behavior of most individuals.

Table 13.—Percentage of red tree voles that continued to use their original nest after they were captured and radiocollared, Douglas County, Oregon, July 2002–September 2003. Sample sizes are in parentheses.

	Females (30)	Males (22)	Overall (52)
Never relocated in original nest	3	18	10
Relocated only once in original nest	3	14	8
Always relocated in original nest	43	23	34
Used multiple nests including original nest	51	45	48

As expected, estimates of home range areas varied depending on the method used (Table 14). However, both methods indicated that tree voles had small ranges, typically encompassing <800 m^2 based on medians (Table 14). Of the 52 radiocollared voles that we observed, 20 had ranges that consisted of the nest tree and a few adjacent trees. The rest of the radiocollared voles used 2–6 nests spaced from 4–131 m apart in different trees. Of the 52 CAP home range estimates, 31 were less than 1,000 m^2. Only 5 voles had home ranges >4,000 m^2, and 2 of these had home ranges that were >10,000 m^2 (Table 14). The frequency of movement among nest trees was highly variable among individuals. Many voles (25 of 52) made few moves to different nest trees during the time they were sampled. In contrast, there were 7 individuals (6 males, 1 female) that moved frequently between multiple nest trees, often revisiting previously used nests throughout the sampling period.

Table 14.—Estimates of home range areas of 52 radiocollared red tree voles in Douglas County, Oregon, July 2002–September 2003. Estimates were based on the 100% Minimum Convex Polygon (MCP) method and the Crown Area Polygon (CAP) method, a modification of the MCP method in which we connected the outer edges of the crowns of trees in which voles were located.

					Home range (m²)	
Vole ID[a]	Vole age	Forest Age (yrs)	Days tracked	Nests used	CAP	MCP[b]
Females						
TCF12	AD	55	112	1	36	2
GRF15	AD	22	46	1	44	NA
TCF07	AD	37	183	1	45	NA
RFF01	AD	37	13	1	60	NA
TCF04	SUB	55	92	1	65	NA
GRF02	AD	39	59	1	92	18
GRF01	SUB	39	79	1	97	NA
GRF07	AD	34	53	1	256	NA
GRF05	AD	34	46	1	266	98
RFF04	AD	223	42	2	292	NA
GRF12	AD	22	99	2	364	84
GRF17	AD	39	28	1	411	39
TCF05	AD	55	61	1	460	93
GRF03	AD	39	57	1	541	272

Table 14.—Continued.

Vole ID[a]	Vole age	Forest Age (yrs)	Days tracked	Nests used	Home range (m^2)	
					CAP	MCP[b]
BRF01	AD	223	45	2	604	NA
TCF08	AD	55	101	1	916	361
GRF08	AD	34	78	1	946	508
TCF02	SUB	250	81	2	1,233	578
TCF11	AD	250	42	2	1,331	381
GRF16	AD	39	86	5	1,404	795
GRU01	SUB	34	48	3	1,446	934
TCF10	AD	55	137	3	1,450	956
GRF10	AD	39	24	3	1,859	1,185
TCF09	AD	37	24	2	2,142	1,396
TCF06	AD	55	307	4	2,271	1,549
GRF04	AD	39	48	2	2,465	1,472
GRF11	AD	39	258	4	2,978	2,134
TCF03	AD	37	198	2	3,016	2,170
GRF13	AD	22	150	5	3,473	2,705
GRF06	AD	39	47	3	10,083	7,654
Females $\overline{X} \pm SE$					1,354 ± 353	1,153 ± 333
Medians					760	687
Males						
TCM02	AD	250	59	1	86	NA
GRM03	AD	22	22	2	111	6
GRM09	AD	22	8	2	127	NA
GRM01	AD	31	16	1	133	26
GRM16	SUB	22	64	1	148	16
GRM07	AD	39	42	2	151	NA

Table 14.—Continued.

Vole ID[a]	Vole age	Forest Age (yrs)	Days tracked	Nests used	Home range (m^2) CAP	Home range (m^2) MCP[b]
GRM05	AD	39	40	2	177	NA
RFM01	AD	223	57	1	400	94
GRM08	SUB	39	52	4	507	131
GRM12	AD	223	41	1	616	112
GRM11	AD	34	33	2	493	97
GRM02	AD	31	47	1	700	364
TCM07	AD	250	75	2	760	164
RFM02	SUB	223	35	2	822	244
TCM03	AD	250	47	4	1,205	600
TCM06	AD	250	71	3	1,660	951
GRM06	AD	223	129	4	2,470	1,518
RFM03	SUB	143	72	2	2,754	1,906
TCM04	AD	250	78	2	4,222	2,806
GRM10	AD	22	93	5	6,906	5,895
TCM05	AD	55	99	6	7,761	6,374
GRM15	SUB	39	38	4	10,308	8,453
Males $\overline{X}$ ± *SE*					1,932 ± 608	1,652 ± 608
Median					658	304
All voles						
$\overline{X}$ ± *SE*					1,599 ± 327	1,378 ± 333
Median					658	543

[a] First 2 letters indicate study area: TC = Taft Creek, BR = Boulder Ridge, GR and RF = Yellow Creek. Third letter indicates sex.

[b] Sample excluded 12 radiocollared voles that were located only in 2 different trees, which resulted in no estimate with the MCP method.

Estimates of mean home range area did not differ between males and females based on the 100% Minimum Convex Polygon method ($t = 0.50$, *d.f.* = 38, $P = 0.62$) or Crown Area Polygon method ($t = 0.53$, *d.f.* = 49, $P = 0.59$). Estimates of mean home range area also did not differ between voles occurring in young and old forest (Table 15). Both males and females typically spent most of their time in a single nest, with occasional visits to satellite nests within 4–131 m from the primary nest. The mean number of nest trees used by individual voles was greater ($t = 2.05$, *d.f.* = 50, $P = 0.046$) for males (3.0 ± 0.4, range = 1–6, $n = 20$) than for females (2.1 ± 0.3, range = 1–5, $n = 32$).

Table 15.—Mean (95% *CI*) home range size comparison between radiocollared red tree voles in young and old forest in Douglas County, Oregon, July 2002–September 2003.

	Mean home range size (m^2)			
	Young forest	Old forest	*t* values	*P* values
100% MCP	1,579 (817–2,341)	850 (390–1,310)	0.50 (*d.f.* = 38)	0.62
CAP	1,703 (849–2,557)	1,318 (720–1,916)	1.09 (*d.f.* = 49)	0.28

Multimodel Regression Analysis of Covariates of Home Range Size.—The model that best described the variation in size of home ranges included only the number of days in the sampling period (Table 16). Three other models were competitive with the best model, including the no-effects model and models that included the effects of days sampled + forest age and days sampled + sex (Table 16). Akaike weights summed across models indicated that the number of days in the sampling period made the largest relative contribution to model fit (0.734) followed by forest age (0.333), sex (0.255), vole age (0.185), and study area (0.067). The amount of total variation in home range size explained by the best model was 0.07. Thus, most of the variation was not explained by any of the variables included in the analysis.

Table 16.—Model selection results from the analysis of factors influencing home range size (CAP method) of red tree voles at the Yellow Creek and Taft Creek Study Areas in Douglas County, Oregon, July 2002–September 2003.

Model structure[a]	K^b	AIC_c	ΔAIC_c	w_i^c
days	3	44.179	0.000	0.222
days + forest	4	44.578	0.399	0.182
days + sex	4	45.172	0.993	0.135
no-effects model	2	45.612	1.433	0.109
days + age	4	46.450	2.271	0.071
forest	3	46.634	2.455	0.065
days + area + forest	5	46.786	2.607	0.060
sex	3	47.568	3.389	0.041
days + sex + age	5	47.599	3.420	0.040
age	3	47.866	3.687	0.035
days + sex + age + forest	6	49.109	4.930	0.019
sex + age	4	49.925	5.745	0.013
days + sex + age + area + forest	7	51.579	7.400	0.005
sex + age + area + forest	6	53.869	9.690	0.002

[a] Covariates indicate model structure for number of days in the sampling period (days), sex, vole age at initial capture (age), study area (area), and forest age (forest),.

[b] Number of parameters estimated.

[c] Model weight.

Frequency of Movements.—The odds of detectable movement between successive relocations was 1.27 times greater for males than for females (95% *CI* = 1.05–1.53, *n* = 2,199). On average, sequential relocations were in the same tree as the previous location 69% of the time for females and 64% of the time for males.

Number of Nests Used per Month.— On average, the number of nests used per month was 2.01 for males (95% *CI* = 0.12–2.85) and 1.06 for females (95% *CI* = 0.53–1.59). The average number of nests used per month was slightly lower in old forest ($\bar{X}$ = 1.21, 95% *CI* = 0.69–1.72) than in young forest ($\bar{X}$ = 1.56, 95% *CI* = 0.94–2.18). The model that best described the variation in mean number of nests used per month included the effects of sex + forest age (Table 17). A model that included only the effect of sex also fit the data reasonably well (Table 17). Akaike weights summed across models indicated that the effect of sex of the vole made the largest contribution to model fit (0.802) compared to 0.467 for forest age, 0.158 for vole age, and 0.158 for study area. The total amount of variation explained by the best models was 0.14. Thus, most of the variation in number of nests used per month was not explained by any of the variables included in the analysis.

Table 17.—Model selection results for the analysis of factors that influenced the number of nests used per month by red tree vole in Douglas County, Oregon, in July 2002–September 2003. The best model is listed first, with other models listed in order of increasing AIC_c values.

Model[a]	K^b	AIC_c	ΔAIC_c	w_i^c
sex + forest	4	53.669	0.000	0.406
sex	3	54.199	0.530	0.311
no-effects model	2	56.239	2.570	0.112
sex + age + area	5	58.003	4.334	0.046
age	3	58.250	4.581	0.041
sex + age + area + forest	6	58.390	4.721	0.038
age + area	4	59.330	5.661	0.024
forest	3	60.417	6.748	0.014
age + area + forest	5	61.608	7.939	0.008

[a] Covariates include model structure for effects of sex, forest age (forest), vole age (age), and study area (area).

[b] Number of parameters in model.

[c] Model weight.

Mean Minimum Distance Moved Per Day.—The mean minimum distance moved per day (MMDM) by females was 3.4 m ± 0.6 (range of individual means = 0.1–15.6 m) and did not vary among months of the year ($F = 1.14$, *d.f.* = 11, 95, $P = 0.34$; Fig. 15). MMDM for males (5.6 m ± 1.8, range of individual means = 0.2–32.7 m) did not differ substantially from females ($t = 1.59$, *d.f.* = 130, $P = 0.12$). Males had slightly higher MMDM in January–July than in the rest of the year ($F = 1.72$, *d.f.* = 11, 44, $P = 0.10$; Fig. 15). This increase in male movements corresponded roughly with the period when most females were lactating or had litters.

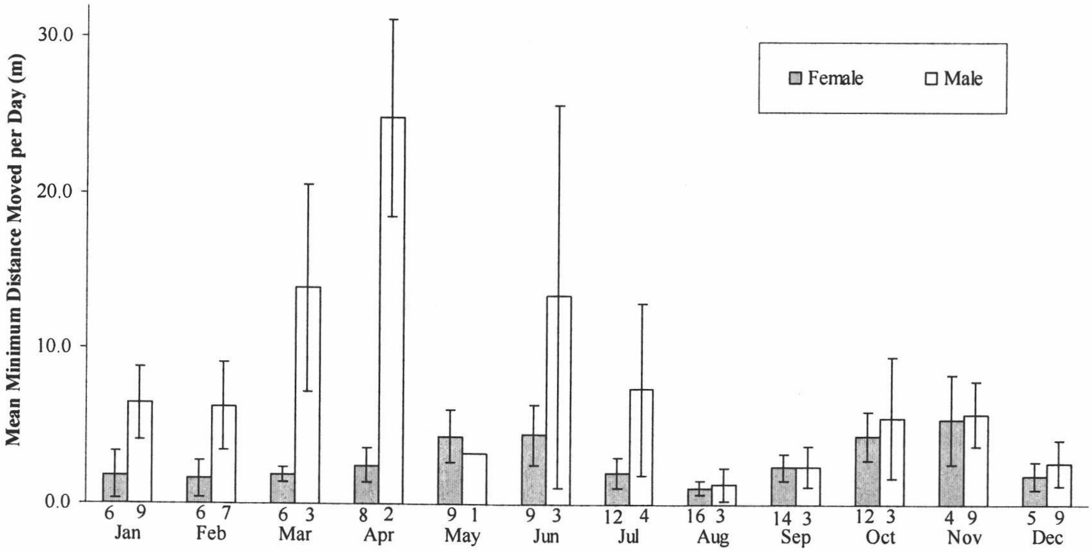

Fig. 15.—Mean minimum distance moved per day (± 1 *SE*) by radiocollared red tree voles during different months of the year in Douglas County, Oregon. Data subdivided by month. Sample sizes are under the columns.

Home Range Overlap.—Adults were normally solitary, but we confirmed 15 cases where voles used nests after the previous occupant died ($n = 7$) or was occupying another nest at the time ($n = 8$). Two nests were occupied by 3 different adult voles on separate occasions. The median number of days between confirmed use of the same nest by different voles was 15.5 days ($\overline{X} \pm SE = 54.9 \pm 4.6$, range = 1–287). Simultaneous occupancy of nests by adult males and females was observed on 2 occasions, once in January and once in February. On both occasions, males visited female nests for a single night and returned to their primary nests by the next morning.

Movements on the Ground.—Of 2,478 radio telemetry locations of live voles, all but 6 were in trees. The 6 exceptions were all cases in which we found voles on the ground as they moved from 1 tree to another. On 1 of these occasions, a vole was observed diving into an underground tunnel as the observer approached at night. In another case, a vole was seen just as it was being captured and killed by a dog that was accompanying the observer. The rarity of ground detections, and many cases where we watched voles travel between trees after flushing them from their nests, indicated that voles generally preferred to travel from tree-to-tree via interconnecting branches, but would travel on the ground if necessary. For example, we documented 2 males that alternated between nests on opposite sides of 22-m-wide gravel logging roads where there were no connecting tree limbs over the roads and the only possible pathway between nests was on the ground. We also found 11 voles in old forests that occupied nests in ≥2 trees that had no interconnecting branches with other trees. These animals were obviously making occasional trips to the ground to move between trees. Thus our data clearly indicate that voles occasionally traveled on the ground in situations where they did not have the option of traversing from tree-to-tree. However, the rarity of terrestrial locations in our sample suggested that, when they came to the ground, voles moved quickly between trees, spending little time on the ground. None of the radiocollared voles were found in ground nests at any time during the study, unless they were dead and cached by predators (see Survival and Predation).

DISPERSAL

The 43 adults that we radiotracked were all residents that remained in the same areas until they died, or until their transmitters quit or were removed. Of the 9 subadults that we monitored, 2 were radiocollared as juveniles in their respective natal nests. Three of the 9 subadults stayed in the same nest for the duration of the study, and 6 moved to new nests before they settled. Straight-line horizontal dispersal distances of the 6 subadults that moved, including the 2 that were marked as juveniles, averaged 55.8 m ± 13.1 (range = 3–75 m). One male juvenile was radiocollared when he was ≈ 37 days old (mass = 17 g) and dispersed when he was ≈ 60 days old. He used multiple trees before becoming stationary in a tree approximately 50 m horizontal distance from the natal nest tree. We were unable to find his radiocollar despite a systematic search of the tree. The second juvenile was radiocollared when she was ≈ 34 days old (mass = 16 g) and dispersed from her natal nest when she was ≈ 57 days old. Within 4 days of leaving her natal nest, she settled at a new nest 75 m from her natal nest. She stayed at the new nest for 26 days before she was killed by a dog.

SURVIVAL AND PREDATION

The Kaplan-Meier estimate of annual survival of radiocollared voles was 0.13 (95% *CI* = 0.06–0.20; Table 18). Survival was mostly constant throughout the study except during intervals 8–9 (8 October–4 November 2002) when there was a marked increase in mortalities (Fig. 16). Apparent causes of the 8 mortalities that occurred during this 4-week period were weasel (*Mustela* spp.) predation ($n = 3$), owl predation ($n = 3$), and unknown causes ($n = 2$).

In the analysis of factors that influenced survival, the best model included a variable time effect only (Table 19). A model that included the effects of variable time + vole mass at first capture was within 2 $\mathrm{AIC_c}$ units of the best model, and therefore was competitive with the best model (Table 19). There was little support for models that included age or sex effects on survival. Akaike weights summed across models indicated that the variable time effect made the largest contribution to model fit (1.00) compared to 0.32 for mass at first capture.

Of 61 voles that we radiocollared, 25 were predated, 6 were confirmed dead from unknown causes, 1 died when its foot became entangled in the radiocollar, 3 were still alive when their radios-transmitters failed, 11 either removed their collars or had their collars removed by predators, 3 were still alive when their radiocollars were removed at the end of the study, and 12 simply disappeared due to unknown causes.

Table 18.—Survival estimates for radiocollared red tree voles in Douglas County, Oregon, based on 2-week intervals from July 2002–September 2003. Probability of survival from time *t* to *t*+1 was calculated from the binomial estimator $s(t) = 1\text{-}d(t)/r(t)$ with $d(t)$ = number of deaths and $r(t)$ = number at risk during each interval. Cumulative survival function is $S(t) = \prod s(t)$.

Interval	$r(t)$	$d(t)$	Censored[a]	$s(t)$	$S(t)$	Variance	95% *CI*
1	5	0	0	1.00	1.00	0.00	1.00–1.00
2	9	0	2	1.00	1.00	0.00	1.00–1.00
3	10	0	0	1.00	1.00	0.00	1.00–1.00
4	16	0	0	1.00	1.00	0.00	1.00–1.00
5	17	0	1	1.00	1.00	0.00	1.00–1.00
6	13	1	2	0.92	0.92	0.07	0.78–1.06
7	16	0	0	1.00	0.92	0.06	0.80–1.05
8	13	5	2	0.62	0.57	0.10	0.37–0.82
9	14	3	1	0.79	0.45	0.09	0.27–0.62
10	15	0	1	1.00	0.45	0.09	0.28–0.61
11	15	1	0	0.93	0.42	0.08	0.26–0.58
12	14	0	1	1.00	0.42	0.09	0.27–0.58
13	18	3	2	0.83	0.35	0.07	0.22–0.48
14	17	0	0	1.00	0.35	0.07	0.21–0.48
15	12	3	0	0.75	0.26	0.06	0.13–0.39
16	9	2	3	0.78	0.20	0.06	0.08–0.36
17	9	0	1	1.00	0.20	0.06	0.08–0.32

Table 18.—Continued.

Interval	*r*(*t*)	*d*(*t*)	Censored[a]	*s*(*t*)	*S*(*t*)	Variance	95% *CI*
18	11	0	1	1.00	0.20	0.05	0.10–0.31
19	12	0	1	1.00	0.20	0.05	0.10–0.30
20	12	0	1	1.00	0.20	0.05	0.12–0.30
21	9	2	1	0.78	0.16	0.05	0.06–0.25
22	11	0	1	1.00	0.16	0.04	0.07–0.24
23	13	0	0	1.00	0.16	0.04	0.08–0.24
24	13	2	2	0.85	0.16	0.04	0.08–0.24
25	11	0	1	1.00	0.13	0.04	0.06–0.21
26	12	0	0	1.00	0.13	0.04	0.06–0.20
27	11	2	0	0.82	0.11	0.03	0.05–0.17
28	10	0	0	1.00	0.11	0.03	0.05–0.17
29	8	1	1	0.88	0.10	0.03	0.03–0.16
30	8	3	1	0.63	0.06	0.02	0.02–0.10
31	3	0	0	1.00	0.06	0.03	-0.01–0.1

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[a] Indicates number that were censored in each interval because (1) voles could not be relocated or their radiocollars were removed, or (2) were killed by their radiocollars or by a dog.

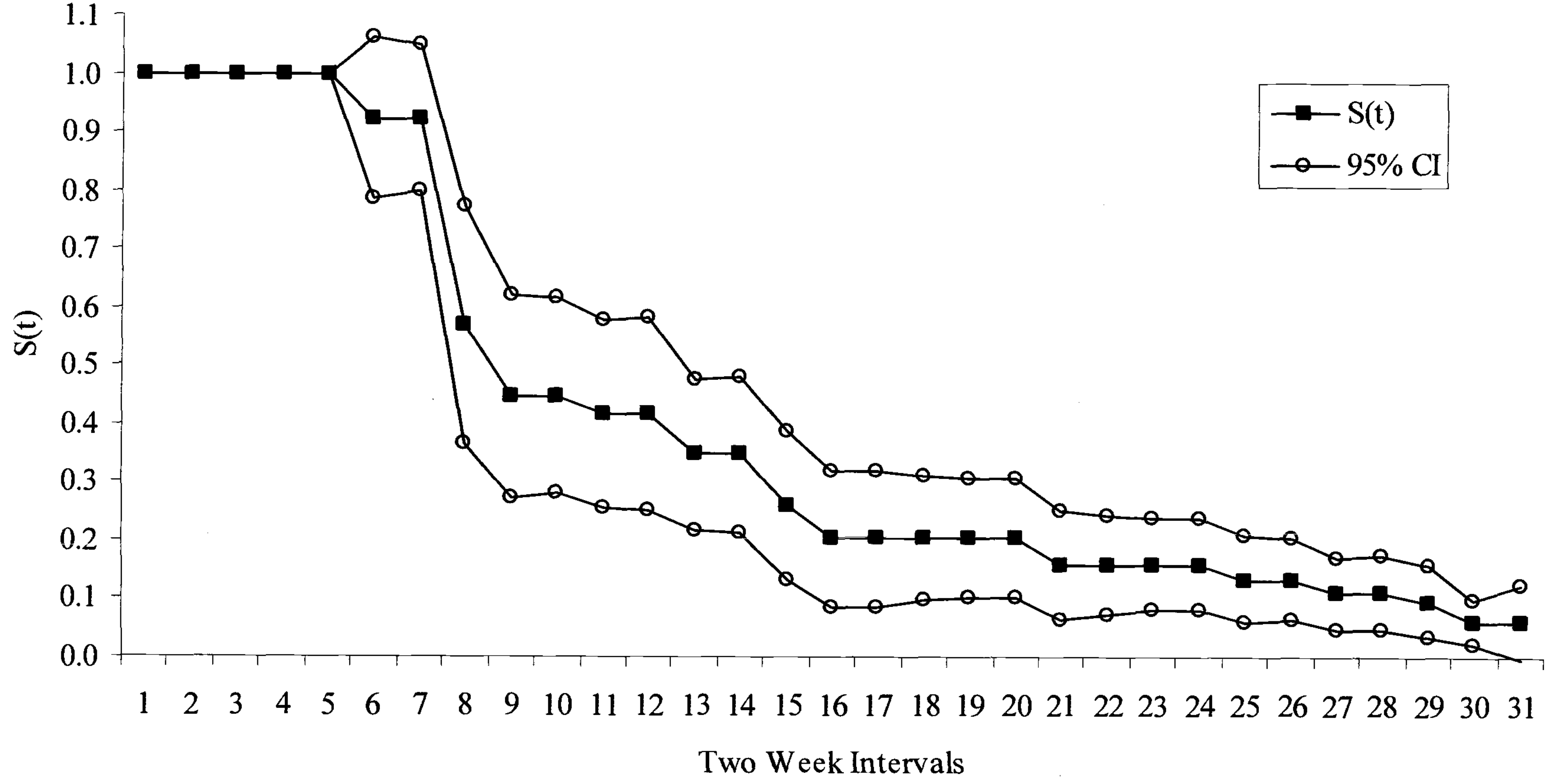

Fig. 16.—Kaplan-Meier survival estimates calculated at 2-week intervals for 61 radiocollared red tree voles in Douglas County, Oregon, July 2002–September 2003.

Table 19.—Model selection results from analysis of bi-weekly survival of radiocollared red tree voles in Douglas County, Oregon, July 2002–September 2003. The best model is listed first with other models listed in order of increasing AIC_c values.

Model structure[a]	K[b]	AIC_c	ΔAIC_c	w_i[c]
S(t)	31	338.4	0.0	0.73
S(t + mass)	32	340.4	2.0	0.27
S(constant)	1	394.7	56.3	0.00
S(forest)	2	395.8	57.4	0.00
S(age)	2	396.5	58.2	0.00
S(T)	2	396.6	58.2	0.00
S(sex)	2	396.7	58.3	0.00
S(sex*forest)	4	399.4	61.0	0.00
S(age*forest)	4	399.6	61.3	0.00
S(sex*age)	4	400.0	61.6	0.00
S(sex*age*forest)	8	405.7	67.3	0.00
S(mass)	1	914.8	576.4	0.00

[a] Covariates indicate model structure for variable time effects (t), linear time effects (T), forest age (forest), and age, sex or mass of the vole at first capture. The S(constant) model included no-effects of age, sex, forest or time on survival.

[b] Number of parameters in model.

[c] Model weight.

Of the 25 voles killed by predators, evidence at the scene suggested that 15 (60%) were killed by weasels (*Mustela* spp.; Fig. 17), 3 (12%) were killed by owls, 1 (4%) was killed by a gopher snake (*Pituophis catenifer*), 1 (4%) killed by a dog, and 5 (20%) were killed by unknown predators (Appendix B). Of the 15 voles killed by weasels, 13 were females. Remains of voles killed by weasels were found in a variety of locations, including tunnels inside decaying logs (*n* = 5), subterranean runways or nests (*n* = 4), on limbs in trees (*n* = 2), on the ground (*n* = 3), or in tree vole nests (*n* = 1; Appendix B). Of the 15 voles killed by weasels, 8 (53%) were mostly or entirely consumed except for bits of fur, 3 (20%) were intact, and 4 (27%) were mostly intact except the brains had been eaten. In 2 cases, it was clear that weasels had climbed into vole nests to capture voles, because there was fresh weasel scat in the nests that the voles had been occupying prior to death. The 5 cases of predation where the predator was unknown included 4 cases where radiocollars were recovered on the ground below nests that had been ripped apart, and 1 case in which we found a radiocollar and vole fur on the ground. The 6 voles that died from unknown causes were all found on the ground with minimal to moderate trauma, including the body of 1 underweight female. The gopher snake that ate the vole was found in a subterranean tunnel approximately 20 cm below the surface and 18 m from the voles nest tree. An x-ray of the snake revealed that the snake had swallowed the vole with the transmitter still in place. The snake regurgitated the vole and radiocollar approximately 6 days after eating the vole and was returned to where it was captured.

Fig. 17.—Nest of a red tree vole TCF08 that was predated by a weasel. The body of the vole was located on the ground 5 m from the nest tree with most of her head eaten. Examination of the nest revealed the top partially torn apart, exposing the tunnel that led to the main nest chamber used by the female.

REPRODUCTION

When capturing voles we did not tear nests apart, so we did not usually see juveniles when we chased their mothers from the nest. However, we did detect a few litters while examining nests in January (1 litter with 1 juvenile), March (2 litters with 1 juvenile), May (1 litter with 1 juvenile, 2 litters with 2 juveniles), June (1 litter with 1 juvenile), July (1 litter with 2 juveniles), and August (1 litter with 2 juveniles). Females that were captured or recaptured on 67 occasions were either lactating or recently post-lactating on 50% of these occasions. The combined data from all sources indicated that breeding occurred throughout the year, with the peak reproductive period from February–September (Fig. 18). Of 9 nests that contained juveniles, no females were found in 5. It was unknown whether females temporarily or permanently left the nest, were hiding in the nest, or had been predated.

We also examined reproductive data for a sample of 301 female tree voles that were captured in the wild and deposited in museums, along with information on their reproductive condition (156 red tree voles, 145 Sonoma tree voles). Based on the percentage of females with litters (*n* = 186) or uterine embryos (*n* = 301), the combined data from museum specimens indicated that breeding occurs throughout the year with peak reproduction occurring from February–August (Figs. 19). Another indication of trends in the annual breeding chronology was the percentage of adult females in museums that had 0, 1, or 2 litters of juveniles in their nests when they were captured (Fig. 20). The percentage of females with 2 litters of different age young in their nests increased from February through July and declined to 0 between September and January, except for a single case in December (Fig. 20).

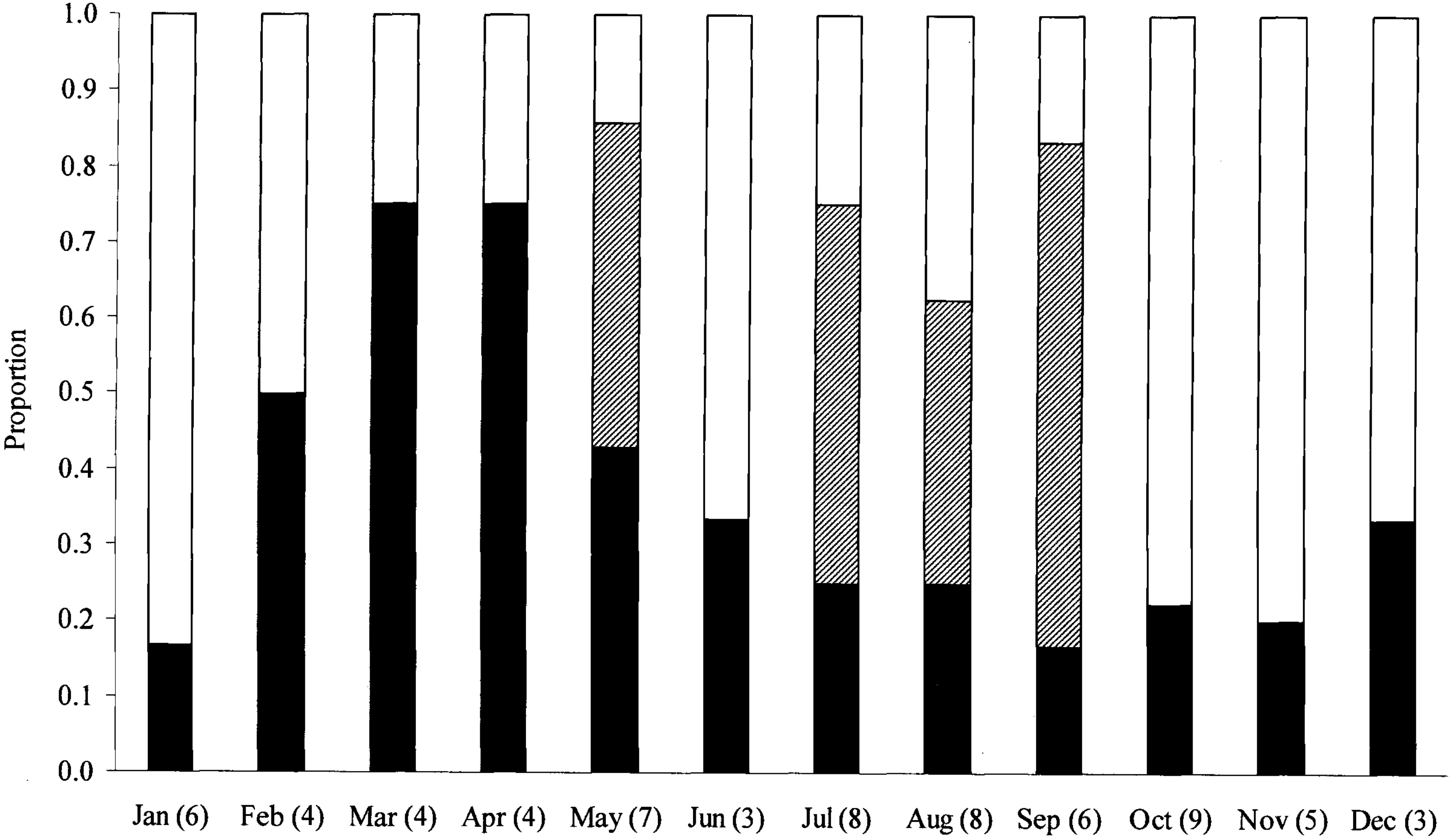

Fig. 18.—Proportion of female red tree voles in breeding condition, subdivided by month in Douglas County, Oregon, July 2002–September 2003. Samples for each month indicate the proportion of females with young (dark shading), females with evidence of recent lactation (diagonal bars), and females without evidence of breeding (unshaded area). Sample sizes are in parentheses.

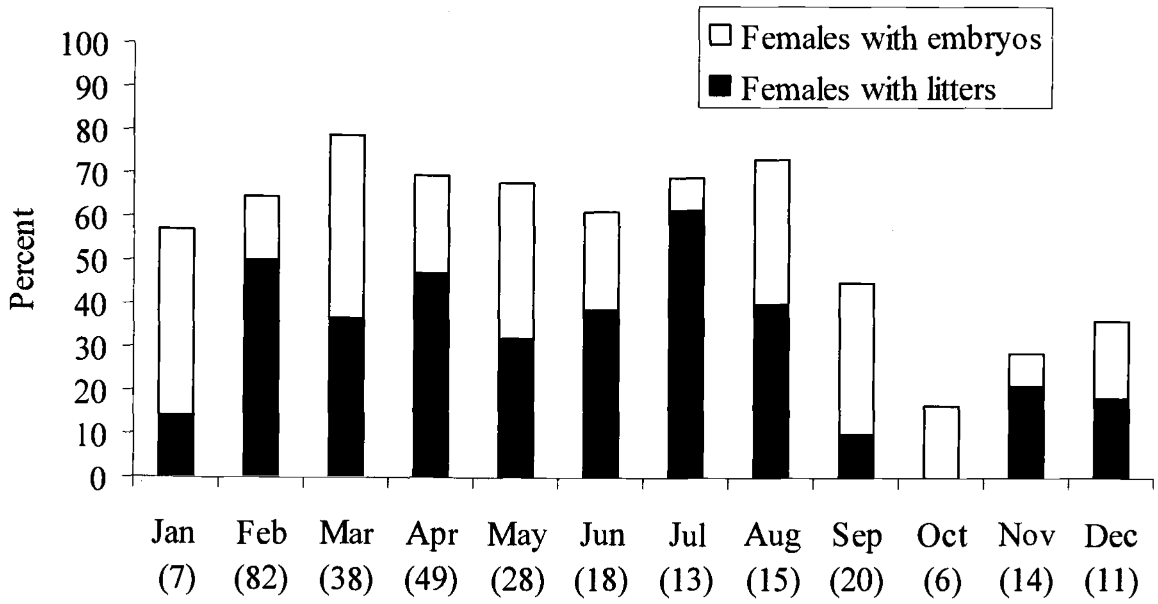

Fig. 19.—Percentage of adult female tree voles in museum collections that had uterine embryos or young at the time of capture. Sample included 156 red tree voles and 145 Sonoma tree voles. Monthly sample sizes are in parentheses.

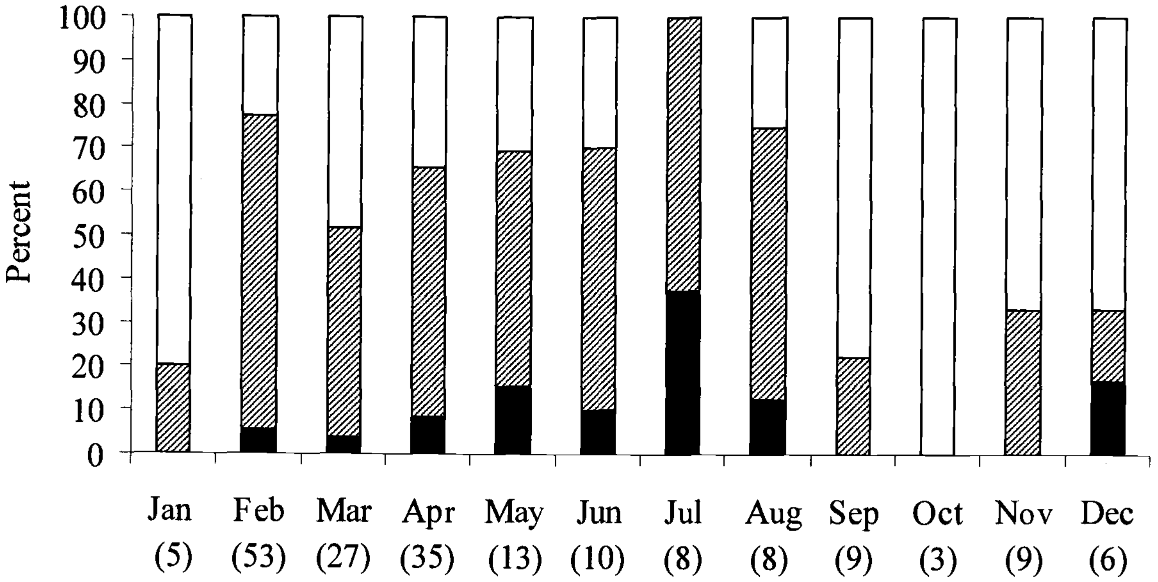

Fig. 20.—Percentage of adult female tree voles in museum collections that had 0 (unshaded area), 1 (diagonal bars), or 2 (dark shading) litters in the nest at the time of capture. Sample included 88 red tree voles and 98 Sonoma tree voles. Monthly sample sizes are in parentheses.

DETECTING VOLES WITH THE INFRARED IMAGER

We were able to detect voles with an infrared imager in 33 of 74 cases (45% detection rate). Voles were be detected only at fairly close range, and only if they were near the periphery of their nests. Voles located deep inside large nests were difficult to detect because the nest material acted as an insulation barrier or the decomposing vegetation and fecal pellets inside large nests created so much heat that the voles were not separable from the rest of the nest. The mean height of nests in which we detected voles with the imager was 6.5 m ± 0.3 (range = 3.7–9.4 m). Although not always useful, the imager was useful at times. For example, 1 vole was detected with the imager as it moved along a branch close to the nest. In another case, we used the imager to detect a vole with a failed radiotransmitter in a nest 7.2 m above the ground. This vole was recaptured by probing the nest at the precise location of the thermal image and catching the vole after it jumped from the nest to the ground. We also used the infrared imager to locate a dead vole that was accidentally stepped on after it jumped from the nest and escaped in dense ground cover.

DISCUSSION

NESTS

Although many researchers have noted that female tree voles tend to have larger nests than males, only one provided quantitative data regarding such differences. Maser (1966:82) reported mean length, width, and depth of 6 nests occupied by males ($\overline{X}$ = 32 x 28 x 25 cm) and 21 nests occupied by females ($\overline{X}$ = 45 x 37 x 28 cm). Estimates of volume calculated from these measurements indicate that female nests in his sample averaged over twice as large as male nests (46,620 cm^3 versus 22,400 cm^3). Compared to the Maser study, our estimates of mean nest volume were considerably larger for both sexes (females = 58,665 ± 8,382 cm^3, males = 39,711 ± 8,674 cm^3). Both studies clearly demonstrate that females tend to occupy larger nests than males.

With the exception of females with young, our radiocollared voles lived solitary lives. When males did visit female nests, it was only for a single night and they returned to their own nests by the next morning. These observations are supportive of Howell (1926:57) who stated that tree voles have "...a markedly solitary disposition, the females usually being truculent and intolerant of other individuals." Our review of field notes, museum specimens, and the literature indicated that previous researchers who have studied tree voles have found only single adult voles or females with young in most nests searched (Taylor 1915; Howell 1926; M. L. Johnson field notes on file at UWBM). One exception was reported by Benson and Borell (1931) who found an adult male and a young subadult female in the same nest.

Except for one case in which M. L. Johnson (field notes on file at UWBM) captured an adult male tree vole in a nest that was simultaneously occupied by a western grey squirrel (*Sciurus griseus*), we found no cases in which tree voles shared nests with other mammals or birds. Clouded salamanders (*Aneides ferreus*) were the only vertebrate that concurrently occupied nests with tree voles in our study. C. Maser also found clouded salamanders co-habiting nests with red tree voles (field notes on file at the James R. Slater Natural History Museum, University of Puget Sound, PSM) and a number of observers have found arboreal salamanders (*A. lugubris*) in nests with Sonoma tree voles (Benson and Borell 1931; Maser 1966; M. L. Johnson field notes on file at UWBM; W. W. Dalquest field notes on file at Museum of Vertebrate Zoology, University of California, Berkeley, MVZ). The warm, damp compost that accumulates in old tree vole nests is probably an ideal micro-habitat for tree-dwelling salamanders, especially because of the large concentrations of invertebrates that also live in tree vole nests (Maser 1966).

One-third of tree vole nests that we examined had evidence of occupancy by different species at different times. Numerous other authors have also documented that tree voles frequently occupy abandoned bird, squirrel, and woodrat nests (Jewett 1920; Benson and Borell 1931; Clifton 1960; Maser 1966).

Data from numerous other studies indicate that the majority of tree vole nests are in the lower third of the live crown (Zentner 1977; Vrieze 1980; Gillesberg and Carey 1991; Meiselman 1992). We found that most of the active nests in old forests were in the lower third of the live crown, but the majority of active nests in young forests were located in the upper 2/3rds of the live crown where these nests were most commonly supported by forked trunks, broken tops with multiple leaders, or dense limb whorls. These types of nest support structures are obviously important for tree voles and are often uncommon in managed stands that have tall, straight boles with few deformities.

However, it is unclear if the absence of tree voles in many young forests is due to the lack of suitable nest support structures or to other factors.

We found that a majority of tree vole nests were in trees on SSE aspects. Howell (1926) and Meiselman and Doyle (1996) also found a preponderance of tree vole nests on southerly aspects. Meiselman and Doyle (1996) proposed that voles might select south aspects to take advantage of higher solar exposure in winter.

TERRESTRIAL ACTIVITY

Our data, and the considerable numbers of tree voles that have been captured in pitfall traps (Appendix C) confirm that tree voles regularly travel on the ground to move between trees. The fact that a few male tree voles have been found nesting in burrows (Howell 1926; Maser et al. 1989; Thompson and Diller 2002) and that samples of voles collected from arboreal nests are often dominated by adult females, has led many authors to speculate that many or even most male tree voles live in burrows in the ground, especially during the dry summer months (Taylor 1915; Howell 1926; Anthony 1928; Cahalane 1947; Ingles 1947; Maser 1966; Nowak 1983). Although he found no tree voles nesting on the ground, Hamilton (1962) speculated that tree voles might nest in burrows during winter because their arboreal nests might not provide enough insulation during cold weather. We found no support for this hypothesis, as none of our radiocollared voles nested on the ground at any time of the year, regardless of their sex, age, or status. Thus, we think that most of the speculation about frequent use of ground nests by tree voles is mistaken, especially in areas like our study area, where live tree crowns are high above the forest floor. We think that biased sex ratios in samples of tree voles collected from arboreal nests or from pitfalls are the result of methodological bias and are not indicative of high use of ground nests by male tree voles.

HABITAT ASSOCIATIONS

In our study, we found approximately equal numbers of active vole nests in young and old forests. While it is tempting to use these findings to refute the numerous claims that tree voles are most abundant in old forests (Meslow et al. 1981; Franklin and Spies 1986; Carey 1989, 1996; Aubry et al. 1991; Gillesberg and Carey 1991; Meiselman and Doyle 1996) or that young forests are populations sinks for tree voles (Carey 1991; Huff et al. 1992), this is not an appropriate use of our data for at least 2 reasons. First, we selected our study areas because we had data from previous surveys in which tree voles were found to be fairly common in these areas. Second, the methods that we used to locate and capture voles may not have been equally efficient in old and young forests. Thus, our study areas were not randomly selected, and our capture methods were probably not without bias. Having said this, we also think that much of the published rhetoric about the relative abundance of tree voles in young and old forests is also based on data that are easily challenged. For example, generic suggestions that all young forests are populations sinks for tree voles (Carey 1991; Huff et al. 1992) are not supported by any data, and the claim that tree voles are "...largely restricted to old growth forests..." (Aubry et al. 1991:294) seems difficult to resolve with the large number of tree voles that we and many other researchers have captured in young forests (Jewett 1920; Howell 1926; Clifton 1960; Maser 1966; Thompson and Diller 2002; M. L. Johnson field notes on file at UWBM).

Based on higher numbers of trees voles captured in pitfall traps in old forests than in young forests, many authors have speculated that tree voles are more abundant in old forests than in young forests (Corn and Bury 1986, 1991; Aubry et al. 1991; Gomez and Anthony 1998; Martin and McComb 2002). While this may be true, we also suspect that pitfall data may be a biased estimator of tree vole abundance relative to stand age. In our sample, large trees in old forests tended to have less connectivity with adjacent trees than did trees in young stands. Thus, it may be that, in order to move between trees, tree voles must descend to the ground more often in old forests than in young forests. This would predispose them to higher capture rates in pitfall traps in old forests than in younger forests. We know of no way to test this hypothesis, but we do think it warrants caution in the interpretation of data from pitfall sampling.

With the exception of a tree vole that was caught in a pitfall trap in a clear-cut >200 m from the nearest forest (Corn and Bury 1986) and a vole caught in a live-trap in a clearcut (Borrecco 1973), there is little direct evidence that tree voles will readily cross large areas of non-forest. However, Biswell and Meslow (1994) observed radiocollared tree voles that crossed logging roads and other canopy gaps that were ≤30 m in width, and 2 of our radiocollared voles occasionally moved between nests on opposite sides of a 22-m-wide gravel road. These results suggest that small forest gaps are no great impediment to movements of tree voles, but we can not rule out the possibility that voles could have reduced survival if they have to descend to the ground to cross openings. The extent to which larger openings impede movements of tree voles is unclear, but Howell (1926) suggested that large expanses of non-forest could act as a barrier to movements by tree voles, resulting in the gradual decline or extirpation of tree vole populations in isolated patches of forest.

GROUND-BASED ESTIMATES OF NEST STATUS

We found that the majority of the nests not previously located from the ground and subsequently located by radiotracking voles were difficult or impossible to see from the ground. This result is in agreement with Howell (1926) who suggested that it was difficult to estimate the abundance of tree voles in a given area because many nests cannot be seen from the ground. We also found that nests of female voles tended to be larger than nests of males and that we were able to correctly determine the status of active tree vole nests only 66% of the time based on visual examination of nests from the ground with the aid of binoculars. These observations led us to conclude that (1) ground-based surveys of tree vole nests will greatly underestimate the number of active vole nests in a given area, regardless of forest age, (2) ground surveys are probably biased towards detection of female nests because the large size of female nests probably makes them more visible, and (3) visual examination of nests from the ground is not a reliable method for determining which nests are occupied by tree voles, especially in old forests where many nests are located high above the ground. Thus, we believe that ground-based surveys of tree vole nests may provide a rough estimate of the relative abundance of tree voles in different forest age classes, but that detectability of nests may be slightly lower in old forests than in younger forests. This could result in underestimates of relative abundance of tree voles in old forests compared with younger forest. There is no obvious solution to the latter problem, but at the very least, all visible nests should be climbed to ensure that status of visible nests is correctly determined.

POPULATION DENSITY

Because they cannot be easily trapped, virtually nothing is known about local or temporal variation in population density of tree voles. The only systematic attempt to document tree vole density was conducted by Maser (1966), who searched for and dissected all nests in a 12.4 ha stand of young Douglas-fir and hardwoods west of Monroe in Lane County, Oregon. He located and dissected 36 tree vole nests, 13 of which were occupied by tree voles, including 10 adult females, 2 adult males, and 28 juveniles. This suggested a minimum adult density of 0.16 males and 0.81 females per ha.

Our study was not a population study, but we did find that the mean number of active nests used by adult voles was 2.2, and that approximately 78% of active nests were not visible or difficult to see from the ground. Theoretically, it should be possible to use these numbers to estimate adult population size based on counts of active nests from ground-based surveys, assuming that an area was searched thoroughly, and that all nests detected were climbed to confirm their status. However, any such estimate would be crude because it would involve numerous assumptions about differences in detectability of nests in different forest types and between nests of males and females. Additional telemetry data from other study areas would be useful for calibrating this type of population estimate.

MELANISTIC TREE VOLES

The high proportion of melanistic individuals observed in the Yellow Creek Study Area was only the second record of melanistic tree voles. J. P. Hayes (pers. comm.) collected 2 melanistic tree voles (1 adult, 1 juvenile) from separate nests in a sample of 6 females captured in March 1995, 8 km northeast of Waldport, Lincoln County, Oregon, 137 km northwest of the Yellow Creek Study Area. Unfortunately, these specimens were discarded after they died in captivity (M. E. Richmond pers. comm.). We found no other evidence of melanism in a sample of 1,048 tree voles that we examined in museums. Miller (1897:85) described a tree vole at the United States National Museum (USNM030649) that was collected from the Oregon Coast Range as "...pale yellowish drab on the dorsal side". We located an additional 5 museum skins at the United States National Museum and James R. Slater Museum of Natural History, University of Puget Sound (USNM563230, USNM563232, PSM10442, PSM23915, PSM10442) that were unusual cream-colored specimens, all of which were collected in Oregon. We suspect that the presence of melanistic or cream-colored tree voles is the result of local inbreeding resulting from low dispersal distances and isolation.

REVERSE SEXUAL DIMORPHISM

Johnson and George (1991) found that females were larger than males based on 17 body and skull measurements of Sonoma and red tree vole specimens. Verts and Carraway (1998) examined 14 body, skull, and mass measurements of 60 female and 69 male red tree voles and found that females were larger than males. Our sample was consistent with the above findings in that mean mass of females was greater than that of males. We also examined the body measurements (total length, tail length, hind foot and ear) of 6 adult females and 4 adult males that we recovered after they died, and found that mean measurements of females were greater than males (Appendix D).

DIEL ACTIVITY

Tree voles in our study were most active at night and were generally inactive during the day except for movements within the nest. On a few occasions, however, we did see tree voles exit their nests during the day to defecate, groom, or feed while we were in the tree at nest height or in an adjacent tree. These results indicate that tree voles are largely nocturnal and that most diurnal activity is limited to movements within the nest. Observations of tree voles in captivity have indicated diel activity patterns similar to those we observed, in that voles seldom ventured from the nest during the day, and spent most of the day sleeping, with short bouts of feeding in their nests (Howell 1926).

NEST DESERTION

Taylor (1915) and Maser (1966) indicated that tree voles will generally abandoned their nests when disturbed. They did not explicitly state what they meant by disturbance, but we assume they meant the dissection of nests to collect voles. Without providing any data, Zentner (1977) claimed that tree voles usually abandoned their nests for 2–7 days or longer after their nests were climbed, and they often deserted their nests for 1–3 days in response to an observer walking to within sight of a nest. While we do not dispute that tree voles usually abandon their nests when their nests are torn apart, our data from radiocollared voles indicated that most individuals continued to occupy the same nests after we climbed their nest trees and captured them, as long as we did not tear their nests apart. There was no indication that the presence of observers walking about below nests caused radiocollared voles to abandon their nests. Thus, we think Zentner's (1977) claims were unsubstantiated hyperbole.

Most observers who have studied tree voles for long periods of time have noted that there is high turnover of occupied nests (Taylor 1915; Howell 1926; Maser 1966; Zentner 1977; Vrieze 1980; Thompson and Diller 2002; M. L. Johnson field notes on file at UWBM). Our data suggest that much of this is due to high turnover of individuals, mostly caused by predation. Thompson and Diller (2002) also suggested that predation was the primary factor causing high turnover in unoccupied nests. However, Maser (1966) and M. L. Johnson (field notes on file at UWBM) also suggested that, at least in some cases, the large numbers of nests were abandoned following severe storm events. High turnover due to predation, combined with frequent use of alternative nests within the home range, could explain why we and most previous observers have found many unoccupied nests with evidence of recent use by tree voles (Taylor 1915; Howell 1926; M. L. Johnson field notes on file at UWBM).

HOME RANGE AREAS

Although they had no data, some authors have speculated that home ranges of tree voles are small and might consist of the nest tree and a few adjacent trees (Taylor 1915; Brown 1985; Carey 1999). This was the case for 20 of the 52 radiocollared voles that we observed but the other 32 radiocollared voles moved between multiple nest trees and 7 of theses individuals frequently moved between alternate nests within their ranges. Males changed nests more frequently than females, but mean distances moved per day and mean home range size did not differ significantly between males and females. The regression analysis of factors effecting home range size indicated that the models that best fit the data were the no-effects model or models that included the number of days in the sampling period.

Although we could usually tell in which tree a vole was, we usually could not pinpoint the exact location of the vole in the tree. As a result, we often assigned nocturnal locations to the UTM coordinates at the center of the tree, usually the nest itself. For this reason, the data for many individuals consisted of large numbers of locations at the nest, with small numbers of locations in adjacent trees. Because of this problem, we were certain that the 100% MCP method resulted in underestimates of home ranges, and we felt that the Crown Area Polygon method produced a more realistic estimate. The ideal method for estimating ranges of tree voles would be a 3-dimensional method (Koeppl et al. 1977) that would take into account vertical as well as horizontal movements within the forest canopy. We know of no current technology that will produce such data over a sustained period of time for an arboreal animal as small as a tree vole.

The only previous data on movements of tree voles were collected by Biswell and Meslow (1994), who studied a sample of 12 radiocollared tree voles (9 adults and 3 subadults) in the Oregon Coast Range near Corvallis, Oregon in 1992–1994. These voles were observed for periods ranging from 35–106 days, nested entirely in trees, and used from 2–7 nests each. Biswell and Meslow (op cit.) found that the mean 100% MCP range size was 1,139 ± 646 m^2 for 6 adult males (range = 376–3,712 m^2) and 344 ± 270

m^2 for 3 adult females (range 41–883 m^2). These estimates were considerably smaller than the mean MCP ranges in our study (males = 1,652 ± 608 m^2, females = 1,153 ± 333 m^2). Whether these differences were due to shorter tracking periods, small sample size, or real variation among study areas was unclear. Also in contrast to our study and most previous studies, the sample of 9 adults captured by Biswell and Meslow (op cit.) included a preponderance of males (66%).

Most species of Arvicolids that have been studied in the Pacific Northwest have mean ranges that are equal to or larger than those of tree voles, and males of most species tended to have larger ranges than females (Table 20). One exception was that female long-tailed voles (*Microtus longicaudus*) studied by Van Horne (1982) had larger home ranges than males (Table 20). Much of the variation among the studies listed in Table 20 is undoubtedly due to small samples and differences in methodology for estimating home range sizes. Larger home ranges size in male Arvicolids is not surprising given that females are constrained for much of the year to a natal nest, whereas males must travel to search for females. Our data suggested that males moved about more than females in general, and were particularly active in late winter and spring, just before and during the period when most females were either pregnant or raising young.

Table 20.—Mean home range estimates (m^2) of voles reported in previous studies in the Pacific Northwest.

Species	Sex	$\bar{X} \pm SD$	*n*	Range	Method	Location/habitat	Source
Arborimus longicaudus	F	344 ± 270	3	41–883	100% MCP	Oregon/Mature Douglas-fir forest	Biswell and Meslow (1994)
	M	1,139 ± 646	6	376–3,712			
Clethrionomys californicus	F	1,350	18	340–3,220	Adaptive Kernel	Oregon/Mature Douglas-fir forest	Thompson (1996)
	M	7,410	5	5,210–9,160			
Clethrionomys californicus	F	767 ± 227	2	606–927	100% MCP	Oregon/Conifer forest	Talmon and Mills (1994)
	M	2,428 ± 1,401	2	1,437–3,418			
Clethrionomys californicus	F	7,930	8	Not reported	95% circular bivariate	Oregon/Mature Douglas-fir forest	Alexander and Verts (1992)
	M	45,570	12	Not reported			
Microtus longicaudus	F	2,360 ± 576	6	Not reported	95% probability distribution	Alaska/Coniferous forest	Van Horne (1982)
	M	1,615 ± 584	7	Not reported			
Microtus oregoni	F	903	20	Not reported	Exclusive boundary strip	Oregon/Coniferous forest	Gashwiler (1972)
	M	1,745	5	Not reported			
Microtus oregoni	F	2,267 ± 891	—	1,619–4,858	Exclusive boundary strip	Oregon/Unburned clearcut	Hooven (1973)
	M	3,845 ± 1,700	—	2,024–6,883			
Microtus miurus	F	450	—	336–775	100% MCP	Alaska/Tundra-shrub	Batzli and Henttonen (1993)
	M	1,250	—	954–1406			

DISPERSAL

Our data on dispersal behavior of 2 juveniles and 7 subadult tree voles suggest that most tree voles disperse only a short distance before settling. This result would seem to support previous speculation that tree voles are relatively weak dispersers and, therefore, may be slow to colonize new areas and susceptible to local extirpation if they become isolated in patchy environments (Cary 1996, 1999; Maser 1998; Huff et al. 2001). Maser (1998) also suggested that the often patchy distribution of tree vole nests was due to young animals settling near their natal sites. He speculated that dispersal behavior was different in old forests because voles could disperse vertically, with multiple generations living in individual trees. We found no cases where multiple adult females lived in the same trees in either young or old forests, although we did find some cases in which there was more than 1 occupied or recently occupied nests in the same large old-growth Douglas-fir tree.

Although the dispersal distances that we documented were short, we are aware of 1 case in which a radiocollared subadult male tree vole dispersed a straight-line distance of 340 m before its transmitter failed (B. L. Biswell pers. comm.). Another observation that suggested a long distance dispersal event was a tree vole that was captured in a pitfall trap in a clear-cut, >200 m from the nearest forest edge (Corn and Bury 1986).

Without providing any supporting data, Carey (1999) suggested that young forests may serve as barriers to dispersal of tree voles. Our data are too limited to demonstrate any influence of forest age on dispersal of tree voles, but we do suspect that the permeability of young stands to dispersal by tree voles is highly variable, depending on a variety of factors such as crown closure, spacing of trees, and tree structure. Young stands with open canopies and tall, straight tree trunks are probably much more inhospitable to dispersing tree voles than are young stands with dense canopies and high concentrations of trees with structures that provide substrates for temporary or permanent nests (broken tops, fork trunks, dense limb whorls, bushy crowns, etc.) Unfortunately, these hypotheses are nearly impossible to test, because it is unlikely that researchers will ever be able to mark and follow enough tree voles to document the effects of forest age or structure on survival of dispersing tree voles.

We located 3 natal nests containing litters of 1–2 large post-weaned juvenile voles but no evidence of an adult female. B. L. Biswell (pers. comm.) also noted at least 2 similar cases. In these situations, it was not clear if the adult females escaped detection, had been recently predated, or had left the juveniles and moved to another nest. Cockburn (1992) listed evidence of "breeding dispersal" by microtine mothers that moved to a new nest after weaning their young. Our observations do not confirm such behavior in the tree vole, but do raise the possibility that it could occur.

SURVIVAL AND PREDATION

M. L. Johnson (field notes on file at UWBM) and Clifton (1960) kept many tree voles in captivity for over a year with a maximum longevity record of 3 years and 2 months. In the wild, however, survival is undoubtedly much lower than is indicated by data from captive voles. Based on development and wear of molars of 76 non-juvenile Sonoma tree voles captured in the wild, Roberts (1989) estimated that only 33% of males and 45% of females were >6 months of age. Based on the higher proportion of older females in his sample of wild-caught tree voles, Roberts (op cit.) suggested that females had higher survival than males. Our data indicated no sexual differences in survival.

We could not rule out the possibility that radiocollars negatively influenced survival of our voles, but there was little evidence that this was the case with the exception of 1 vole that died when his leg became entangle in the radiocollar. Voles that were recaptured to replace transmitters were heavier than when they were first captured, and only 1 of 31 voles that were recaptured had an abrasion caused by the radiocollar. Thus, there was little indication that radiocollars reduced survival.

Because spotted owls are known to capture large numbers of tree voles (Miller 1933; Forsman 1975; Barrows 1980; Forsman et al. 2004), we expected that owls would be a major cause of tree vole mortality in our study. We were surprised to find that predation by weasels was the main source of tree vole mortality, followed in order of decreasing importance by predation by owls and other species. Of the 15 radiocollared voles that were predated by weasels, 80% were females. Whether this was due to small sample size or some other factor was unknown. Cushing (1985) reported that estrous female deer mice (*Peromyscus maniculatus*) were more susceptible to predation by least weasel (*Mustela nivalis*) than were diestrous mice.

We suspect that the single incidence of predation by a gopher snake was unusual. Gopher snakes are known to climb trees and prey on avian nests (Rodríguez-Robles 2002), but our examination of the nest of the tree vole that was predated by the snake revealed no damage to the nest, so we are unsure if the snake captured the vole on the ground or in the nest tree. We also suspect that the single case of predation by a domestic dog was unusual, although we are aware of at least 2 cases in which domestic cats killed tree voles (C. Maser field notes on file at PSM; C. McCafferty pers. comm.). In addition to spotted owls and the predators documented in our study, many other species are known to feed on tree voles, at least occasionally. These include great horned owls (*Bubo virginianus*—Maser 1966), northern saw-whet owls (*Aegolius acadicus*—Forsman and Maser 1970), long-eared owls (*Asio otus*—Reynolds 1970), ringtails (*Bassariscus astutus*—Alexander et al. 1994), common ravens (*Corvus corax*—L. V. Diller pers. comm.), Steller's jays (*Cyanocitta stelleri*—Howell 1926; K. Burton pers. comm.), northern pygmy-owls (*Glaucidium gnoma*) and red-tailed hawks (*Buteo jamaicensis*—Graham and Mires 2005).

REPRODUCTION

A number of authors have claimed that tree voles breed throughout the year (Maser et al. 1981; Huff et al. 1992; Carey 1999) without providing supporting evidence. Based on data from other species of Arvicolids, Taylor (1915) and Howell (1926) speculated that breeding by tree voles was limited primarily to late winter, spring, and fall. We documented females in reproductive condition or with young in nests throughout the year, with the peak period of reproduction between February and September. A review of museum specimens also indicated that breeding occurs throughout the year with peak reproduction occurring from February–August. The data from our study and from museum specimens both suggest similar seasonal chronologies.

SUMMARY AND RECOMMENDATIONS

Our results support previous studies that indicated that tree voles are solitary, nocturnal, and mainly arboreal but will come to the ground to move between trees that do not have interconnecting branches. We found no evidence of use of ground nests which led us to conclude that use of ground nests by tree voles is a uncommon, at least in forests where the live tree crowns are located high above ground. Tree voles used 1–6 nests within home ranges that varied in size from a single nest tree with adjacent foraging trees to multiple nest trees that were spaced up to 131 m apart. Males moved between nest trees more often than females, but on average, size of home ranges did not differ between the sexes. Dispersal distances of 2 juveniles from their respective natal nests were only 50–75 m, suggesting low dispersal abilities of tree voles. However, records of tree voles that moved >200 m have been documented in other studies, indicating that, at least occasionally, tree voles are capable of moving considerable distances between nests.

Radiocollared voles had low annual survivorship and a high rate of predation, most of which was due to weasels. Presence of weasel scat in tree vole nests indicated that at least occasionally, weasels captured tree voles by climbing trees and capturing voles in their nests. Other documented predators were owls, a gopher snake, and a dog. All of the above life history traits, along with small litters, and a long gestation period, suggest that tree vole populations probably grow at a slow rate even under optimum conditions.

Our sample of radiocollared voles included more females than males, a situation that has been noted in most previous studies in which observers searched for nests from the ground, and then climbed trees to capture voles. In contrast, our examination of museum specimens indicated that tree voles collected by loggers included nearly identical numbers of males and females (60:67), and samples of tree voles collected in pitfall traps were highly biased towards males (101:34). We believe that the skewed sex ratios in samples collected with visual nest searches and pitfall traps are due to methodological bias. On average, nests of female tree voles were larger and more conspicuous than nests of males, which results in more female nests being detected during visual searches. In addition, male tree voles move between nests more frequently than do females, which may account for the higher numbers of males captured in pitfall traps. In contrast, sex ratios of voles captured by loggers are probably the least biased method for estimating population structure because both sexes are equally likely to be captured when trees are felled and disoriented or dead voles are found among the debris.

Of the 61 tree voles that we radiocollared, 41 were in young forests that were regenerating on areas that were clear-cut and replanted in 1948–1979, and 20 were in old forests dominated by mature or old-growth trees that were 110–250 years old. The preponderance of radiocollared voles in young forest was not intentional. Rather, it was due to the fact, that despite a concerted effort, we were unable to capture as many voles in old forest as in young forests. Several sources of bias could have caused this result. Principal among them was the fact that nests were more difficult to see when they were high up in big trees with complex structure, and that big trees are more difficult to climb than small trees. Thus, it was usually possible to climb several small trees in the time it takes to climb a large tree.

In many recent publications, biologists have suggested that tree voles are most common in old forests and are uncommon or absent in young forest (Corn and Bury

1986; Carey 1989, 1996; Aubry et al. 1991; Huff et al. 1992). Carey (1991, 1999) further hypothesized that old forests are more stable environments for tree voles and that young forests were unstable, rapidly changing habitats with lower food availability for tree voles than old forests. Based on our experience, we think that these opinions about tree voles are considerable over-simplifications of the actual relationships between tree voles and young forests. While we agree that old forests are probably a more stable environment for tree voles, and that many young stands have low densities of tree voles, we, and many others, have found that some young forests have relatively high numbers of tree voles, including many breeding females (Jewett 1920; Howell 1926; Clifton 1960; Maser 1966; Thompson and Diller 2002; M. L. Johnson field notes on file at UWBM). While these results are often ignored or discounted because they are based on non-random collection methods, we believe they actually indicate that young forests play an important role in the dispersal and persistence of tree vole populations and should not be dismissed as unimportant or unsuitable habitat for tree voles. In many areas young forests may be the only chance for persistence of the species, especially in landscapes where old forests have been largely eliminated or are restricted to remnant patches interspersed within extensive areas of young forest. Unfortunately, the plethora of recently published opinion pieces about tree vole associations with old forest have led many forest managers to believe that young forests are unimportant for the persistence of tree voles, and that thinning or pruning of young stands will have few negative consequences for tree voles. As a result, young forests are often targeted for thinning projects, with negative consequences for the tree voles that are present. In our opinion, this aspect of the ecology of the tree vole is poorly understood, and greatly in need of further investigation.

Until better information is available on the factors that influence patterns of abundance and distribution of tree voles, managers should consider non-treatment of forest stands occupied by tree voles as an option for management, especially in regions such as the northern Coast Range of Oregon, where recent surveys suggest that tree voles are extremely uncommon (USDA Forest Service and USDI Bureau of Land Management Survey and Manage Program Interagency Species Management System, ISMS, unpubl. data). Trees with broken tops, densely spaced branch clusters, deformed limbs, bushy crowns, and forked trunks should be retained in managed forests as they are important habitat components for arboreal species like tree voles.

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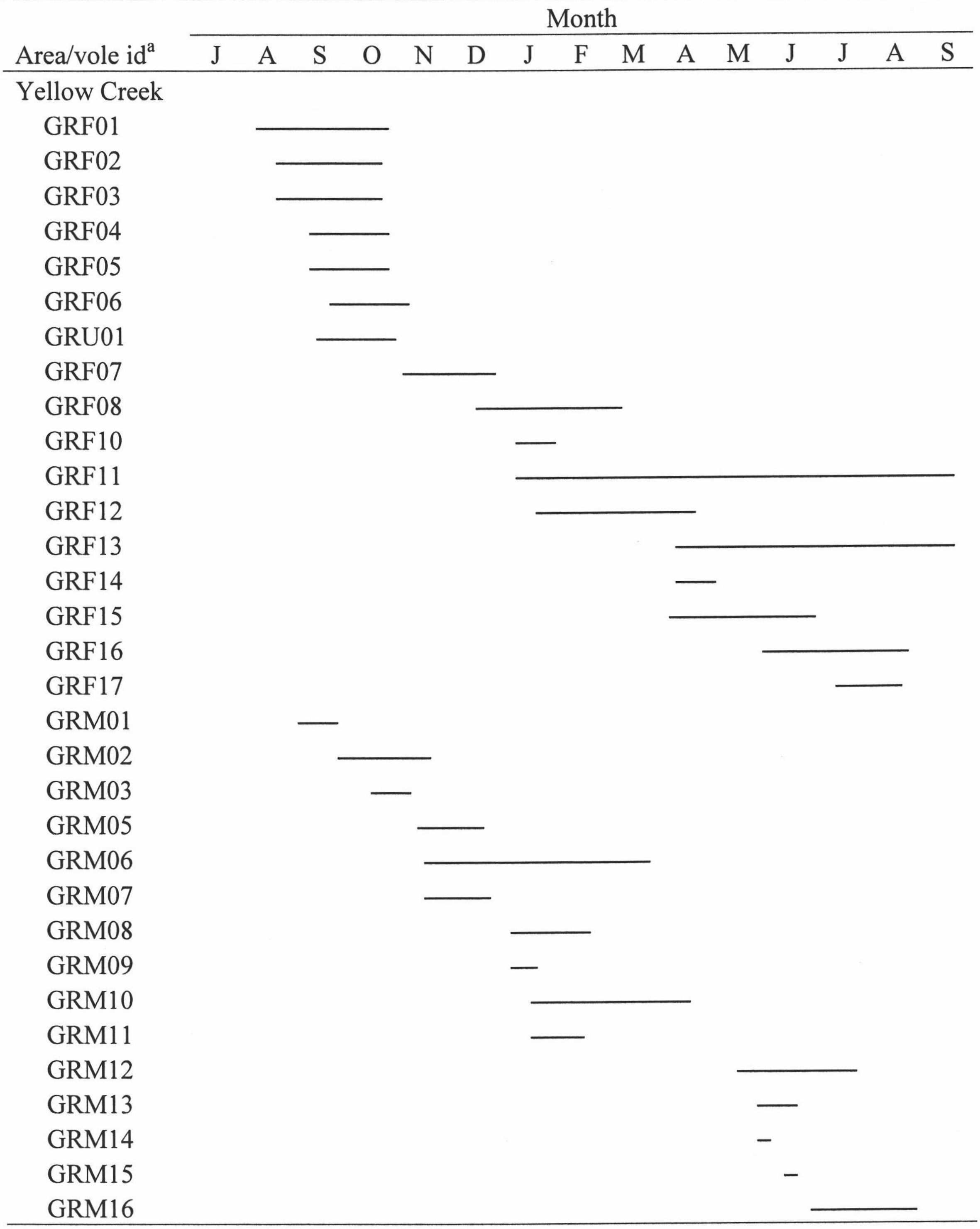
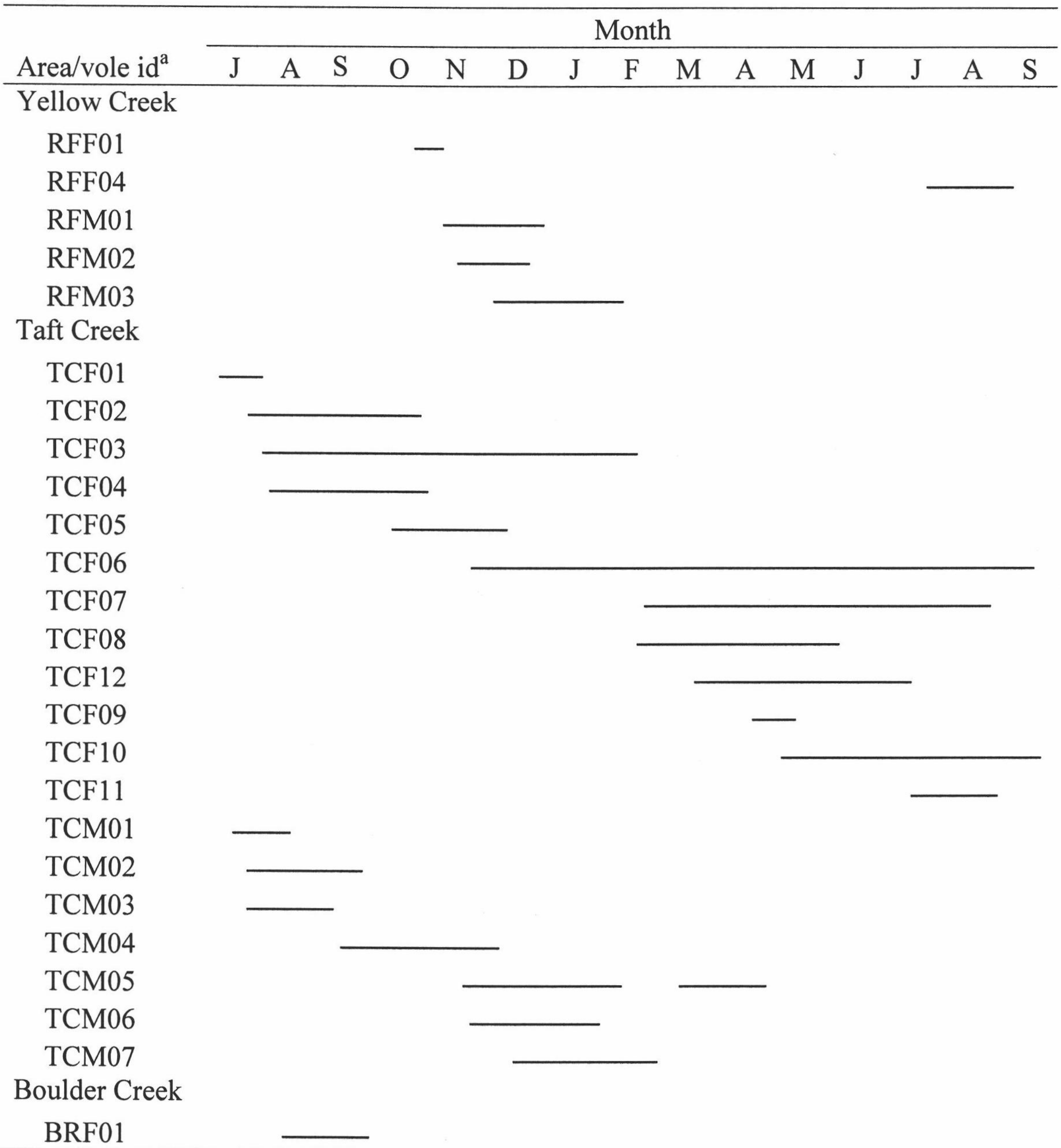
APPENDICES

Appendix A.—Monthly tracking periods for 57 radiocollared red tree voles in Douglas County, Oregon, July 2002–September 2003. Third letter indicates sex (M = male, F and U = Female). Sample excludes 5 juveniles.



Appendix A.—Continued.



[a] First 2 letters indicate study area: TC = Taft Creek, BR = Boulder Ridge, GR and RF = Yellow Creek. Third letter indicates sex, and number indicates vole number.

Appendix B.—Suspected causes of mortality of radiocollared red tree voles in Douglas County, Oregon, July 2002–September 2003.

Vole	Sex	Age	Suspected cause	Evidence	Distance from nest (m)
GRF08	F	AD	Predation	Radiotransmitter signal weak before loss of signal. Nest ripped apart.	0
GRF17	F	AD	Predation	Radiocollar found on ground 63.2 m from nest that was ripped apart.	63
GRM09	M	AD	Predation	Radiocollar and fur along recovered on ground.	81
GRM16	M	SUB	Predation	Radiocollar found under nest tree among ripped apart nest material.	3
TCM02	M	AD	Predation	Radiocollar found under nest tree among ripped apart nest material.	0
GRF05	F	AD	Owl	Intact body cached face down 5.8 m up a tree on a single branch.	26
RFF01	F	AD	Owl	Intact body cached face down 11.6 m up a tree on a single branch.	55
TCF04	F	SUB	Owl	Intact body cached face down 10.2 m up a tree on a single branch.	104
GRF13	F	AD	Snake	Vole located inside gopher snake (*Pituophis catenifer*).	18
RFM01	M	AD	Unknown	Radiocollar located in 4 cm wide and 3 cm deep crack on top of a log.	97
GRF06	F	AD	Unknown	Located on ground with minimal external signs of trauma (small head wounds with blood in ears).	67
GRM02	M	AD	Unknown	Found on ground below nest tree with minimal trauma (abrasions on head with spots of blood by eye).	4
RFM02	M	SUB	Unknown	Found on ground below nest tree with moderate signs of trauma (head and body wounds).	0
TCM06	M	AD	Unknown	Body on ground with moderate trauma. Head wounds and body abrasions.	6
TCF03	F	AD	Unknown	Found on ground below nest tree. Vole looked emaciated (23 g).	0

Appendix B.—Continued.

Vole	Sex	Age	Suspected cause	Evidence	Distance from nest (m)
GRF01	F	SUB	Weasel	Radiocollar recovered in tree vole nest along with fresh weasel scat.	0
GRF02	F	AD	Weasel	Radiocollar and fur recovered in decay class IV log with fresh weasel scat.	76
GRF03	F	AD	Weasel	Radiocollar and fur recovered in decay class III log with weasel scat.	29
GRF07	F	AD	Weasel	Body cached in decay class IV log.	215
GRF10	F	AD	Weasel	Radiocollar and fur recovered 22 cm underground in subterranean runway.	43
GRF12	F	AD	Weasel	Radiocollar and 2 coast moles (*Scapanus orarius*) recovered in subterranean weasel nest.	160
GRF14	F	AD	Weasel	Radiocollar and deer mouse (*Peromyscus maniculatus*) head and tail recovered under forest duff.	2
GRF15	F	AD	Weasel	Vole recovered in subterranean runway.	60
GRM07	M	AD	Weasel	Body cached in decay class III log.	195
GRM11	M	SUB	Weasel	Found cached on its back 9.4 m up in a tree with most of body and head eaten.	40
GRM15	M	SUB	Weasel	Radiocollar and tree vole fur recovered in subterranean nest made of moss and shredded bark.	21
TCF05	F	AD	Weasel	Brains and part of body eaten, cached on its back on a branch 9.8 m up in a tree. Tail half the original length.	6
TCF07	F	AD	Weasel	Radiocollar located in subterranean runway 6.0 m from the ripped apart nest.	6
TCF08	F	AD	Weasel	Body recovered on ground below nest with most of head eaten. Nest ripped apart.	6
TCF12	F	AD	Weasel	Body recovered on ground with part of face and brains gone. Pair of puncture wounds 0.9 mm apart on maxilla.	65
GRU01	F	SUB	Dog	Subadult female killed on ground by dog that was accompanying observer.	0
GRM10	M	AD	Study	Foot caught between neck and radiocollar	0

Appendix C.—Number of tree voles captured per 10,000 trap nights in published studies in which pitfall traps were used to sample small mammals in western Oregon and northern California.

Source	Study location	No. of trap nights	Small mammals captured	Tree voles captured	Tree voles per 10,000 trap nights	Proportion of mammals that were tree voles
Corn & Bury (1986)	Cascade Mountains	38,880	2,104	18	4.6	0.0085
Manning & Maguire (1999)	Cascade Mountains	21,168	1,265[a]	1	0.5	0.0008
Corn & Bury (1991)	Coast Ranges	108,864	3,047	13	1.2	0.0043
Gilbert & Allwine (1991)	Cascade Mountains	ND[b]	ND	9	ND	ND
Gomez & Anthony (1998)	Coast Ranges	100,800	9,723	13	1.3	0.0013
Martin & McComb (2002)	Coast Ranges	127,900	16,892	42	3.3	0.0025
Ralph et al. (1991)	Klamath Mountains	141,120	ND	22	1.6	ND
Raphael (1988)	Northwest California[c]	898,431	4,914	19	0.2	0.0038

[a] T. Manning pers. comm.

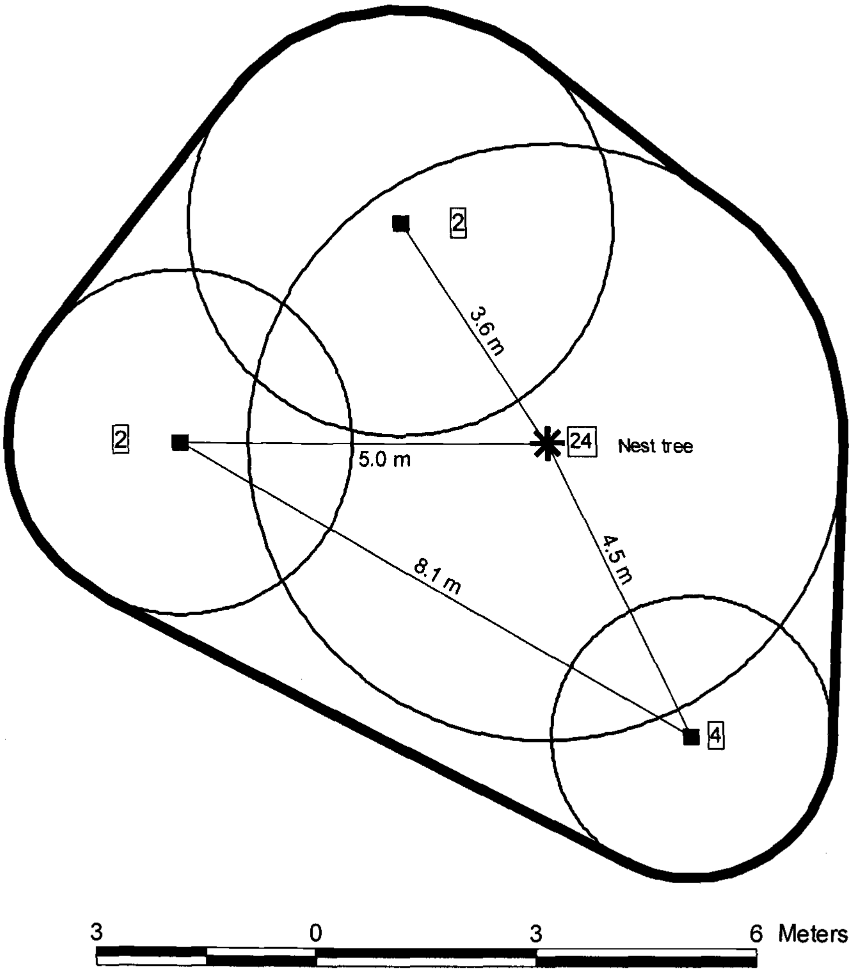
[b] ND = data not provided.

[c] Tree voles that were captured in this study were south of the Klamath River, which is within the range of the Sonoma tree vole (*Arborimus pomo*).

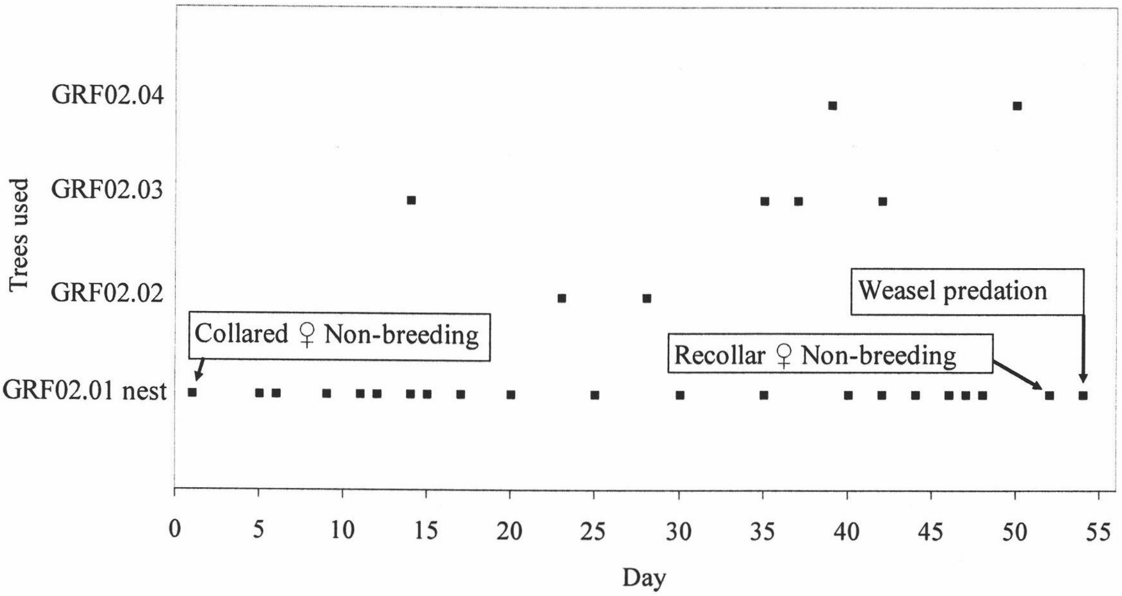
Appendix D.—List of red tree vole specimens sent to the University of Washington Burke Museum (UWBM) from the radiotelemetry study in Douglas County, Oregon, July 2002–September 2003.

Vole id	Catalog number	Pelage color	Sex	Age	Mass (g)	Body measurements (mm)			
						Total	Tail	Foot	Ear
GRF05	78042	Red	F	AD	34.0	183	73	20	14
RFF01	78033	Red	F	AD	31.0	182	72	18	10
TCF03	78048	Red	F	AD	23.0	175	69	18	12
TCF04	78041	Red	F	AD	29.0	172	72	20	9
GRF07	78052	Red	F	AD	31.0	171	64	19	13
GRF06	78037	Black	F	AD	25.0	159	68	20	11
RFF02	78036	Gray	F	Sub	21.0	154	69	20	11
GRF09	78050	Gray	F	Sub	22.0	152	65	20	12
GRU01	78030	Red	F	Sub	21.7	151	57	20	10
RFF03	78038	Gray	F	Sub	18.5	131	47	19	10
TCF05	78039	Red	F	AD	—	—	—	—	—
TCM06	78051	Red	M	AD	29.5	170	67	19	10
GRM07	78035	Red	M	AD	29.1	168	64	20	11
GRM02	78034	Black	M	AD	22.0	164	68	19	10
GRM04	78031	Red	M	AD	28.0	157	61	19	10
RFM02	78029	Red	M	AD	26.0	151	59	18	7
GRM11	78040	Black	M	AD	—	—	—	—	—
BRJ02	78044	Gray	U	Juv	5.5	71	19	—	—
BRJ01	78043	Gray	U	Juv	5.3	79	22	—	—
GRJ03	78045	None	U	Juv	3.5	57	12	—	—

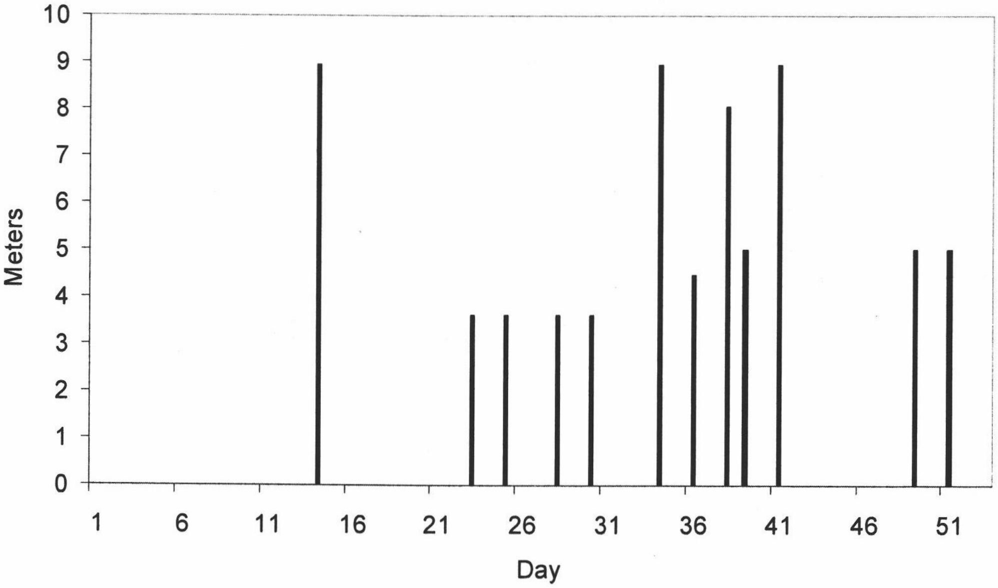
Appendix E.—Examples of small, medium and large home range areas and movements of red tree voles that were radiotracked in Douglas County, Oregon, July 2002–September 2003. Data for each vole include 3 figures, one that illustrates the home range, another that illustrates the frequency of relocations in the initial nest and other trees or nests, and another that illustrates distances moved between locations collected on different days. In the home range figures, known nest trees are indicated by an asterisk (*) and other locations are indicated by solid boxes (■). The number of relocations in each tree is indicated in a box along with a unique code for each tree. Thin straight lines indicate minimum distance moved between locations. Circles indicate horizontal crown area of trees in which voles were located. The thick dark line connecting the outer edges of tree crowns indicates the Crown Area Polygon (CAP) home range. The 100% MCP (not shown) was the area within a convex polygon connecting the outermost locations of the tree bole point locations. In the nest occupancy figure, codes for unique trees in which voles were located are labeled on the Y axis. First 2 letters indicate study area, third letter indicates sex, next 2 numbers indicate vole number that was first located in the tree, and 2 digits after the decimal indicate tree number.



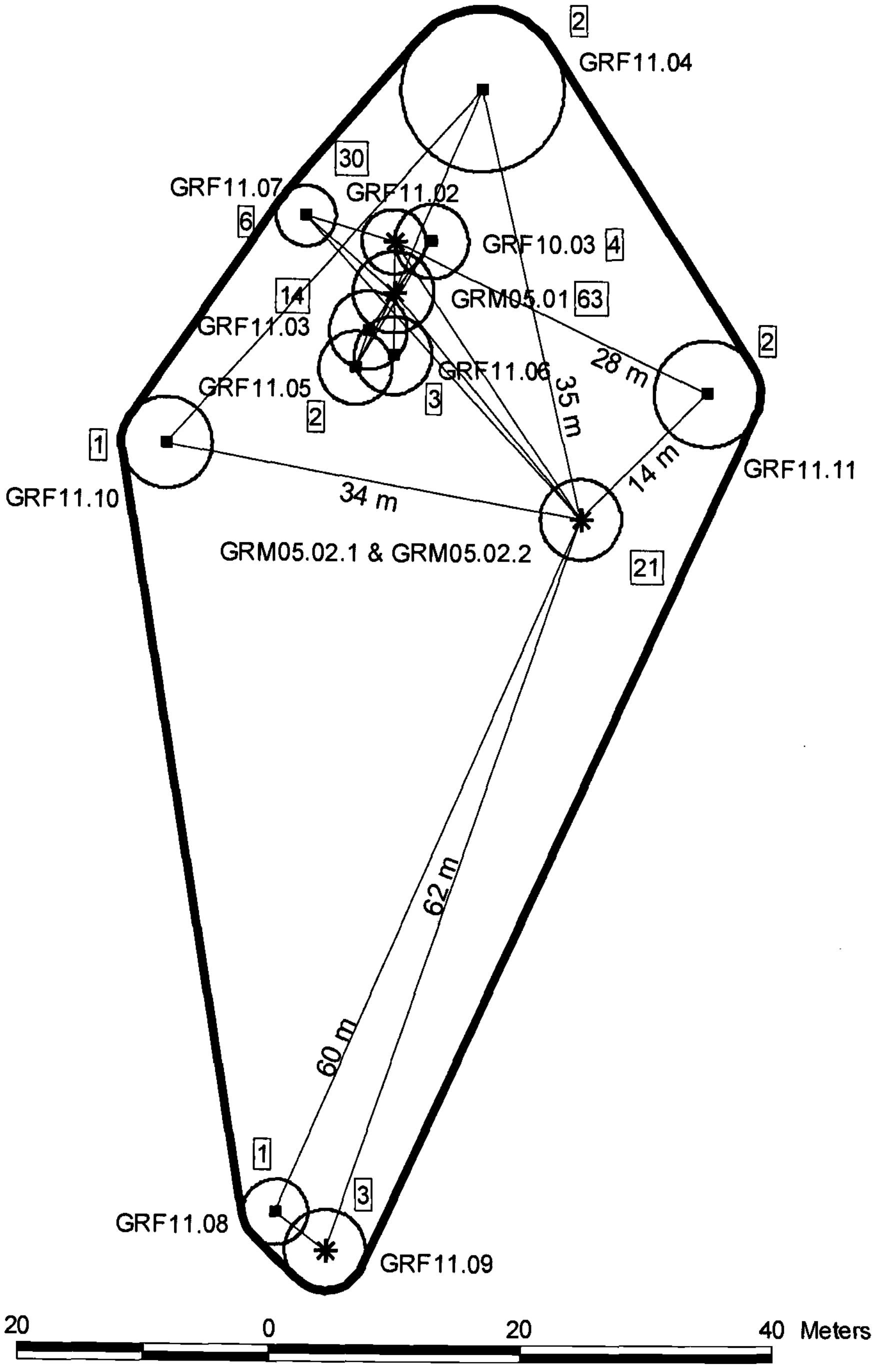
Appendix E-1A.—Home range area of Yellow Creek adult female tree vole GRF02. She was tracked for 59 days (26 August–24 October 2002) in a 39-year-old forest before she was killed by a weasel. Home range estimates were 92 m^2 (CAP) and 18 m^2 (100% MCP).



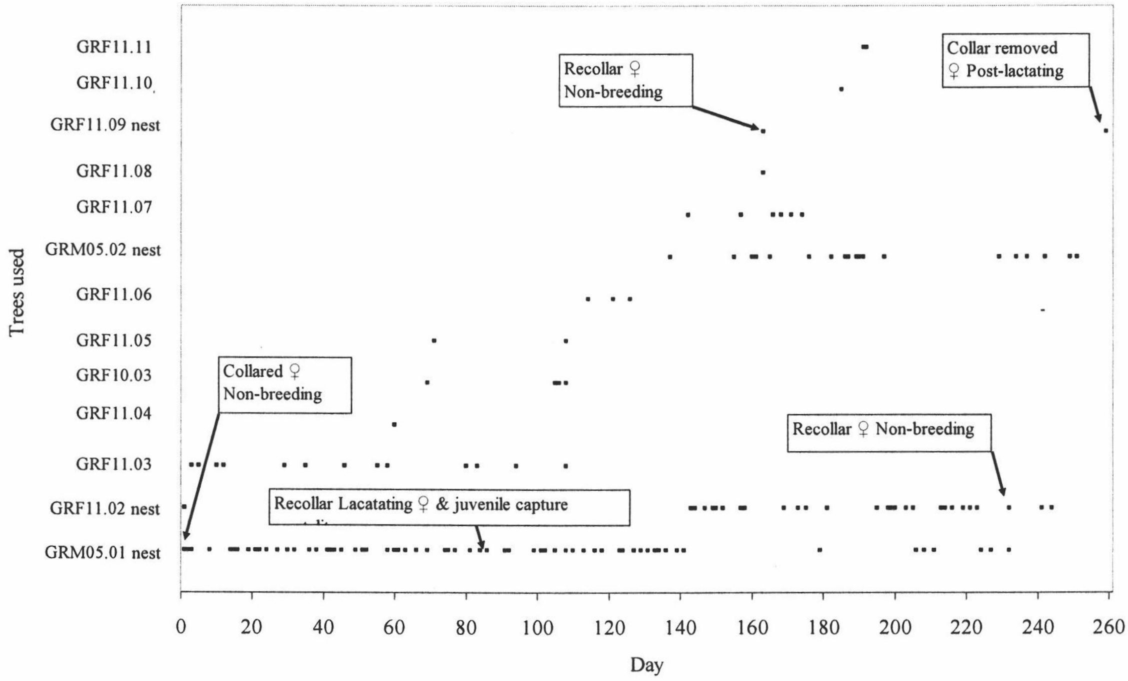
Appendix E-1B.—Frequency of relocations of Yellow Creek adult female tree vole GRF02 in different trees.



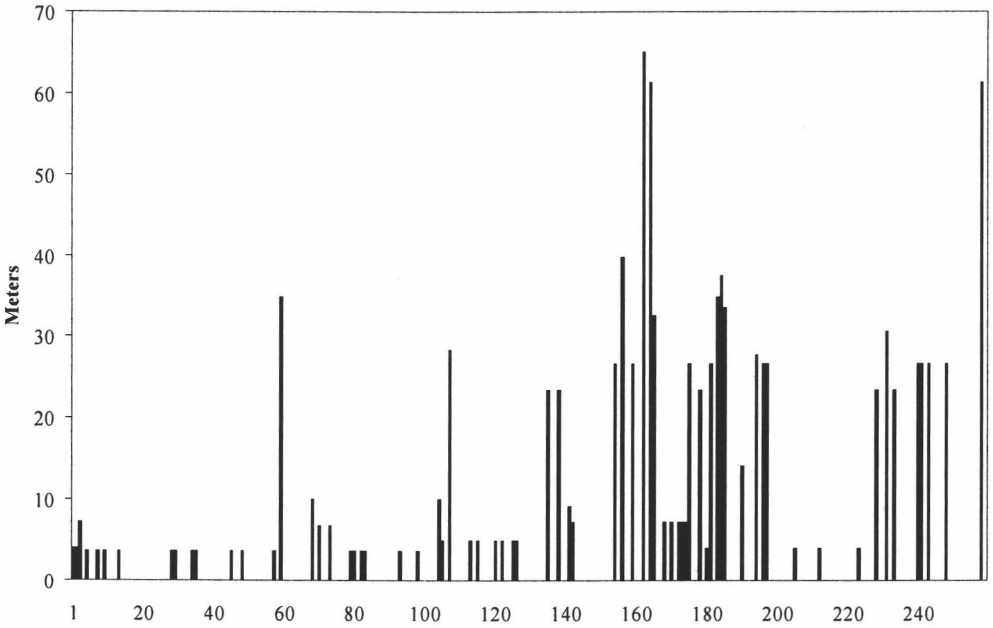
Appendix E-1C.—Minimum distance between sequential relocations of Yellow Creek adult female tree vole GRF02.



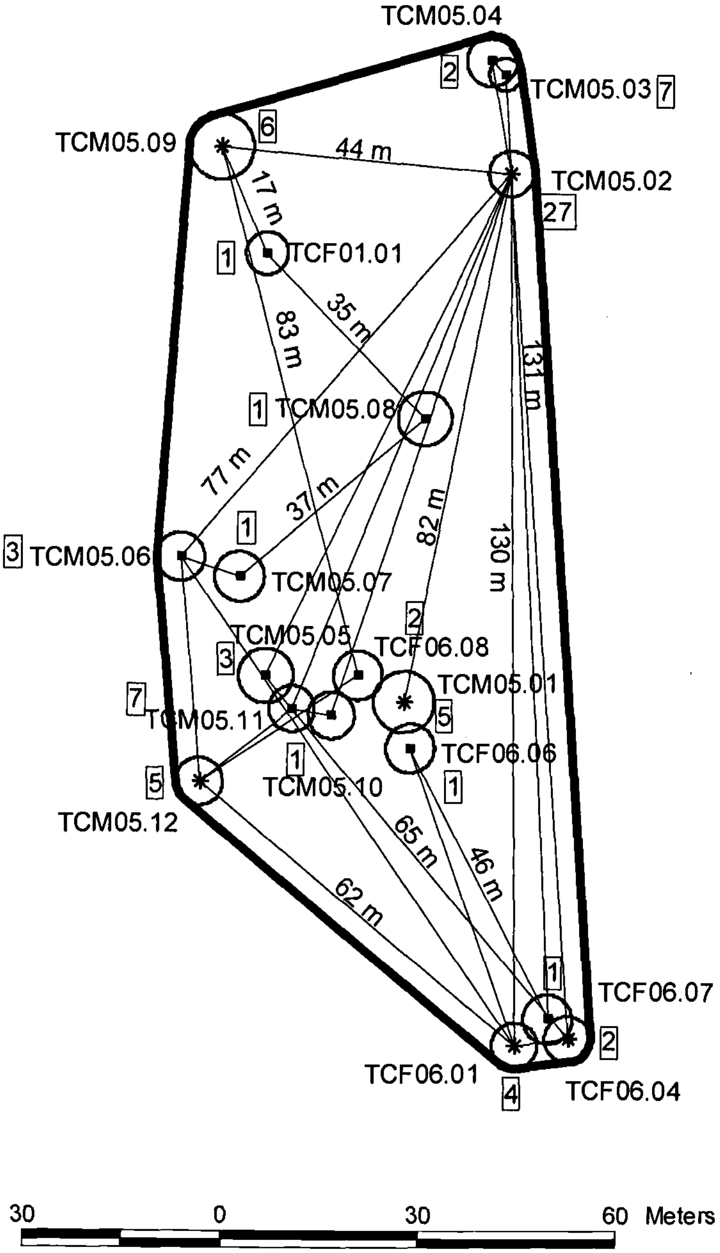
Appendix E-2A.—Home range area of Yellow Creek adult female tree vole GRF11. She was tracked for 258 days (7 January–22 September 2003) in a 39-year-old forest before her radiocollared was removed at the end of the study. Home range estimates were 2,978 m^2 (CAP) and 2,134 m^2 (100% MCP).



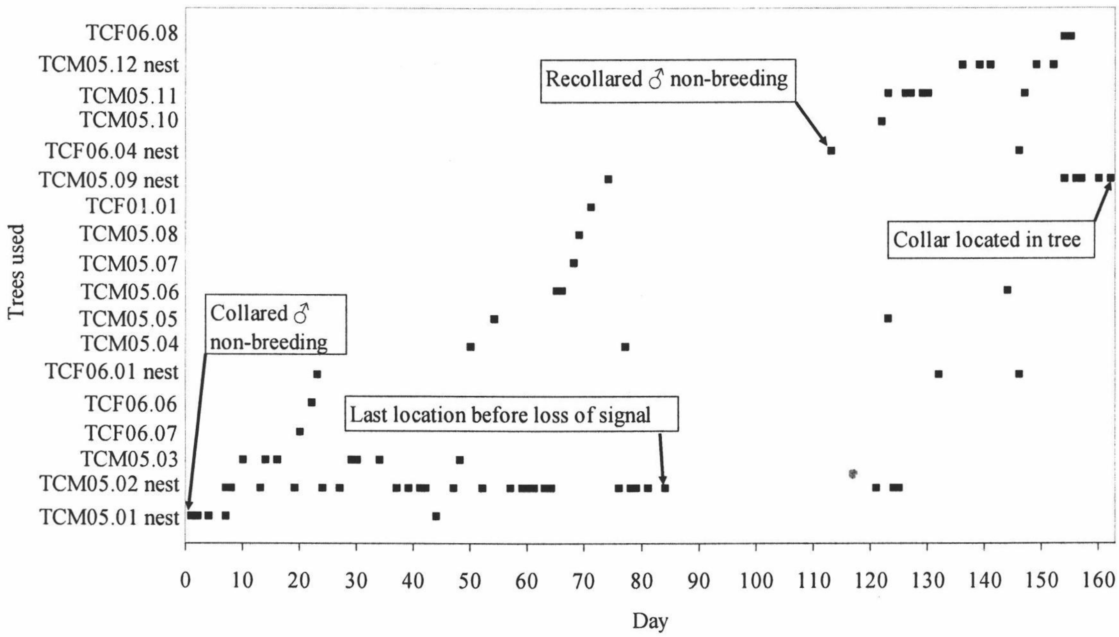
Appendix E-2B.—Frequency of relocations of Yellow Creek adult female tree vole GRF11 in different trees.



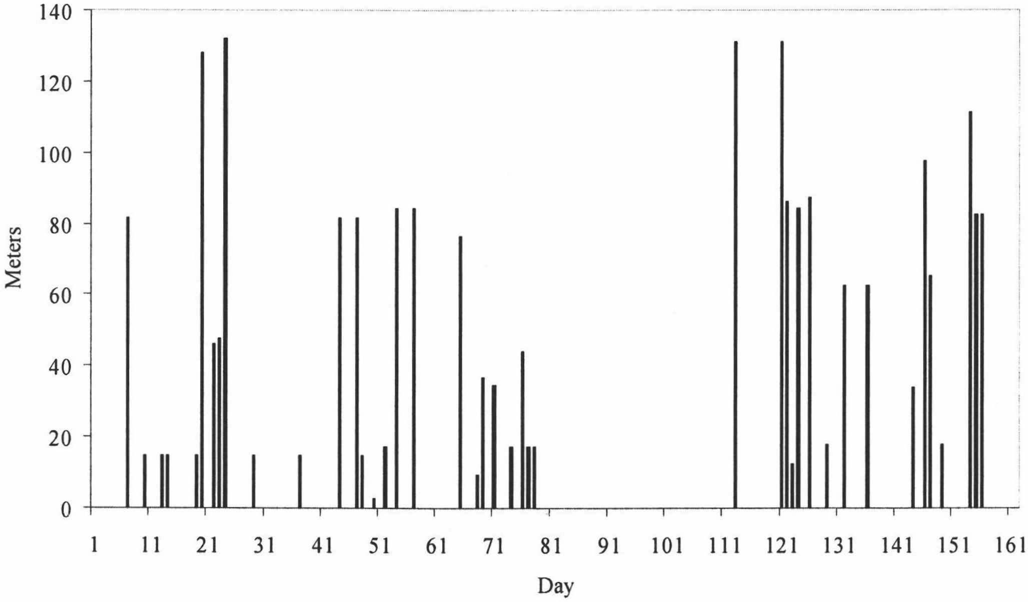
Appendix E-2C.—Minimum distance between sequential relocations of Yellow Creek adult female tree vole GRF11.



Appendix E-3A.—Home range area of Taft Creek adult male tree vole TCM05. He was tracked for 99 days (30 November 2002–6 May 2003) in a 54-year-old forest before we found his radiocollar hanging in a tree. Home range estimates were 7,761 m^2 (CAP) and 6,374 m^2 (100% MCP).



Appendix E-3B.—Frequency of relocations of different trees by Taft Creek adult male tree vole TCM05.



Appendix E-3C.—Minimum distance moved between sequential relocations of Taft Creek adult male tree vole TCM05.