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Home Range Areas and Activity Patterns of Red Tree Voles *(Arborimus longicaudus)* in Western Oregon

Abstract

We radiocollared 45 red tree voles *(Arborimus longicaudus)* in western Oregon and monitored their movements during July 2002-September 2003. We predicted that home range areas would be larger in young forests than in old forests and that males would have larger home ranges and use more nests than females. We tracked individual voles for 82 ± 9 days (mean ± SE; range = 24-307 days). Voles were active primarily at night, although we did see voles outside their nests during the day on two occasions. Of the 45 voles, 18 (4 males, 14 females) occupied a single nest tree aud adjacent foraging trees that had interconnecting branch pathways with the nest tree. The other 27 voles (11 males, 16 females) used >2 nest trees (range = 2-6). Average distauce between alternate nests use by individuals was 45 ± 5 m (range = 4-162 m). Estimates of mean (± SE) and median home range size were 1,732 ± 366 m^2 and 760 m^2, respectively (range = 36-10,308 m^2). Little variation in home range size was explained by gender or age of voles, or by forest age. However, females occupied fewer nests aud made fewer movements between nest trees than males. Male home ranges were larger than females during late winter and spring during the peak breeding period (2,475 ± 1,076 m^2 aud 790 ± 239 m^2, respectively). We did not detect use of ground nests by radiocollared voles, but we did document occasional cases where voles moved on the ground between nest trees.

Introduction

Tree voles *(Arborimus longicaudus, A. pomo)* are endemic to the coniferous forests of western Oregon and the coastal ranges of California north of San Francisco (Bailey 1936, Hayes 1996). They are the most unique microtine rodent in North America because they are predominantly arboreal, have small litters and long gestation periods compared to other microtines, and feed exclusively on the needles and twig bark of conifers (Howell 1926, Benson and Borell 1931, Hamilton 1962). Tree voles are solitary except for brief periods when males visit female nests to breed (Taylor 1915, Howell 1926, Forsman et al. 2009). Their nests are typically located in the live crowns of trees, where conifer needles are easily accessible (Gillesberg and Carey 1991, Meiselman and Doyle 1996, Thompson and Diller 2002). Although tree voles are thought to live throughout the year in arboreal nests, the sex ratio of adult tree voles captured in arboreal nests is skewed towards females (Taylor 1915, Howell 1926, Hamilton 1962). This, and the fact that a few tree voles have been found in terrestrial nests, led Howell (1926) and Hamilton (1962) to suggest that tree voles, especially males, frequently live in ground nests and only live in arboreal nests during part of the year. This has never been confirmed, despite the fact that many researchers have attempted to study tree voles.

Although many tree voles have been captured alive and studied in captivity (Howell 1926, Clifton 1960, Hamilton 1962, Johnson 1973), little is known about their population ecology, space-use, or dispersal in the wild because they are difficult to study using conventional small mammal sampling techniques (Maser et al. 1981, Smith et al. 2003b, Swingle et al. 2004). As a result, there is considerable uncertainty regarding how tree vole populations will respond as humans systematically modify forest succession and change the distribution and structure of forests in which the species occurs (Carey 1996, Verts and Carraway 1998). It is thought that tree vole numbers are declining as their preferred habitat becomes increasingly fragmented and reduced in extent by timber harvest, fires, and conversion of forest lands to non-forest

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uses (Huff et a1. 1992, Smith et al, 2003 b, Forsman et al. 2004). However, documentation of the actual rates or areas of decline is lacking.

Conservation of uncommon and unevenly distributed species like tree voles requires knowledge of movements, especially home ranges and dispersal relative to different forest types. We used radiotelemetry to document movements and diel activity patterns of red tree voles in western Oregon. Our primary objectives were to document home range areas and number of nests used by tree voles and to evaluate the influence of gender, age, forest age, and the number of days in the sampling period on estimates of home range size. We hypothesized that male ranges would be larger than female ranges because males would be actively searching for receptive females, whereas reproducing females would remain close to their nests when raising young. Our second hypothesis was that ranges of voles in young forest would be larger than in old forest because voles in small trees would have to utilize multiple trees to avoid over-utilization of the needles and twigs in the nest tree.

Study Area

We conducted field work in two study areas in Douglas County, Oregon, from July 2002 - September 2003. The Yellow Creek Study Area was in the Coast Ranges, 32 km N of Roseburg *(43°29'48" N,* 123°24'53" W), and the Taft Creek Study Area was in the Cascade Mountains, 45 km E of Roseburg (43°12'36" N, 122°48'15" W). Both areas were in mountainous terrain covered by forests dominated by Douglas-fir *(Pseudotsuga menziesiii.* Other tree species commonly associated with Douglas-fir were western hemlock *(Tsuga heterophylla),* grand fir *(Abies grandis),* bigleaf maple *(Acer macrophyllum),* western redcedar *(Thuja plicata),* golden chinquapin *(Castanopsis chrysophylla),* Pacific madrone *(Arbutus menziesii),* and incense-cedar *(Calocedrus decurrens).* Vegetation on both areas included a mixture of young forests (22-55 yrs old) regenerating on old clear-cuts, intermixed with mature and old-growth forest (110-260 yrs old). Regardless of age, forests on both study areas typically had high (>70%) canopy closure. Both areas were characterized by cool wet winters and warm, dry summers (Franklin and Dyrness 1973).

Methods

Capture and Radiocollar Attachment

We located voles by searching for their arboreal nests as we walked or drove through forested areas. We investigated 1,151 potential nests by climbing trees to determine if they were occupied by voles. We captured voles by probing their nests with a stiff piece of wire, and capturing them by hand or in nets as they ran from the nest (28%) or jumped to the ground (72 %). We used the wire probe because we did not want to influence vole behavior or survival by damaging their nests.

Upon capture we fitted each vole with a radiocollar (Models BD-2C, BD-2NC, or MD-2C; Holohil Systems, Carp, Ontario, Canada). We used three different collar sizes (0.6, 1.0, 1.6 g) depending on the mass of the vole, so that total mass of collar and transmitter was <5% of an individual's body mass. We classified voles as juveniles, subadults, or adults based on mass, pelage color, and external evidence of reproductive condition (Clifton 1960, Hamilton 1962, Maser and Storm 1970). Gender of voles was determined using molecular data (n = 38) or morphological evidence such as visible mammae, descended testes, and distance between the urogenital opening and anus (n = 7). Molecular determination of gender was based on a polymerase chain reaction (PCR) analysis of DNA extracted from a tissue sample from the tip of the tail (Bryja and Konecny 2003, Bellinger et al. 2005). After installing the radiocollar we released each vole at the base of the tree from which it was captured. The handling sequence from capture to release took about 20 min. All procedures met the guidelines recommended by the American Society of Marnmalogists, Animal Care and Use Committee (Gannon et al. 2007) and were conducted under Oregon State University Animal Care and Use Permit 3091.

Rad iotracking

We used hand-held radio receivers (Model R-1000, Connnunications Specialists, Orange, CA or Model TR-2, Telonics Inc., Mesa, AZ) and hand-held H-antennas (Model RA-2AK, Telonics Inc.) to relocate radiocollared voles. We used a series of triangulations to home in on the transmitter signal until the vole was located in a specific tree directly above the observer. 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, 2,166 (86%) were determined to the nearest tree, 312 (12%) were narrowed down to a cluster of trees within a 10 m radius, and 59 (2%) were discarded because we could not get an accurate location. Based on 129 cases where we triangulated on voles from the ground and then climbed trees to determine their exact locations, we found that mean telemetry error was 1.50 m ± 0.02 m (SE; range = 0-21.0 m), and that we correctly identified the tree in which the vole was located 77% of the time. When a vole was found in a different tree than the one it had been occupying during previous locations, we conducted a diurnal 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 tree.

Sampling Schedule and Diel Activity Patterns

All voles were monitored until they died, or until their transmitters either failed or were removed. We used two sampling methods to monitor radio-collared voles. The first method was to record a single location for each vole every other night, using a systematic sampling schedule to ensure that observations of each vole were evenly distributed throughout the night (Otis and White 1999). On average, we relocated individual voles 4.2 ± 0.1 (SE) times per week.

The second method was to randomly select a vole and monitor it continuously for a l-hr period, using changes in signal strength and location to determine if the vole was moving about or stationary at the nest. We used the latter method 1-4 times per week, with a maximum of one vole monitored on the same day or night, and we systematically spaced the l-hr sampling intervals so that we obtained approximately equal amounts of data throughout the night. During continuous monitoring, we scored the level of activity during each l-hr period as 1 (inactive-no movement), 2 (moderately active-occasional movement), or 3 (highly active-frequent movement) and we recorded whether the vole used >1 trees. To evaluate differences in the level of activity at different times of the night we subdivided the data from the sampling periods into 2-hr intervals, beginning at sunset and ending at sunrise. We then used t-tests to compare mean activity levels of males and females in each 2-hr interval at night and during the diurnal interval (all l-hr samples collected between sunrise and sunset). Unless the vole moved from one tree to another during a continuous monitoring period we only recorded a single location for the entire period.

Estimation of Home Range

Although it was usually possible to identify the tree in which a vole was located, we could not reliably determine whether a vole was in its nest or out on a limb in the nest tree. For this reason we always recorded locations at the center of the tree in which the vole was located. If we used these locations with convex polygon or kernel estimators the results would have underestimated space-use because our locations were not accurate enough to capture the occasions when voles were foraging out on limbs around the nest, especially in cases where the majority of relocations were in one or a few nest trees (Hansteen et al. 1997). Therefore, we used a method that we referred to as the Crown Area Polygon (CAP) to estimate the horizontal area used by each vole. The CAP method was based on the same principal as the 100% Minimum Convex Polygon method (Mohr 1947) except that, instead of connecting the outermost points where the animal was detected, we connected the outer edges of the crowns of the trees in which the animal was detected (Figure 1). With this method we assumed that, at least occasionally, voles foraged to the outer ends of the limbs in the trees in which they were located. We believe this is a reasonable assumption considering that tree voles feed primarily on new growth from the outer ends of limbs (Howell 1926, Walker 1930), and that video observations of tree voles revealed that they regularly ran in and out on all of the limbs surrounding their nests while they were foraging at night (Forsman et a1. 2009).

To estimate home ranges, we used a compass and laser to determine the distance and direction between the boles of all trees used by each vole. We imported these data into Program Arc View 3.2 (ESRI, Inc., Redlands, CA) and used the Distance and Azimuth Tools extension (Jenness Enterprises, www.jennessent.com) to determine the coordinates of each location. We also imported circular estimates of the crown area of each tree into Arc View. The latter estimates were computed based on the average of two measurements of crown width taken at right angles on each tree. The area within the CAP was then estimated from the digitized convex polygon connecting

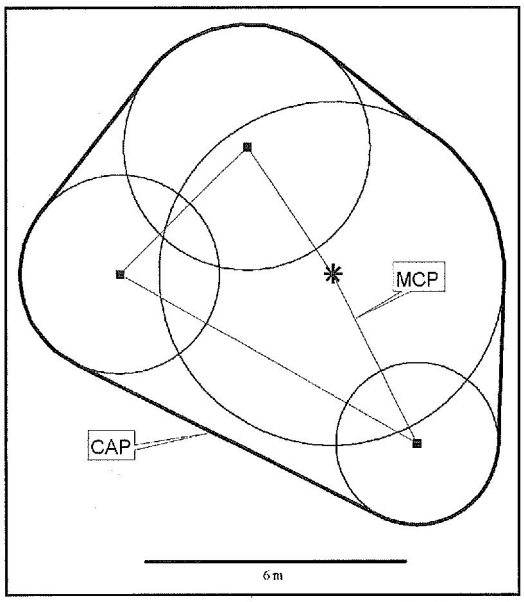

Figure 1. Two-dimensional home range area of red tree vole (*Arborimus longicaudus*) female #2 estimated with the Crown Area Polygon (CAP) method. Asterisk indicates bole of nest tree, squares indicate boles of foraging trees, and circles indicate the crown area of each tree in which the vole was located. The area of the home range that would have been obtained with the more traditional Minimum Convex Polygon method (MCP) is shown for comparison.

the crowns of trees in which the vole was located (Figure 1). In all estimates of home range we did not concern ourselves with autocorrelation in the data, because Otis and White (1999) demonstrated convincingly that autocorrelation is generally a non-issue in tests of hypotheses regarding home range size, and that intensive sampling leads to improved estimates of spatial use.

We used t-tests and linear regression for univariate tests of association between variables. We used the multi-model information-theoretic approach (Burnham and Anderson 2002) to evaluate a set of *14 a priori* linear models that included the additive effects of gender, age, study area, number of days in the sample period, and forest age on estimates of the number of trees used by individual voles and estimates of home range size. We were especially interested in relationships between gender, forest age, and home range attributes because some have suggested that male tree voles live most of the time in ground nests (Howell 1926), and because differences in home range size in different forest types could help to understand the relative energetic costs of living in young versus old forests. For these analyses we divided forests into two age classes; young forest (22-55 yrs old) consisted primarily of even-aged stands of Douglas-fir growing on areas that had been clear-cut and reforested and old forest (110-260 yrs old) included a diverse mix of medium to large trees growing on areas that had not been logged. We used Akaike's Information Criterion (AIC_c) corrected for small sample size to rank models, and Akaike weights (w_i) to evaluate model likelihood (Akaike 1973, Burnham and Anderson 2002). For this analysis, any model within 2 AIC_c units of the best model was considered competitive with the best model (Burnham and Anderson 2002). We estimated the amount of variance explained by the best model as the difference in residual variance between the best model and the no-effects model using the estimates of residual variance computed with program STATGRAPHICS (STSC, Inc. 1988). Because home range estimates tended to be skewed towards smaller areas, we log-transformed the data to improve normality before conducting analyses. However, we present the untransformed estimates in the text because we think they are biologically more meaningful.

Gender Differences in Movements and Nest Tree Fidelity

To evaluate the hypothesis that male and female voles were equally likely to change locations between subsequent relocations, we coded each relocation as a 0 if the vole was located in the same tree as the previous radiotelemetry location or 1 if it was at a different location. Then we subdivided the data by gender in a 2 x 2 contingency table and computed the log odds ratio of the likelihood of movement between successive relocations of males and females (Ramsey and Schafer 2002). We also subdivided these data by season in order to examine seasonal differences in the amount of movement between trees within the home range. We used $P<0.05$ as the criteria for significance in statistical tests, and $P = 0.05$-0.10 as suggestive, but inconclusive evidence. All means are expressed ± 1 SE.

Results

Of 50 voles radiocollared we excluded 5 that were tracked for <24 days because a plot of mean home range size relative to the number of days in the observation period indicated that estimates

of mean home range size increased rapidly for the first 10-20 days that voles were tracked, and then began to level off. On average, home range size by day 24 reached 80% of the eventual 100% CAP range.

The 45 non-juveniles observed included 38 adults (12 males, 26 females) and 7 subadults (3 males, 4 females). The sample included 33 voles (6 males, 27 females) in young forest, and 12 voles (9 males, 3 females) in old forest. Of the 45 voles, 26 were radiocollared one time only, and 19 were recaptured and recollared on 1 (n= 14), 2 (n= 3), or 3 (n= 2) occasions to replace transmitters that failed or were about to fail. On average, voles were observed for 82 ± 9 days (range = 24-307 days). After they were radiocollared, 82% of the voles continued to occupy the same nest where they were originally captured, and 90% were found at least once in their original nest, which led us to believe that our methods did not greatly disrupt the behavior of most individuals.

Diel Activity Patterns

Data from 213 continuous monitoring sessions indicated that voles were largely active at night and spent the daylight hours in their nests. There were no differences in mean activity levels of males and females in any of the 2-hr intervals after sunset (all $P > 0.25$), so we combined the data for males and females for comparisons among the 2-hr intervals (Figure 2). During 192 1-hr intervals at night, voles were highly active in 118 intervals (61%), moderately active in 55 intervals (29%), and inactive in 19 intervals (10%). In contrast, in 21 1-hr intervals during the day, voles were inactive in 9 intervals (43%), moderately active in 12 intervals (57%), and highly active in no intervals. 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 movements 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. Virtually all diurnal activity seemed to consist of movements within the nest, except for two cases in which we found voles huddling on limbs outside their nests during the day.

Home Range Attributes

Of the 45 voles, 18 (4 males, 14 females) had home ranges that consisted of a single nest tree

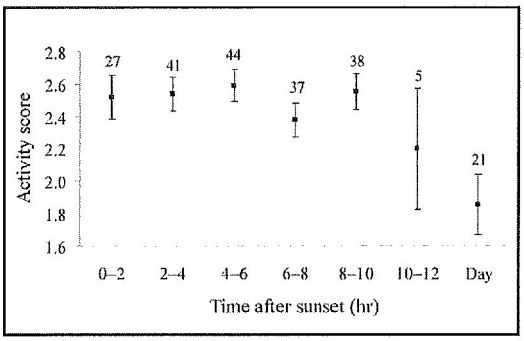

Figure 2. Mean activity scores (± 1 SE) of radiocollared red tree voles (*Arborimus longicaudus*) during diurnal hours (day) and during six 2-hr intervals starting at sunset in western Oregon, July 2002–September 2003. Means indicate average of activity scores recorded in the field (low = 1, moderate = 2, high = 3). Numbers above SE bars indicate the number of 1-hr sampling intervals used to calculate means.

and a few adjacent trees, and 27 (11 males, 16 females) used 2-6 nests that were 4-162 m apart (mean = 45 m ± 5 m). Mean nest height was 16.0 ± 0.7 m (n = 112, range = 5.1-42.7 m). Estimates of mean home range size did not differ between males and females or between forest age classes (Table 1). Although the direction of the differences in the means seemed to provide weak support for our *a priori* hypotheses, the means were strongly influenced by a few outliers, and when we compared medians rather than means, the patterns were actually the opposite of what we predicted. That is, median home range areas were smaller in young forest than in old forest and were smaller for males than for females (Table 1).

The mean number of nest trees used by males and females was 2.67 ± 0.41 and 2.03 ± 0.23, respectively ($t = -1.44$, $P = 0.16$). The model that best described variation in the number of nest trees used included the additive effects of gender and days in the sample period (Table 2). The only competitive model was one that included the effects of days in the sample period, with no additive gender effect (Table 2). Akaike weights (w_i) summed across models indicated that days in the sampling period made the largest contribution to model fit (0.90), compared to 0.56 for gender, 0.24 for vole age, 0.17 for forest age, and 0.03 for study area (Table 2). However, the amount of the total variation explained by the best model was only 17%, indicating that most of the variation in the number of nest trees used was unexplained by our models (Figure 3A).

TABLE 1. Home range estimates (m^2) for radiocollared red tree voles (*Arborimus longicaudus*) in western Oregon.

	Young forest			Old forest			All voles[1]	Comparison of means[2]	
Gender	n	Mean ± SE	Range	n	Mean ± SE	Range	Mean ± SE	*t*	*P*
Males	6	2,665 ± 1,482	148–7,761	9	1,360 ± 430	86–4,222	1,882 ± 637	-0.85	0.43
Females	27	1,735 ± 511	36–10,308	3	952 ± 331	292–1,331	1,657 ± 462	-0.50	0.62
All	33	1,904 ± 490	36–10,308	12	1,258 ± 329	86–4, 222	1,732 ± 366	-0.28	0.78
		Median			Median		Median		
Males		500			822		760		
Females		700			1,233		808		
All		541			1,014		760		

[1] *t*-test of means for males and females was $t = 0.28$, $P = 0.78$).
[2] Comparison of means in young versus old forest.

TABLE 2. Model selection results from the analysis of potential factors influencing the number of nest trees used by red tree voles (*Arborimus longicaudus*) in western Oregon. The best model is listed first, with other models listed in order of increasing ΔAIC_c) values.

Model structure[1]	*K*	MLE	AIC_c	ΔAIC_c	w_i
gender + days	4	1.80	35.34	0.00	0.368
days	3	1.94	36.43	1.09	0.214
gender + age + days	5	1.79	37.81	2.47	0.107
forest + days	4	1.92	38.26	2.92	0.085
age + days	4	1.94	38.84	3.50	0.064
no-effects model	2	2.17	39.15	3.81	0.055
gender	3	2.11	40.18	4.84	0.033
gender + age + forest + days	6	1.79	40.48	5.14	0.028
area + forest + days	5	1.91	40.61	5.27	0.026
age	3	2.16	41.34	6.00	0.018
forest	3	2.17	41.36	6.02	0.018
gender + age	4	2.10	42.34	7.00	0.011
gender + age + area + forest + days	7	1.79	43.25	7.91	0.007
gender + age + area + forest	6	2.07	46.93	11.59	0.001

[1] Covariates indicate model structure for gender, number of days in the sampling period (days), vole age at initial capture (age), study area (area) and forest age (forest). *K* is the number of parameters in the model, MLE is the maximum likelihood estimate, AIC_c is Akaike's Information Criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c value between the selected model and the best model, and Akaike weight (w_i) is the relative support for each model.

The model that best described the variation in size of horne ranges was the no-effects model. However, four other models were competitive with the best model, including simple univariate models that included gender, vole age, forest age, and days in the sampling period (Table 3). Akaike weights (w_i) were fairly evenly distributed among all of the competing models, suggesting that gender, vole age, forest age, and days in the sampling period all had an effect on home range estimates. However, the full model explained only 7% of the variation in the data, again indicating that most of the variation in horne range size was unexplained by any of our models. The weak relationship between home range size and number of days in the sampling period was also indicated by the low correlation between the number of days in the sampling period and home range size ($r^2 = 0.17$ and 0.02 for males and females, respectively; Figure 3B).

TABLE 3. Model selection results from the analysis of potential factors influencing home range size of red tree voles (*Arborimus longicaudus*) in western Oregon. The best model is listed first, with other models listed in order of increasing ΔAIC_c values

Model structure[1]	K	MLE	AIC_c	ΔAIC_c	w_i
no-effects model	2	2.18	39.30	0.00	0.236
days	3	2.10	39.95	0.66	0.170
age	3	2.15	41.01	1.72	0.100
gender	3	2.15	41.14	1.84	0.094
forest	3	2.16	41.30	2.00	0.087
days + gender	4	2.06	41.50	2.20	0.079
days + forest	4	2.07	41.70	2.40	0.071
days + age	4	2.08	42.00	2.70	0.061
gender + age	4	2.12	42.86	3.56	0.040
days + gender + age	5	2.04	43.58	4.28	0.028
days + area + forest	5	2.06	44.02	4.72	0.022
days + gender + age + forest	6	2.03	46.12	6.82	0.008
gender + age + area + forest	6	2.12	48.02	8.72	0.003
days + gender + age + area + forest	7	2.02	48.74	9.44	0.002

[1] Covariates indicate model structure for number of days in the sampling period (days), gender, vole age at initial capture (age), study area (area), and forest age (forest). K is the number of parameters in the model, MLE is the maximum likelihood estimate, AIC_c is Akaike's Information Criterion corrected for small sample size, ΔAIC_c is the difference in AIC_c value between the selected model and the best model, and Akaike weight (w_i) is the relative support for each model.

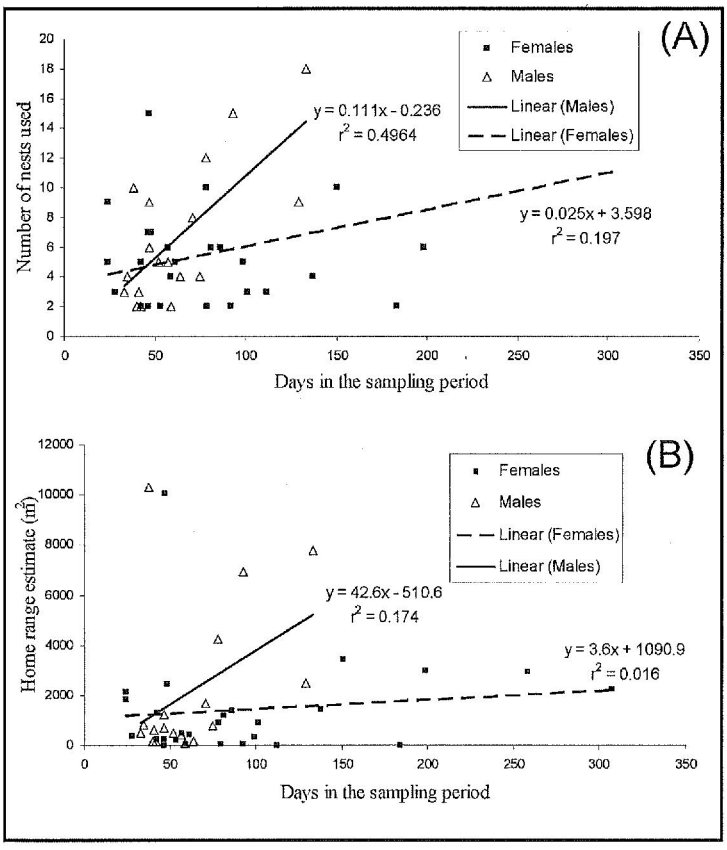

Figure 3. Linear regression of the number of nests used (A) and home range area (B) on the number of days in the sampling period for radiocollared red tree voles (*Arborimus longicaudus*) in western Oregon.

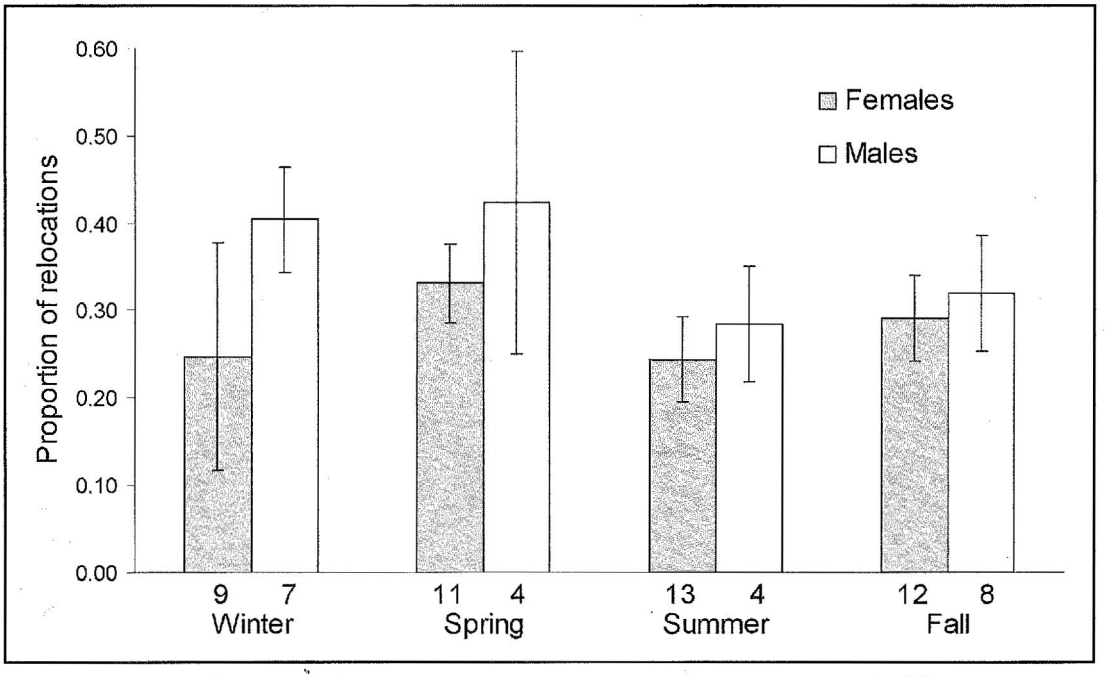

Figure 4. Mean proportion (± 1 SE) of red tree vole (*Arborimus longicaudus*) relocations that were in different trees than the previous location, subdivided by gender and season in western Oregon. The number of voles in each sample is indicated under the bars.

Frequency of Movements Nest Trees

On average, sequential relocations of individual males and females indicated they were in the same tree as the previous location 69% and 64% of the time, respectively. The odds of locating a vole in a different tree than in the previous location was 1.27 times greater for males than females (95% *CI* = 1.05-1.37, n = 2,199). The higher rate of movement by males was most pronounced in late winter through spring (January - June) when females tended to be sedentary and males regularly traveled among trees within their ranges (Figure 4). During this period, the mean home range size of males (2,475 ± 1,076 m^2, n = 8) was nearly three times larger than the mean home range size of females (790 ± 239 m^2, n = 13), but the individual variation in home range size was so great for both sexes that the seemingly large difference between the sexes was only suggestive for a difference (t = -2.078, P = 0.052). During the summer and early winter (July - December), the frequency of movement between sequential relocations was more similar between the sexes (Figure 4), and there was little evidence of a sexual difference in mean home range size of males (1,189 ± 397 m^2, n = 11) and females (1,761 ± 562 m^2, n = 24, t = -0.024, P = 0.981).

Home Range Overlap

Of the females that we observed there were only three individuals whose observation periods overlapped and that occurred close enough together to expect theirranges to overlap. These three females occurred in young forest. The home range of one of these females (#11) overlapped the ranges of the other two (#'s 10 and 16), but not during the same radiotracking period. From 6-30 January 2003 the home range of #11 was confined to three interconnected trees that were entirely subsumed within the range of #10, whose range included a much larger area that included at least three nest trees and five foraging trees (Figure 5A). These two females were found in close proximity (5.2 m) to each other on only one occasion, when #10 was found in a tree whose crown overlapped the nest tree of #11. The #10 female was lulled by a weasel on 30 January 2003 and we eventually marked another female (#16) in the same area on 29 May 2003. This female occupied a range that had little overlap with the range of #11 except

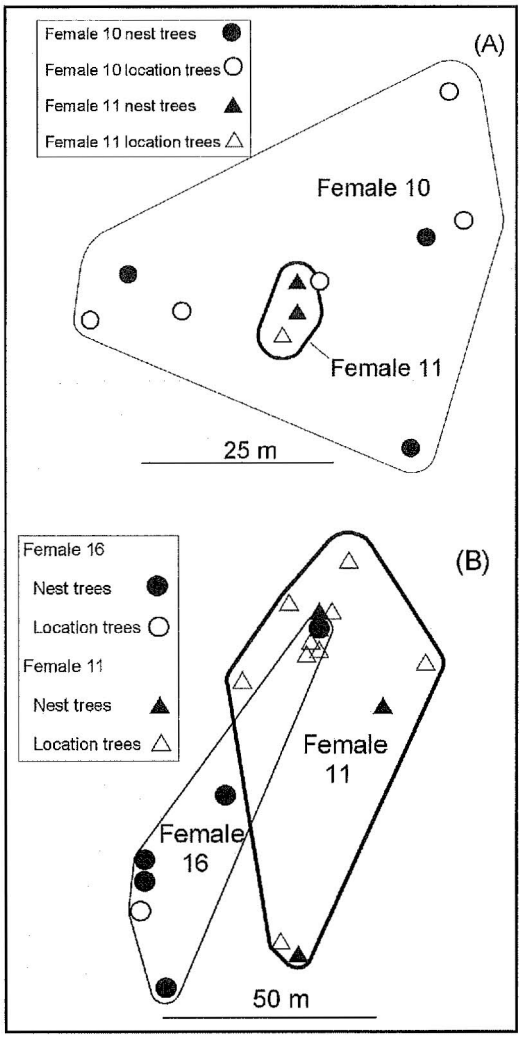

Figure 5. Home range overlap of female tree voles (*Arborimus longicaudus*) in western Oregon. Top map (A) shows locations of females #10 and #11 from 6–30 January 2003 and bottom map (B) shows locations of females #11 and #16 from 29 May–23 August 2003.

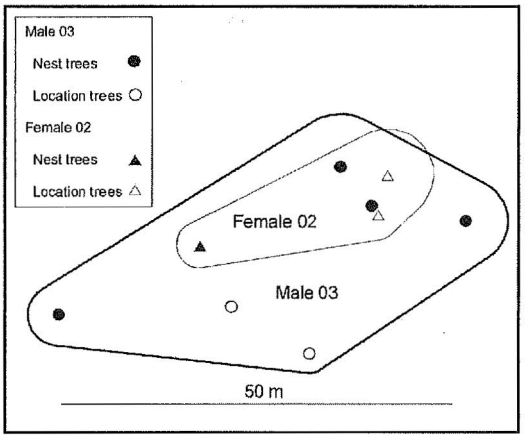

Figure 6. Home range overlap of female #3 and male #2 red tree voles (*Arborimus longicaudus*) in western Oregon from 24 July–9 September 2003.

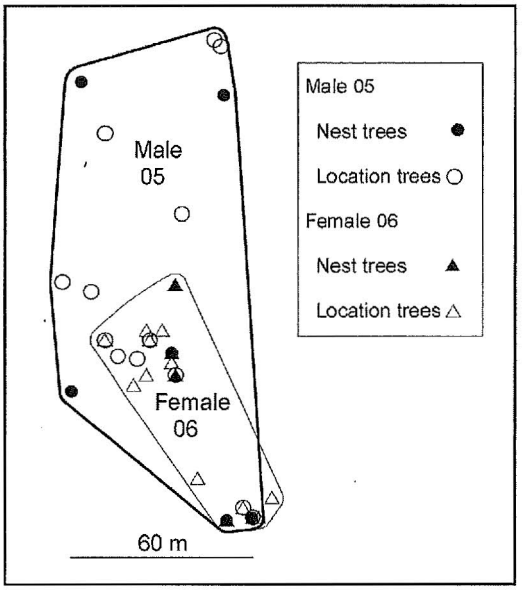

Figure 7. Home range overlap of female #6 and male #5 red tree voles (*Arborimus longicaudus*) in western Oregon from 20 November 2002–8 February 2003 and 12 March–30 April 2003. Male was not located from 9 February–12 March 2003 because of a failed radiocollar.

for one day in which she was found in a nest in a tree whose crown broadly overlapped the tree in which #11 was nesting (Figure 5B). By the next day #16 had moved back to her center of activity consisting of 4 nest trees where 92% of her total relocations occurred and there was no further overlap with #11.

In two cases where we radiocollared a male and female in close proximity to each other we found that the ranges of the males almost completely overlapped the ranges of the females (Figures 6-7). In one case the observation period was in late Summer (24 July - 9 September) in an old forest, and there was little indication of close interactions between the two voles except for one night when they were in trees that were 8.7 m apart (Figure 6). In the other case, the two

voles occupied a young forest and were tracked from 20 November-30 April except for a 22 day period (9 February-12 March) when the male's transmitter died (he was recollared on 13 March). During this time their simultaneous relocations were 65.2 ± 4.6 m apart on average (n = 63), but there were three occasions when they were found in trees whose crowns overlapped each other and one night when they were together in the female's nest tree (Figure 7). This female was lactating in three of four recaptures.

Movements on the Ground

Of 2,537 locations oflive voles, all but six were in trees. The six exceptions were all cases in which we found voles on the ground as they moved from one tree to another at night. The rarity of ground detections and the relatively frequent cases in which we documented travel from tree-to-tree via interconnecting branches indicated that the voles preferred to travel in the forest canopy but would travel on the ground if necessary. For example, there were two adult males that used alternate nests on opposite sides of a gravel logging road that passed through their home ranges. The treeless corridor through which this road passed averaged 22-m wide, and the only possible pathway between nests on opposite sides of the road was on the ground. We also found 11 voles in old forests that occupied nests in >2 trees that had no interconnecting branches with each other or with other trees. These individuals were obviously descending to the ground to move between trees. None of the radiocollared voles were found in ground nests at any time during the study.

Discussion

Although some authors have speculated that tree vole home ranges consist of a single nest tree and possibly adjacent foraging trees (Taylor 1915, Brown 1985, Carey 1999), 60% of the voles we observed used multiple nests in different trees, and some individuals frequently moved between alternate nests throughout the time they were monitored. It is possible that some movement among nests was influenced by our radiocollars or our disturbance of nests, but we suspect that, especially for males and non-breeding females, use of multiple nests is the norm. In other radiotelemetry studies of voles, use of a control group has revealed little evidence of radiocollar effects (Berteaux et al. 1996, Johannesen et al. 1997), but such comparisons were not possible in our study because tree voles are virtually impossible to sample using any conventional small mammal sampling techniques other than radiotelemetry (Swingle et al. 2004).

Although our analysis indicated that males tended to use more nest trees than females, our models were only weakly supportive of the hypothesis that males had largerranges than females. However, male home ranges did tend to be larger than female home ranges during the late winter and spring, just before and during the period when most females were either pregnant or raising young (Swingle 2005). But even then, there was so much variation among individuals that the difference was only marginally significant. Larger home range size of males is a common pattern in micro tines (Gashwiler 1972, Alexander and Verts 1992, Thompson et al. 2009) and in many arboreal rodents (Martin and Anthony 1999, Cotton and Parker 2000, Meyer et al. 2005). This pattern is not surprising given that females are constrained to a maternal nest for much of the year, whereas selection probably favors males that maximize their home range size to breed with as many females as possible (Cotton and Parker 2000). We suspect that variation in home range size of the voles we studied could be better explained if the data were subdivided based on the reproductive status of each vole and if we had included more detailed covariates on vegetation structure in our models. However, this was not possible because we were unable to consistently determine breeding status of individuals and because we did not have funding to collect detailed vegetation measurements at every nest tree.

With the exception of females with young, our radiocollared voles were solitary. Males were infrequently found in the same trees as females, except at night when they occasionally visited female nests, presumably to see if females were receptive to breeding (see Forsman et al. 2009). They always returned to their own nests by the next morning. These observations are supportive of Howell's (1926:57) observation that tree voles have, "... a markedly solitary disposition, the females usually being truculent and intolerant of other individuals." Rare exceptions in which adult male tree voles have been found in nests with females during the day (Benson and Borell 1931) probably represent cases in which males

were visiting receptive females to breed. The rarity of studies finding more than one adult tree vole simultaneously nesting in the same tree leads us to conclude that it is uncommon (even in large old-growth trees) for multiple adults to simultaneously occupy the same tree. Thus, we think that the statement by Maser (1998:223) that, "... multiple generations of tree voles can simultaneously occupy the same old-growth tree .... " may represent the exception rather than the rule for adult tree voles.

Activity levels documented during our 1-hr continuous monitoring periods suggested that tree voles were more active at night than during the day, but there was some uncertainty because it was often difficult to tell the difference between activity that occurred in the nest versus outside the nest, especially at night. Subsequent to our study, Forsman et al. (2009) used video cameras to continuously observe tree vole nests, and documented that activity outside the nest took place almost entirely at night, with rare episodes of diurnal foraging.

We predicted that home ranges of tree voles would be larger in young forest than in old forest because we thought that voles that occupied stands of small trees would have to utilize the crowns of multiple trees in order to find enough food, whereas voles in old trees could find adequate food in the crown of a single large tree. Our results did not support this hypothesis. It is possible that this comparison was confounded by our method of home range estimation, but none of the other possible methods of home range estimation could be used with our data. We found no other studies in which researchers compared home range size of microtines in forests of different age.

An obvious limitation of our data is that we only estimated home ranges in two dimensions because we could not consistently determine the height of voles in trees at night. What is needed to better understand space use by tree voles is a sampling method that would permit calculation of a 3-dimensional home range that would take into account vertical as well as horizontal movements within the forest canopy (Cranford 1977, Koeppl et al. 1977, Meserve 1977). We know of no current technology that will produce such fine scale location data for a small arboreal animal like the tree vole, but it is possible that pit tags with multiple sensors encircling the trunks and limbs of nest trees could produce 3-dimensional data (Harper and Batzli 1996, Dell'omo et al. 1998).

Our data, and the considerable number of tree voles that have been captured in pitfall traps (Corn and Bury 1986,1991; Raphael 1988; Gilbert and Allwine 1991; Gomez and Anthony 1998; Manning and Maguire 1999; Martin and McComb 2002), confirm that tree voles will travel on the ground to move between trees in situations where they do not have the option of traversing from tree-to-tree via interconnecting branches. However, the rarity of terrestrial locations for both males and females in our sample suggested that, when they did come to the ground, voles moved quickly between trees, spending little timeon the ground. Thus, our study provides little support for the hypothesis that large numbers of male tree voles reside in ground nests, as has been suggested by some (Taylor 1915, Howell 1926, Maser 1966). Hamilton (1962) speculated that tree voles might be more likely to nest in burrows during winter because their arboreal nests might not provide enough thermal insulation during cold weather. We found no support for this hypothesis, as none of our radio collared voles nested on the ground at any time of the year. However, the voles that we studied were initially captured by searching for arboreal nests and chasing the voles out of those nests. Therefore, we cannot discount the possibility that there was a ground-dwelling segment of the population that we overlooked. One potential method for further investigation of the use of ground nests by tree voles is the use of trained dogs to locate nests (Smith et al. 2003a, McKay et al. 2008). We have not tried this, but it certainly should be considered in the future.

In an attempt to explain why he found few tree voles in isolated patches of forest surrounded by pastures or cutover areas, Howell (1926:40) suggested that extensive areas of non-forest may be a barrier to movement of tree voles. This hypothesis has been repeated by others (Carey 1996, 1999; Harris 1984) but has not been tested. We could not test this hypothesis directly, but our data clearly show that tree voles can and do at least occasionally move short distances across small forest openings or across small logging roads that were less than 25 m wide. We saw no cases in which tree voles moved across large areas of non-forest, and we suspect that large non-forest openings do act as barriers to dispersal, and that long-term persistence of tree voles in any given forest area depends on the size and connectivity

of the remaining stands, as well as the structure of the forest canopy. Experimental tests of these hypotheses would be extremely difficult, but retrospective surveys of tree voles in heavily disturbed forest areas may provide insights regarding the rate of dispersal and recolonization relative to the distance from the nearest refugia.

There is considerable evidence from trapping studies (Corn and Bury 1986, 1991; Raphael 1988; Gilbert and Allwine 1991; Gomez and Anthony 1998; Manning and Maguire 1999; Martin and McComb 2002) and nest surveys (Gillesberg and Carey 1991, Meiselman and Doyle 1996, Jones 2003, Dunk and Hawley, *In Press)* that indicates that tree voles are most common in old forests. However, they also occur in fairly high numbers in some young stands (Howell 1926, Maser 1966, Thompson and Diller 2002). We think this is an important fact to emphasize because, if the objective is to maintain tree voles in an area, managers may want to forego thinning in young stands that have signs of occupancy by tree voles, or they may want to experiment with variable density thinning (Franklin et al. 1997, Carey 2003) in those stands in order to retain patches of densely spaced trees with interconnected branch pathways and with the types of structural attributes that provide support for tree vole nests in young trees (deformed limbs, broken or forked tree tops, epicormic branching).

Another finding from our study with important implications for both scientists and managers is that approximately 48% of the nests used by our radiocollared voles could not be seen from the ground (Swingle 2005). The proportion of nests that could not be seen from the ground was particularly high in old forests (54%) and relatively high in young forest (44%). This means that it is not possible to estimate the number of voles or vole nests per unit area without climbing large numbers of trees, and even then it is difficult to estimate the number of voles from nest counts because (1) some nests will still be missed, (2) some individuals occupy multiple nests, and (3) it is impossible to tell which nests are actually occupied without dissecting or probing the nests. Even if the objective is to just compare the relative abundance of tree vole nests in young stands and old stands we think that climbing trees to the top is the only way to obtain reasonable estimates, because so many nests in old trees are hidden high in the canopy or inside tree cavities.

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Literature Cited

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* B. N. Petrov and F. Csaki (editors), Second International Symposium on Information Theory, Akaderniai Kiado, Budapest, Hungary. Pp. 267-281.

Alexander, L. E, and B. T. Verts. 1992. *Clethrionomys californicus.* Mammalian Species 406:1-6.

Bailey, V. O. 1936. The marrunals and life zones of Oregon. North American Fauna 55:1-416.

Bellinger, M. R., S. M. Haig,E. D. Forsman, and T. D. Mullins. 2005. Taxonomic relatiouships among *Phenacomys* voles as inferred by cytochrome *b.* Journal of Marnmalogy 86:201-210.

Benson, S. B., and A. E. Borell. 1931. Notes on the life history of the red tree mouse *Phenacomys longicaudus.* Journal of Marnmalogy 12:226-233.

Bertcaux, D., F. Masseboeuf, T. Bonzom, T. Bergeron, D. W. Thomas, and H. Lapierre. 1996. Effect of carrying a radiocollar on expenditure of energy by meadow voles. Journal of Mammalogy 77 :359-363.

Brown, E. R. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. USDA Forest Service, Pacific Northwest Region R-6-F&WL-192. Portland, OR.

Bryja, T., and A. Konecny. 2003. Fast sex identification in wild rnammals using PCR amplification of the *Sry* gene. Folia Zoologica 52:269-274.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition Springer-Verlag, New York.

Carey, A. B. 1996. Interactions of Northwest forest canopies and arboreal mammals. Northwest Science 70:72-78.

Carey, A. B. 1999. Red tree *vole/Arborimus longicaudus. In* D. E. Wilson and S. Ruff (editors), The Smithsonian Book of North American Mammals. Smithsonian Institution Press, Washington, D.C. Pp. 620-622.

Carey, A. B. 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. Forestry 76:127-136.

Clifton, P. L. 1960. Biology and life history of the dusky tree vole *Phenacomys silvicola* (Howell). M.A. Thesis, Walla Walla College, Walla Walla, WA.

Corn, P. S., and R. B. Bury. 1986. Habitat use and terrestrial activity by red tree voles *(Arborimus longicaudusi* in Oregon. Journal of Mammalogy 67:404-406.

Corn, P. S., and R. B. Bury. 1991. Small mammal communities in the Oregon Coast Range. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (technical coordinators), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report PNW-GTR-285. Pacific Northwest Research Station, Portland, OR. Pp. 241-254

Cotton, C. L., and K. L. Parker. 2000. Winter habitat and nest trees used by northern flying squirrels in subboreal forests. Journal of Mammalogy 81:1071-1086.

Cranford, J. A. 1977. Home range and habitat utilization by *Neotoma fuscipes* as determined by radiotelemetry. Journal of Mammalogy 58:165-172.

Dell' omo, G., R. F. Shore, and H. Lipp. 1998. An automated system, based on microchips, for monitoring individual activity in wild small mammals. Journal of Experimental Zoology 280:97-99.

Dunk, J. R., and J. J. U. G. Hawley. *In Press.* Red tree vole habitat suitability modeling: implications for conservation and management. Forest Ecology and Management.

Forsman, E. D., R. G. Anthony, and C. J. Zabel. 2004. Distribution and abundance of red tree voles in Oregon based on occurrence in pellets of northern spotted owls. Northwest Science 78:294-302.

Forsman, E. D., J. K. Swingle, and N. R. Hatch. 2009. Activity patterns and behavior of red tree voles *iArborimus longicaudusi* based on continuous video monitoring of nests. Northwest Science 83 :262-272.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis.

Franklin, J. F., D. R. Berg, D. A. Thronburgh, and J. C. Tappeiner. 1997. Alternative silvicultural approaches to timber harvesting: variable retention systems. *In* K. A. Kohm and J. F. Franklin (editors), Creating a Forestry for the 21st Century. Island Press, Washington D.C. Pp.I11-139.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88: 809-823.

Gashwiler, J. S. 1972. Life history notes on the Oregon vole, *Microtus oregoni.* Journal of Mammalogy 53:558-569.

Gilbert, F. F., and R. Allwine. 1991. Small mammal communities in the Oregon Cascade Range. In L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff (technical coordinators), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA Forest Service General Technical Report PNW-GTR-285. Portland, OR. Pp. 257-267.

Gillesberg, A. M., and A. B. Carey. 1991. Arboreal nests of *Phenacomys longicaudus* in Oregon. Journal of Mammalogy 72:784-787.

Gomez, D. M., and R. G. Anthony. 1998. Small manunal abundance in riparian and upland areas of five seral stages in western Oregon. Northwest Science 72:293-302.

Hamilton, W. J.,III, 1962. Reproductive adaptations of the red tree mouse. Journal of Mammalogy 43:486-504.

Hansteen, T. L., H. P. Andreassen, and R. A. Ims. 1997. Effects of spatiotemporal scale of autocorrelation and home range estimators. Journal of Wildlife Management 61 :280-290.

Harper, S. J., and G. O. Batzli. 1996. Monitoring use of runways by voles with passive integrated transponders. Journal of Mammalogy 77:364-369.

Harris, L. D. 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. The University of Chicago Press, Chicago, IL.

Hayes, J. P. 1996. *Arborimus longicaudus.* Mammalian Species No. 532:1-5.

Howell, A. B. 1926. Voles of the genus *Phenacomys.* North American Fauna 48: 1-66.

Huff, M. H., R. S. Holthausen, and K. B. Aubry. 1992. Habitat management for red tree voles in Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-302. Pacific Northwest Research Station, Portland, OR.

Johannesen, E., H. P. Andreassen, and H. Steen. 1997. Effect of radiocollars on survival of root voles. Journal of Mammalogy 78:638-642.

Johnson, M. L. 1973. Characters of the heather vole, *Phenacomys,* and the red tree vole, *Arborimus* . .Tournal of Mammalogy 54:239-244.

Jones, J. M. 2003. Habitat associations and ecology of the Sonoma tree vole *(Arbo}'inzus POl11o)* in northwestern California. M.S. Thesis, Humboldt State University, Arcata, CA.

Koeppl, J. W., N. A. Slade, K. S. Harris, and R. S. Hoffman. 1977. A three-dimensional home range model. Journal of Mammalogy 58:213-220.

Manning, T., and C. C. Maguire. 1999. A new elevation record for the red tree vole in Oregon: implications for National Forest management. American Midland Naturalist 142:421-423.

Martin, K. J., and R. G. Anthony. 1999. Movements of northern flying squirrels in different-aged forest stands of western Oregon . .TournaI of Wildlife Management 63:291-297.

Martin, K. J., and W. C. McComb. 2002. Small mammal habitat associations at patch and landscape scales in western Oregon. Forest Science 48:255-264.

Maser, C. O. 1966. Life histories and ecology of *Phenacontys albipes, Phenacomys longicaudus, Phenacomys silvicola.* M.S. Thesis, Oregon State University, Corvallis.

Maser, C. 1998. Mammals of the Pacific Northwest: From the Coast to the High Cascades. Oregon State University Press, Corvallis.

Maser, C., and R. M. Storm. 1970. A Key to Microtinae of the Pacific Northwest. Oregon State University Book Stores, Corvallis.

Maser, C., B. R. Mate,.T. F. Franklin, and C. T. Dyrness, 1981. Natural history of Oregon Coast mammals. USDA Forest Service General Technical Report PNW-133. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

MacKay, P., D. A. Smith, R. A. Long, and M. Parker. 2008. Scat detection dogs. *In* R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray (editors), Noninvasive survey methods for carnivores. Island Press, Washington, D.C. Pp. 183-222.

Meiselman, N., and A. T. Doyle. 1996. Habitat and microhabitat use by the red tree vole *(Phenacomys longicaudusi.* American MidJand Naturalist 135:33-42.

Meserve, P.L. 1977. Three-dimensional home ranges of Cricetid rodents. Journal of Mammalogy 58:549-558.

Meyer, M. D., D. A. Kelt, and M. P. North. 2005. Nest trees of northern flying squirrels in the Sierra Nevada. Journal of Mammalogy 86:275-280.

Mohr, C. O. 1947. A table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63: 1039-1044.

Ramsey, F. L., and D. W. Schafer. 2002. The Statistical Sleuth: A Course in Methods of Data Analysis. 2nd Edition, Duxbury, Pacific Grove, CA.

Raphael, M. G. 1988. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. 111 R. C. Szaro, K. E. Severson, and D. R. Patton (technical coordinators), Management of Amphibians, Reptiles, and Small Mammals in North America. USDA Forest Service General Technical Report RM-166. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Pp. 23-3l.

Smith, D. A., K. Ralls, A. Hurt, B. Adams, M. Parker, B. Davenport, M. C. Smith, and J. E. Maldonado. 2003a. Detection and accuracy rates of dogs trained to find scats of San Joaquin kit foxes *(Vulpes macrotis mutica).* Animal Conservation 6:339-346.

Smith, W. P., R. G. Anthony, J. R. Waters, N. L. Dodd, and C. J. Zabel. 2003b. Ecology and conservation of arboreal rodents of western coniferous forests. *In* C. J. Zabel and R. G. Anthony (editors), Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America, Cambridge University Press, Cambridge, UK. Pp. 157-206.

STSC, Inc. 1988. STATGRAPHICS: User's Guide. *STSC,* Inc., Rockville, MD.

Swingle, J. K. 2005. Daily activity patterns, survival, and movements of red tree voles (*Arborimus longicaudus)* in western Oregon. M.S. Thesis, Oregon State University, Corvallis.

Swingle, J. K., E. D. Forsman, and S. G. Sovern. 2004. A method for live-trapping tree voles. Northwestern Naturalist 85:134-135.

Taylor, W. P. 1915. Description of anew subgenus *(Arborimus)* of *Phenacomys,* with a contribution to knowledge of the habits and distribution of *Phenacomys longicaudus* True. Proceedings of the California Academy of Sciences (Series 4) 5:111-161.

Thompson, .TL., and L. V. Diller. 2002. Relative abundance, nest site characteristics, and nest dynamics of Sonoma tree voles on managed timberlands in coastal northwest California. Northwestern Naturalist 83:91-100.

Thompson, R. L., C. L. Chambers, and B. C. McComb. 2009. Western red-backed vole in the Oregon Cascades. Northwest Science 83:46-56.

Verts, B. J., and L. N. Carraway. 1998. Land Mammals of Oregon. University of California Press, Berkeley.

Walker, A. 1930. Notes on the forest *Phenacomys.* Journal of Mammalogy 11:233-235.

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