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Behavior of Red Tree Voles *(Arborimus longicaudus)* Based on Continuous Video Monitoring of Nests

Abstract

We used video cameras to observe the activity patterns and behavior of three female red tree voles *(Arborimus longicaudus)* and their young in arboreal nests in western Oregon. Observation periods at the three nests were 63, 103 and 148 days. All three voles were primarily nocturnal, but occasionally foraged for brief periods during the day when they had large young in the nest. The median time when voles began and ended activity was 95 min after sunset and 1-68 min before sunrise, respectively. The median amount of time spent outside the nest at night was 27 min (range = 0-712 min), and most of this time was spent foraging. Nocturnal activity consisted primarily of long periods inside the nest interspersed with short periods of intensive foraging, during which voles ran out of the nest, harvested cuttings and hauled them back to the nest. Cuttings were stored inside the nest or on top of the nest. The mean number of foraging bouts per night was 3.4 ± 0.1 (range = 1-13), and the mean number of cuttings harvested per night was 20.4 ± 3.5 (range = 0-75). Females harvested more cuttings when they had large young in the nest and there was no evidence that they ate anything but the needles and bark of the cuttings that they brought to their nests. All three females produced litters while we observed them (1, 2, and 3 litters, respectively). Juveniles first began to explore outside the nest when they were 30-35 days old and dispersed when they were 47-54 days old. During the last two weeks before they dispersed the juveniles spent considerable time outside the nest at night, becoming increasingly adept climbers and gradually beginning to harvest their own food. Dispersal of siblings occurred on the same night and appeared to be precipitated by female aggression towards the young.

Introduction

Tree voles *(Arborimus longicaudus, A. pomo)* have long intrigued biologists because they are almost exclusively arboreal, have unusual life history attributes compared to other microtines, and because there is concern that their populations may be declining as old forests are cut and replaced with intensively managed young forest (Taylor 1915, Howell 1926, Walker 1928, Benson and Borell 1931, Clifton 1960, Hamilton 1962, Maser 1966, Huff et a1. 1992, Hayes 1996, Thompson and Diller 2002, Forsman et al. 2004). Because of these concerns, there has been a recent resurgence of interest in tree voles, including a number of papers published on their genetic structure (Bellinger et al. 2005, Blois and Arbogast 2006, Miller et al. 2006), distribution (Forsman et a1. 2004, *in press),* movements (Swingle 2005, Swingle and Forsman 2009), and interspecific relationships (Forsman and Swingle 2007). In addition, the USDA Forest Service and USDI Bureau of Land Management have conducted extensive surveys for tree voles since 2001, greatly increasing our understanding of the distribution of tree voles and of their relative abundance in different forest types (Dunk and Hawley *in press).* Despite the considerable amount of new information, however, there is still much that is unknown about tree voles, particularly as regards their population trends, energetics and behavior. For example, Swingle and Forsman (2009) documented that tree voles are primarily nocturnal, but their radiotelemetry methodology did not allow them to discriminate between activity that took place outside versus inside the nest. Adult tree voles are solitary, and when raising young, females typically occupy a single large brood nest (Taylor 1915, Howell 1926, Swingle 2005). Although tree voles have been observed in captivity (Clifton 1960, Hamilton 1962), there are no data on their foraging behavior or on the developmental behavior of their young in the wild.

In 2006-2007 we used video cameras to document activity patterns and behavior of three adult

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female red tree voles and their young at tree nests in western Oregon. In this report we summarize our observations on the behavior of adult and juvenile voles, including the timing and duration of various types of activity, development and dispersal behavior of juveniles, and behavior of males that visited female nests.

Study Area

The three nests observed were located in the foothills of the Coast Ranges near Corvallis, Benton Co., Oregon. The Oak Creek and Peavy nests were on Oregon State University McDonald Research Forest, 8.5 km NW and 10.6 km N of Corvallis, respectively (44°37'17" N, 123°20'5"W and 44°39'42" N, 123°15'2" W). The Greasy Creek nest was on land administered by the USDI Bureau of Land Management, 19.3 km SW of Corvallis (44°27'43" N, 123°27'17"W). The Peavy and Oak Creek nests were in mixed-age forests of Douglas- fir *(Pseudotsuga menziesiii,* grand fir *(Abies grandis)* and big leaf maple *(Acer macropliyllum),* in which the dominant overstory conifers were 150-220 yrs old. The Greasy Creek nest was in a 35-yr-old stand of Douglas-fir regenerating on an old clear-cut.

Methods

Tree Vole Nests

The Peavy nest was located 27.4 m above ground in a 146-cm-dbh Douglas-fir and the Oak Creek nest was located 14.3 m above ground in the deformed top of a 51-cm-dbh grand fir. The Greasy Creek nest was 5.1 m above ground in the forked trunk of a 42-cm-dbh Douglas-fir. All three nests were typical brood nests constructed by female tree voles, consisting of large, densely compacted accumulations of conifer twigs, needles, and resin ducts interlaced with tunnels leading to living chambers and fecal latrines (Maser 1966). Resin ducts, which the voles removed from conifer needles when feeding, were used to line tunnels and living chambers. On top of, and inside the entry tunnels of these nests, the voles accumulated a daily supply of food, which consisted exclusively of fresh green cuttings harvested from the tips of conifer branches.

Data Collection and Analysis

We mounted a video camera (Sentinel Magnum 4 video system, Sandpiper, Inc., Manteca, CA) about 1.5 m above each nest, aiming downward so that we could continuously monitor activity on the top and sides of the nest and on the limbs and trunk of the tree adjacent to the nest. The camera operated with ambient light during the day and infrared light at night and recorded the data on a hard drive (100-160 GB) located in a waterproof container on the ground. We used a 130-amp-hr 12 volt deep cycle marine battery to power the camera and recorder. We changed hard drives and batteries every 2-3 days and downloaded the video onto 500-GB LaCie hard drives (Hillsboro, OR) for viewing, editing, and long-term storage. To summarize the data from each nest we recorded the start and stop times of all activity observed, subdivided by activity type.

We recorded the type, number, and length of all items brought to nests during foraging bouts, including live conifer branchlets (hereafter called "cuttings"), dead twigs, and lichens.

We estimated the amount of time spent in different activities relative to sunrise and sunset, and the total length and biomass of cuttings brought to the nest. To evaluate the relationship between nesting status and amount of food brought to the nest we compared the mean number and mass of cuttings brought to the nest per day during periods when females had large young in the nest and periods when they had no young or young that were too small to venture outside the nest at night. We estimated the length of each cutting brought to the nest by visually converting the length of each cutting to a proportion of vole body length as we watched voles carry cuttings across the nest. We then converted the visual estimates to cm by multiplying the proportional length estimate of each cutting times 10.6 cm, which was the mean body length of 189 adult female red tree voles in a sample of museum specimens that we examined. We then summed the total length of all cuttings harvested each day and night and computed daily averages for each female and for the sample of three females. To estimate the mean number, wet mass, and dry mass of needles harvested per day we multiplied the mean length of cuttings harvested per day by mean estimates of the number, wet mass, and dry mass of needles cm^{-1} in a sample of 10 Douglas-fir cuttings and 10 grand fir cuttings that we measured, weighed, and dried for 48 hrs in a drying oven at 60° C (Douglas fir = 16.52 ± 1.22 needles cm^{-1}, 0.186 g cm^{-1} wet mass, 0.073 g cm^{-1} dry mass; grand fir = 10.66 ± 1.02 needles

cm^{-1} 0.220 g cm^{-1} wet mass, 0.079 g cm^{-1} dry mass). We included the stem of the cuttings in our estimates of wet and dry mass because we and others (e.g., Maser 1966) have observed that tree voles often eat the bark from the stem in addition to eating the needles.

We recorded all male visits to each nest and whether copulation was observed on each visit. Even when copulation was not observed, males were usually easy to identify because of their smaller size and furtive behavior as they investigated nest entrances to locate females. We documented the behavior and development of juveniles from the time they first began to explore outside the nest until they dispersed. Age of juveniles at various stages of development was estimated based on their size and physical behavior, and on dates when we observed their mothers copulate. For estimates of juvenile age based on observed dates of copulation we assumed a mean gestation period of 28 days (Clifton 1960, Hamilton 1962).

We used paired z-tests or univariate analysis of variance to compare means, and X^2 tests to compare medians (Zar 1974). All means are presented as $\bar{X} \pm 1$ SE. In eases where mean estimates were strongly skewed by a few outliers we used medians rather than means to describe the timing and duration of activity. We used Program SPSS (SPSS Inc., Chicago, IL) for all computations and statistical tests.

Results

We analyzed 6,696 hrs of video, including 2,184 hrs at Peavy, 3,384 hrs at Oak Creek, and 1,128 hrs at Greasy Creek. Observation periods were 9 February - 25 May 2006 at Peavy (103 days), 6 February - 3 July 2007 at Oak Creek (148 days), and 23 October - 24 December 2007 at Greasy Creek (63 days). All three nests were occupied by single adult females and their young. The Peavy and Oak Creek females raised three and two litters to dispersal age respectively, while we observed their nests, and were raising additional litters when they were apparently preyed upon. The Greasy Creek female had two large young that dispersed nine days after we installed the camera on her nest. There was no indication that she either bred or had additional litters before she disappeared on 24 December 2007.

On the first night of observation at Peavy we found that the female had three small juveniles that were just beginning to venture outside the nest. We could not be absolutely sure of the age of these juveniles, but based on comparisons with subsequent litters in which we knew the approximate age of the young, we estimated that the young in the first litter were ca 30 days old when first observed on 9 February 2006. The female at Oak Creek female had no young when the camera was installed on 6 February 2007, but based on the fact that ajuvenile began to venture outside the nest on 5 April we estimated she became pregnant on 6 February and had a litter on 6 March. She was observed copulating on 16 March and had a second litter on ca 13 April. The young from her two litters dispersed on 1 May and 9 June, respectively.

Activity Periods

All three females were primarily nocturnal, and two were almost exclusively so (Figure 1). Nocturnal activity typically began 1-2 hrs after sunset (grand median = 95 min, 95% CI = 90-100 min, range = 12-735 min), and ceased 2-5 hrs before sunrise (grand median = 168 min, 95% CI = 151-191 min, range = 14-726 min). The Greasy Creek and Oak Creek females were seen outside the nest during the day on only rare occasions when they emerged briefly, harvested 1-6 cuttings, and then went back inside (Figure 1b, c). The Peavy female was slightly more inclined to forage during the day, especially when she had large young (Figure 1a). She was seen outside the nest during the day on 11 of the 94 days for which we had complete data, spending an average of 1.47 ± 0.55 min day^{-1} (range = 0-36 min) foraging during diurnal hours. Eight of these occasions occurred in the late afternoon, presumably after she and her young had consumed all of the cuttings inside the nest (Figure la).

Although diurnal activity outside the nest was uncommon, interior renovation of nests and retrieval of cuttings that were stored at the nest entrance were common during the day at all nests, occuring on an average of $36 \pm 28\%$ and $61 \pm 28\%$ of the days that we observed nests, respectively. Interior renovation was observable because the top of nests would bulge outward as the voles pushed or pulled materials about inside their nests. In most cases ($91 \pm 17\%$, n = 3 nests) retrieval of cuttings during the day was detected when a cutting was gradually pulled inside the nest entrance without the vole exposing itself. Less commonly, females

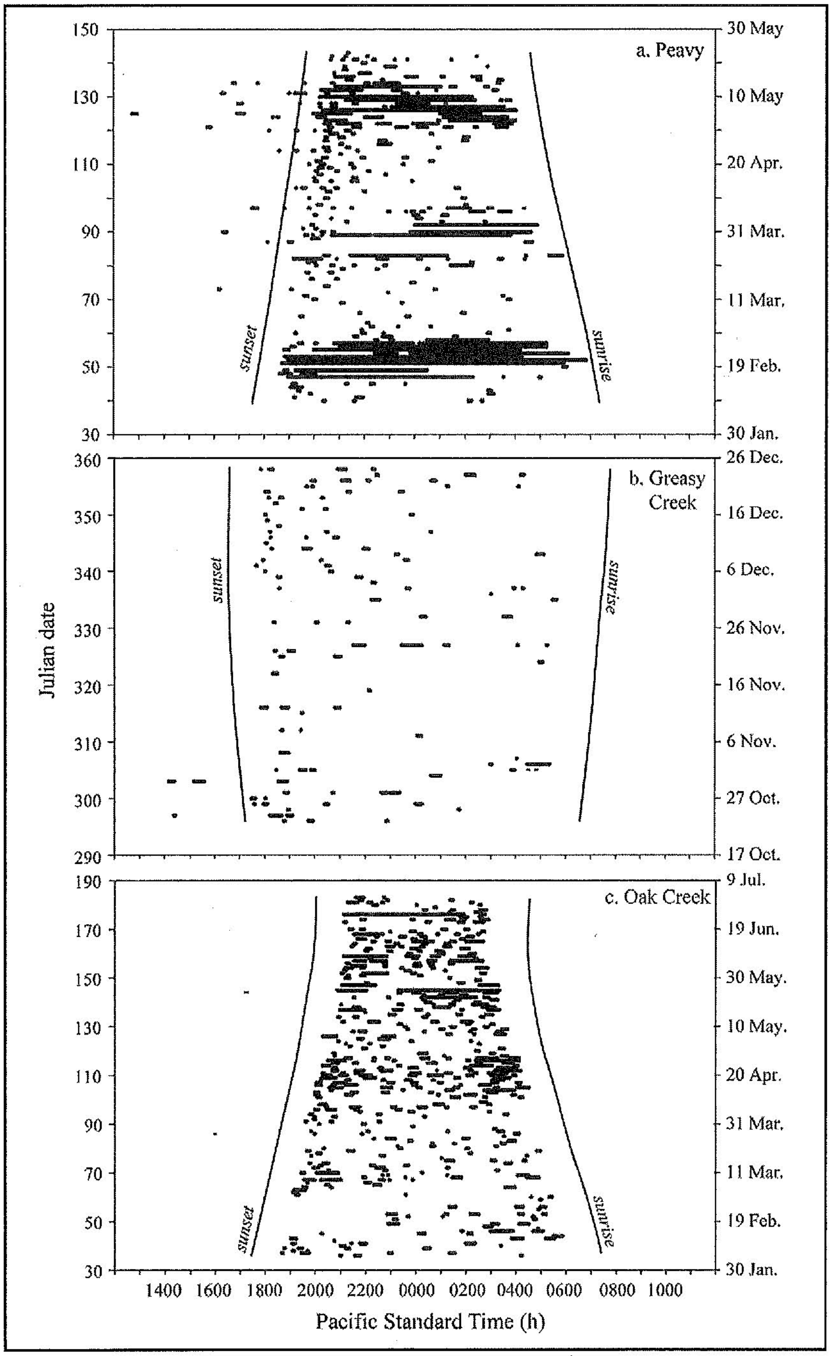

Figure 1. Diel activity periods of three adult female red tree voles (*Arborimus longicaudus*) in western Oregon. Time on x-axis indicates time of day in 2-hr intervals centered on midnight (0000 hrs) Pacific Standard Time. Curved vertical lines indicate sunset (left) and sunrise (right) and dashed horizontal lines indicate time intervals when the voles were active outside their nests. Each row of data is for one 24-hr day in the sampling period. Sampling periods are indicated by Julian dates on the left and corresponding calendar dates on the right.

TABLE 1. Mean estimates (± 1 SE)[1] of the number of foraging bouts and the number, total length, mass, and individual length of cuttings brought to the nest by three adult female red tree voles (*Arborimus longicaudus*) in western Oregon.

Variable	Peavy	Oak Creek	Greasy Creek	Grand mean[2]	Range
Number of bouts per night	3.0 ± 0.2	3.0 ± 0.1	3.6 ± 0.3	3.2 ± 0.2	0–13
Number of cuttings per bout	8.8 ± 2.8	6.9 ± 0.3	4.7 ± 0.3	6.8 ± 1.1	1–49
Number of cuttings per day					
Nocturnal bouts	26.3 ± 1.5	20.7 ± 1.3	14.1 ± 1.8	20.4 ± 3.5	0–75
Diurnal bouts	0.6 ± 0.2	tr[3]	0.2 ± 0.1	0.3 ± 0.2	0–12
24-hr period	26.6 ± 1.6	20.7 ± 1.3	14.2 ± 1.8	20.5 ± 3.6	0–75
Total length of cuttings per day (cm)					
Nocturnal bouts	304 ± 19	253 ± 16	244 ± 31	267 ±19	0–1,275
Diurnal bouts	6 ± 2	9 ± tr	4 ± 2	6 ± 1	0–12
24-hr period	310 ± 18	253 ± 16	245 ± 31	269 ± 21	0–1,275
Wet weight of cuttings per day (g)	58 ± 3	54 ± 3	46 ± 6	52 ± 4	0–237
Dry weight of cuttings per day (g)	23 ± 1	20 ± 1	18 ± 2	20 ± 1	0–93
Length of individual cuttings (cm)	11.5 ± 0.1	12.3 ± 0.1	17.3 ± 0.2	13.7 ± 1.8	1–37
Length of individual dead twigs (cm)	13.7 ± 1.7	17.4 ± 0.9	19.4 ± 0.6	16.8 ± 1.7	2–39

[1]Sample sizes for daily and nightly estimates were 83 (Peavy), 143 (Oak Creek) and 52 (Greasy Creek). Sample sizes for length of bouts and number of cuttings per bout were 266 (Peavy), 430 (Oak Creek) and 155 (Greasy Creek). Sample sizes for length of individual cuttings were 2,409 (Peavy), 2,942 (Oak Creek), and 770 (Greasy Creek). Sample sizes for length of individual dead twigs were 16 (Peavy), 109 (Oak Creek), and 151 (Greasy Creek). Sample size for all grand means was 3.

[2]Grand means = mean of the means of three females.

[3]tr = <0.05

TABLE 2. Median estimates of time spent outside the nest per night and per foraging bout (in min) for three adult female red tree voles (*Arborimus longicaudus*) in western Oregon. Time spent outside nest is subdivided into time spent foraging and storing food versus all other types of activity. 95% confidence limits for population medians are in parentheses.[1]

Activity type	Peavy	Oak Creek	Greasy Creek	Grand median[2]	Range
Foraging and storing	19 (16–25)	29 (23–36)	20 (15–38)	24 (20–27)	0–448
Other activity[3]	0 (0–0)	0 (0–0)	0 (0– 1)	0 (0–0)	0–701
Total time outside	25 (18–32)	31 (24–37)	23 (17–38)	27 (23–32)	0–712
Foraging bout length	6.8 (6.0–7.9)	9.3 (8.7–10.1)	8.2 (7.5–9.0)	8.4 (8.0–8.9)	0.2–443.3

[1] Sample size for Peavy, Oak Creek and Greasy Creek was 84, 142, and 53 nights, and 263, 430, and 157 foraging bouts, respectively.

[2] Grand median is median of all data combined for the three voles (Zar 1974).

[3] "Other" activity included loitering on top of the nest, interactions with males, renovation of nests, retrieving stored clippings, and periods of unknown behavior when females were away from the nest.

darted out of the entrance, grabbed a cutting in the mouth, and dragged it inside.

Nocturnal activity offemales consisted primarily of long periods inside the nest interspersed with short bouts of intensive foraging (Figure 1). The mean number of foraging bouts per night was 3.2 ± 0.2 (Table 1) and the median length of individual foraging bouts was 8.4 min (Table 2). The median time spent outside the nest at night was 27 min (Table 2). Occasionally, females left their nests for extended periods at night and did not return for 2-12 hrs (Figure 1), and on several occasions after her young dispersed, the Greasy Creek female was absent from the nest for one or two nights. It was unclear what the voles were doing during these prolonged absences, but the result was that mean estimates of the duration of nocturnal activity outside the nest were strongly skewed by a few outliers.

The mean number of cuttings brought to the nest was 6.8 ± 1.1 per foraging bout (range = 1-49) and 20.4 ± 3.5 per night (range = 0-75; Table 1). Of 6,421 items brought to nests, 6,121 (95.3%) were cuttings, 276 (4.3%) were dead twigs, and 24 (0.4%) were lichens. The mean number of dead twigs and lichens brought to nests per night was

TABLE 3. Estimated mean length (cm) of individual cuttings, dead twigs, and lichens brought to nests by three adult female red tree voles (*Arborimus longicaudus*) in western Oregon.

Nest	Green conifer cuttings			Dead twigs			Lichens		
	n	$\bar{X} \pm$ SE	Range	n	$\bar{X} \pm$ SE	Range	n	$\bar{X} \pm$ SE	Range
Peavy	2,409	11.5 ± 0.1	1–35	16	13.7 ± 1.7	4–32	1		
Oak Creek	2,942	12.3 ± 0.1	1–37	109	17.4 ± 0.9	2–37	22	8.5 ± 1.0	1–17
Greasy Creek	770	17.3 ± 0.2	3–34	151	19.4 ± 0.6	5–39	1		
Grand means[1]	3	13.7 ± 1.8		3	16.8 ± 1.7				

[1]Grand means are the mean of the means of the three females.

TABLE 4. Mean number and mass (g) of cuttings brought to nests per 24-hr period by adult female red tree voles (*Arborimus longicaudus*) when they had large young versus when they either had no young or only small young.

Variable	Large young not present		Large young present		Comparison of means	
	$\bar{X} \pm$ SE	n	$\bar{X} \pm$ SE	n	Statistic	*P*
Number of cuttings						
Peavy	22 ± 2	41	30 ± 2	45	$F = 6.7$	0.011
Oak Cr	18 ± 2	94	26 ± 2	49	$F = 11.2$	0.001
Greasy Cr	14 ± 2	39	16 ± 4	8	$F = 0.3$	0.616
Grand mean	18 ± 3	3	24 ± 4	3	$t = -3.4$	0.078
Wet weight of cuttings (g)						
Peavy	44 ± 3	43	69 ± 5	38	$F = 17.2$	0.000
Oak Cr	45 ± 4	94	71 ± 6	49	$F = 14.3$	0.000
Greasy Cr	40 ± 5	44	73 ± 24	9	$F = 5.0$	0.029
Grand mean	43 ± 2	3	71 ± 1	3	$t = -11.1$	0.008
Dry weight of cuttings (g)						
Peavy	17 ± 1	43	27 ± 2	38	$F = 17.2$	0.000
Oak Cr	17 ± 1	94	26 ± 2	49	$F = 14.3$	0.000
Greasy Cr	16 ± 2	44	29 ± 9	9	$F = 5.0$	0.029
Grand mean	17 ± 1	3	27 ± 1	3	$t = -11.1$	0.008

1.4 ± 0.9 (range = 0-44) and 0.06 ± 0.02 (range = 0-4), respectively.

The mean length of individual cuttings and dead twigs brought to nests by females was 13.7 ± 1.8 cm and 16.8 ± 1.7 cm, respectively (Table 3). The cumulative length of cuttings brought to nests averaged 269 ± 21 cm day^{-1}, or approximately 4,445 needles of Douglas-fir or 2,700 needles of grand fir per day (Table 1). The estimated total wet and dry mass of cuttings brought to nests averaged 52 ± 4 and 20 ± 1 g day , respectively (Table 1). The number and mass of cuttings harvested per day were greater when females had large young in the nest than when they had no young or small young (Table 4).

Behavior offemales while foraging was rather stereotyped. Foraging bouts usually started when a female arrived at the nest entrance, paused for several sees to several min to look around, and then began to run in and out on the limbs and trunk of the nest tree, rapidly biting off the new growth at the tips of limbs, and dragging the cuttings to the nest. The median amount of time required to run out from the nest, harvest a cutting and bring it back to the nest was 37 sec, and the median time required to store each cutting was 5 sec (Table 5). Although median estimates of the amount of time required to store food were similar for all females, median estimates of the amount of time required to harvest individual clippings differed among females (X^2 =810.9, df = 2, $P < 0.001$, Table 5). During foraging bouts the movements of the voles were often so rapid it was hard to follow them as they scurried in and out of the nest. Cuttings were transported by grasping them in the mouth and dragging them alongside the body or lengthwise over the back. Smaller cuttings and dead twigs were often carried sticking out one side

TABLE 5. Median duration (in secs) of foraging trips and food storing periods of three adult female red tree voles (*Arborimus longicaudus*) in western Oregon.

Nest	Foraging trip[1]			Food storage[1]		
	Median	95% CI	Range	Median	95% CI	Range
Peavy	28	28–29	5–3,412	5	5–5	1–249
Oak Creek	41	40–42	4–17,176	5	4–5	1–251
Greasy Creek	64	61–66	4–3,563	4	3–4	1–62
Grand median	37	36–38	4–42,079	5	4–5	1–460

[1]Number of foraging trips and storing events at each nest was: Peavy (2,476; 2,431), Oak Creek (3,135; 3,074), Greasy Creek (961, 934).

of the mouth at odd angles to the line of travel. When coming down the trunk with large cuttings, voles typically let the cutting dangle below them until they reached the nest, and then reverted to dragging the cutting behind them. Regardless of cutting size, voles always traveled head-first when going up or down the trunk, and virtually always stayed in direct contact with the trunk or limbs. On rare occasions they jumped between the nest and adjacent limbs, but such leaps were limited to only a few ern. Although females occasionally harvested cuttings or dead twigs that were over 30 cm long, these large loads were difficult for them to handle, and it was not unusual to see long cuttings become snagged on limbs or on the debris on top of the nest. This usually precipitated a brief period of jerking and tugging to get the cutting loose. If the cutting remained stuck the vole would eventually drop it and go after another one.

The median amount of time spent outside the nest per night in activities other than foraging was zero for all three females (range = *0-70/min;* Table 2). Activity other than foraging was mostly limited to occasional brief periods when females loitered on top of the nest, retrieved clippings, or interacted with males. However, the amount of time spent in other activities was extremely variable, and as mentioned earlier, there were occasions when females were gone for much of the night, doing something away from the nest.

Reproductive Behavior and Juvenile Development

All three nests were visited by males, but the percent of nights when males visited was highly variable among nests (48% at Peavy, 12% at Oak Creek, 25% at Greasy). Visits typically began when a male appeared from up or down the trunk or from one of the limbs surrounding the nest and began to investigate the top of the nest. Males were usually easy to identify because of their nervous behavior as the sniffed around the entrance to the nest, darted in and out of the nest entrance, or skulked on top of the nest. In most cases, these visits lasted only a few min and males left after being ignored or chased by the females. When males were persistent and females were unreceptive, the males would eventually give up and leave after being repeatedly nipped and chased by females. In all of these interactions, the slightly larger size and dominant behavior of females was evident. On three occasions, copulation was observed on top of the nest or on limbs adjacent to the nest or both, and involved rapid circling prior to the male mounting the female.

Young born in two litters, presumably from the observed copulations, were first observed coming to the nest entrance, or just outside the nest entrance, 58 days and 63 days after copulation was observed, respectively. Assuming a gestation period of 28 days (Clifton 1960, Hamilton 1962), we estimated that the juveniles in these two litters were 30 and 35 days old, respectively, when they first began to emerge from the nest. Juvenile behavior and tenure at the nest was similar for all six litters observed. The first trips outside the nest were very tentative and limited to peeking from the entrance or crawling about just outside the entrance. Within 2-6 days of their first appearance juveniles began to explore the top of the nest, crawling about somewhat aimlessly before retreating back inside the nest. During the next two weeks they spent increasing amounts of time outside the nest at night, milling about on top of the nest and gradually spending more and more time climbing on the trunk and limbs near the nest. Initial climbing attempts were tentative and clumsy, and the juveniles ventured only a few centimeters up the trunk or out onto limbs before crawling back onto the nest. Like the adults, climbing was always head-first, regardless of whether they were going up or down the trunk. After they had been venturing outside the nest for 7-10 days (age ca 40 days), juveniles began to climb with increasing skill, and within two weeks (age ca 44 days) they were making regular trips up the trunk and out the limbs around the nest. The earliest age at which they began to bring cuttings back to the nest was ca 33 days (range = 33-41 days). At the Peavy nest the number of cuttings brought back to the nest by juveniles gradually increased with age, and during the last week before they dispersed, siblings harvested an average of 8.0 ± 3.6 cuttings per night (range = 0-21, n = 3 litters,). At the Oak Creek nest, where both litters consisted of a single juvenile, we saw only one case in which a juvenile brought a cutting to the nest. On average, cuttings brought to the nest by juveniles were about half as long ($\bar{X}$ = 7.2 ± 0.3 cm, n = 3 litters) as the cuttings brought to the nest by the adult females $\bar{X}$ = 13.7 ± 1.8 cm, n = 3 females).

Juveniles in the two litters of known age dispersed when they were 47 and 57 days old, respectively. This was 17 days and 22 days after they first began to venture out of the nest, respectively. Dispersal in the four litters with multiple siblings appeared to be simultaneous, with littermates leaving the nest on the same night. It was unclear if dispersal was voluntary or was triggered by female aggression. We saw two interactions between females and their young that suggested that females became aggressive towards their young as the young approached dispersal age, especially if the female had another litter of small young in the nest. In one particularly violent case, the Peavy female knocked one of her juveniles down and repeatedly nipped at it until it fled the nest and did not return.

Discussion

Although Swingle and Forsman (2009) concluded that tree voles were active primarily at night, their telemetry locations were not accurate enough to determine how much time the voles spent in their nests versus moving about in the forest canopy. Our observations corroborate their findings that tree voles are primarily nocturnal and also demonstrate that, on most nights, breeding females spend most of their time inside the nest, coming out for relatively brief periods at night to forage. Diurnal foraging was rare and limited primarily to occasions when females had overlapping litters in the nest and food demand was high. The small amount of time spent outside of nests by female tree voles probably reflects strong selection for minimizing exposure to predators, especially owls and weasels, which are major predators on tree voles (Forsman and Maser 1970, Forsman et al. 2004, Graham and Mires 2005, Swingle 2005).

Based on their behavior when chased from their nests during the day, tree voles have acquired a reputation for being slow, docile and somewhat clumsy climbers (Taylor 1915, Howell 1926, Jewett 1930, Bailey 1936). We reached a very different opinion based on our observations of tree voles at night, when we found that they were very coordinated climbers and spent most of their time running rapidly up and down tree trunks and in and out on limbs, while carrying bulky loads. We suspect that tree voles have acquired a reputation for being slow and clumsy primarily because most previous observations have been based on voles that were chased from their nests during the day. In these situations tree voles often seem confused and try to hide by huddling motionless on a tree trunk or limb or under debris on the ground, and if chased they typically run only a short distance before trying to hide again. Their rapid, non-stop behavior when foraging at night was in marked contrast to their behavior during the day.

Our results support previous studies that indicated that female tree voles are solitary, largely arboreal, and have high nest fidelity (Howell 1926, Maser 1966, Maser et al. 1981, Swingle and Forsman 2009). The vast majority of activity at night consisted of foraging bouts that were restricted to the trunk or limbs of the nest tree, or possibly adjacent trees with interconnecting branches. However, there were occasional periods at night when females left their nests and did not return for up to 12 hrs. During these prolonged absences it was unclear if they were making exploratory trips to the ground or to other trees or were feeding or resting elsewhere in the nest tree. Swingle (2005) observed a number of cases in which radiocollared females left their nests in the evening, spent the night in nearby trees, and then returned to their nests before dawn. The behavior of the female at Greasy Creek was especially unpredictable after her last litter dispersed in early November, and she sometimes disappeared for 1-2 days at a time. It is possible in the latter case that this non-breeding female was using multiple nests in different trees, a behavior that was typical of 60% of the 45 voles that were radiotracked by Swingle and Forsman (2009).

The voles we observed appeared to feed exclusively on fresh cuttings of the conifers in which they lived, and possibly an occasional lichen. They appeared to ignore the insects, spiders, and salamanders that were often seen on top of their nests (Forsman and Swingle 2007). Howell (1926:52) estimated that a captive 20-g female tree vole removed the needles from 168 cm and 180 cm of Douglas- fir cuttings on two sequential days. He estimated that this was the equivalent of 2,310 needles (17.5 g wet wt) and 2,476 needles (19.0 g wet wt), respectively. Based on these data he concluded that the vole ate about, "... 100 needles per hour, day and night," and that it consumed approximately 90% of its body mass in food every 24 hrs. Howell noted that his calculations did not account for the amount of food that was discarded by the vole, but he suggested that any food discarded was offset by the amount of bark that was consumed and not accounted for by his methods. Although this assumption is questionable, his study suggests that tree voles spend much of their time eating, and consume prodigious amounts of needles relative to their body size. Our estimates of the mean total length ($\bar{X}$ = 269 ± 21 cm) and wet weight ($\bar{X}$ = 52 ± 4 g) of cuttings brought to the nest per night by adult females were considerably greater than Howell's estimates of daily food consumption, which was not surprising given that the females we observed were raising juveniles during much of the time that we observed them, and that at least some of the food brought to the nest was wasted because it dried out before it could be consumed.

Although it is well documented that tree voles have small litters (1-4), and that their young develop slowly compared to other microtines (Clifton 1960, Hamilton 1962) there is little information on the age at which tree voles become independent. Based on observations of captive and wild tree voles, Hamilton (1962:500) estimated that weaning took place when juveniles were 30-40 days old, well in advance of dispersal. This is about the same age at which we first began to see juveniles venturing outside the nest at night. Our observations indicate that young tree voles do not disperse until they are at least 47-57 days old, and Swingle (2005:63) estimated that radio-collared juveniles in two different nests dispersed when they were 57 and 60 days old, respectively. Juveniles were almost completely dependent on the female for food until they were approximately 35-40 days old, and even thereafter the majority of their food was harvested by the female until they dispersed 2-3 weeks later. Small litter size and comparatively slow development of juvenile tree voles are probably adaptations for an arboreal life and a nutrient-poor diet of conifer needles (Hamilton 1962).

The females at Peavy and Oak Creek produced litters at intervals of about 30-35 days, which indicated a predominant pattern of post-partum breeding in which successive litters overlapped in the nest (Clifton 1960, Hamilton 1962). This pattern was most consistent at Peavy, where the female was almost continuously pregnant from the time we put the camera on her nest in early February until she disappeared on 25 June. During this time she raised three litters to dispersal age, and had at least one other litter in the nest when she disappeared. Although much has been written about the dispersal of voles, the proximal factors that influence dispersal of juvenile micro tines are not well understood, and may differ among species with different social systems (Lidicker 1985, Gaines and Johnson 1987, Tamarin et al. 1990). In our study we observed two cases in which adult females knocked down, nipped at, and chased their young on the same night the juveniles dispersed. Dispersal of littermates occurred on the same night, suggesting that females became aggressive towards all littermates on the same night. Hillborn (1975) and Beacham (1979) suggested that the tendency of sibling voles to disperse at the same time might be genetically based. We think there might be a simpler explanation for such behavior, namely female aggression towards their older young at times when females are caring for another litter or about to have another litter. Aggression of female tree voles towards their large juveniles may be most pronounced in cases where there are overlapping litters in the nest, as was the case in two of the three nests that we observed. Because the potential food supply within easy foraging distance of nests occupied by female tree voles is limited, there may be selection for females to force their young to disperse as soon as they become proficient at foraging for themselves, thereby reducing food competition with the female and her next litter. Forcing large juveniles to disperse may also reduce the likelihood of predation of the female and her small young, as high levels of juvenile activity outside the nest at night undoubtedly increase the odds that predators will be attracted to the nest.

In our study, male tree voles regularly visited the nests of females at night, presumably to monitor female receptiveness to breeding. In most cases males were rebuffed or ignored and departed after only a few minutes. Even in cases where females were receptive, males did not remain at female nests for more than a few hours at night. The amount and pattern of male activity outside the nest probably differs from females, but we could not evaluate this because we did not monitor male nests. We were also unsure if the males we observed were primarily monogamous with a single female or visited the nests of multiple females. Data from radiocollared males observed by Swingle (2005) indicated that some males visited multiple nests within home ranges that encompassed up to 10,000 m^2.

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