2010 Northwest Science 84(3)

James K. Swingle[1], Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

Eric D. Forsman, USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331

and

Robert G. Anthony, U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

Survival, Mortality, and Predators of Red Tree Voles *(Arborimus longicaudus)*

Abstract

Although estimations of vital rates are important to understand population dynamics of small mammals, there is little information on survival rates and causes of mortality for many species. In 2002-2003, we estimated monthly and annual survival of 50 radiocollared red tree voles *tArborimus longicaudusi* during a study of movements and diel activity patterns in western Oregon. Estimated annual survival for both sexes combined was 0.15 (95% CI = 0.06 to 0.31) and was influenced little by mass at initial capture. In the analysis of explanatory variables, we did not find strong effects of gender, vole age. or forest age on survival. We suspect this may have been due to small sample size and low power to detect effects, because some of the point estimates were suggestive of large differences among groups. Most mortality was due to predation, with 15 of 25 deaths attributed to weasels *(Mustela* spp.). Weasels preyed upon significantly more females than males (14: 1, respectively). Other confirmed or suspected predators were owls (*n*= 3), a gopher snake *(Pituophis cateniferi,* and a domestic dog ***(Canis familiaris).*** Although our results did not support the hypothesis that survival of tree voles was higher in old forests than in young forests. we caution that om sample for this comparison was small and recommend that more definitive studies with larger samples be conducted to better elucidate relationships between vital rates of tree voles and forest age and structure.

Introduction

Red tree voles *(Arborimus longicaudus)* are small microtine rodents that are endemic to the coniferous forests of western Oregon and northwestern California, where they are an important prey item of northern spotted owls *(Strix occidentalis caurina)* and other forest birds and mammals (Forsman et al. 2004a, b; Graham and Mires 2005). Tree voles are solitary and primarily arboreal, but occasionally come to the ground to travel between trees if there are no interconnecting branches (Forsman et al. 2009, Swingle and Forsman 2009). They are primarily active at night when they leave the nest to harvest cuttings from terminal tips of conifer branches, which they bring back to the nest and store for consumption later (Taylor 1915, Howell 1926, Forsman et al. 2009). When feeding they eat conifer needles one at a time, after first removing the resin ducts (Benson and Borell 1931). The discarded resin ducts are used to line passageways and living chambers inside the nest (Taylor 1915).

The red tree vole is a species of concern to forest managers because of its association with old forests (Corn and Bury 1991, Dunk and Hawley 2009). In addition, tree voles have small litters, slow growth rates, and a long period of natal dependency compared to other microtines (Clifton 1960, Hamilton 1962, Forsman et al. 2009). This has led to speculation that they may be particularly susceptible to local extinctions due to logging and habitat fragmentation (Corn and Bury 1988, Aubry et al. 1991, Huff et al. 1992, Thomas et al. 1993, Carey 1996). Because of these concerns, the red tree vole in the Coast Ranges is listed as vulnerable on the Oregon list of sensitive species (Oregon Department ofFish and Wildlife 2008), and is on the list of species that federal agencies in Oregon are required to survey and manage in proposed timber sales (USDA Forest Service and USDI Bureau of Land Management 1994, 2001). The U.S. Fish and Wildlife Service is currently conducting a status review of the species to determine if it warrants listing as "threatened" in all or part of its range (USDI Fish and Wildlife Service 2008).

---

[1] Author to whom correspondence should be addressed. E-mail: jimmy.swingle@gmail.com

In 2002-2003, we conducted a radiotelemetry study in which we examined the movements and diel activity patterns of red tree voles in western Oregon (Swingle and Forsman 2009). During that study we monitored the fate of all individuals and attempted to document causes of mortality. In this paper we describe causes of mortality and compare age- and gender-specific survival rates of tree voles in young forests regenerating on clearcuts (22-55 yrs old) versus old forests (110-260 yrs old) that had not been logged. We hypothesized that survival rates would be higher in old forests because there is evidence that tree voles are associated with old forests (Corn and Bury 1991, Dunk and Hawley 2009). We also predicted that males would have lower survival than females because they probably spend more time outside their nests than females, while seeking out females that are sexually receptive.

Study Sites

The study was conducted at three different sites in Douglas County, Oregon. The Yellow Creek study site (43°29'48"N, 123°24'53"W) was located in the southern Coast Ranges, 32 km north of Roseburg. The Boulder Ridge study site (42°57'45"N, 123°40'47"W) was located in the Klamath Mountains, 38 km SW of Roseburg. Both of these study sites were on lands administered by the Roseburg District of the Bureau of Land Management (BLM). The Taft Creek study site (43°12'36"N, 122°48'15"W) was located in the Little River drainage on the west slope of the Cascades Range, 45 km E of Roseburg on lands administered by the Umpqua National Forest. Study sites were selected based on a variety of factors, including known locations of tree voles, good road access, and agency restrictions on where we could conduct research so that our study sites did not conflict with planned timber sales.

All three study sites were characterized by mountainous terrain covered by forests dominated by Douglas-fir (*Pseudotsuga menziesii).* Other trees species that were associated with the Douglas-fir forests were western hemlock *(Tsuga heterophylla),* grand fir *(Abies grandis),* incense-cedar *(Calocedrus decurrens);* bigleaf maple *(Acer macrophyllumi,* golden chinquapin *(Castanopsis chrysophylla),* western redcedar *(Thuja plicata),* Pacific yew *(Taxus brevifolia),* red alder *(Alnus rubra),* and Pacific madrone *(Arbutus menriesii).* Forest structure on the three study sites included a mixture of young forest (22-55 yrs old) regenerating on old clearcuts, intermixed with areas of mature and old-growth forest (110-260 yrs old) that had never been cut (GIS data on file at Roseburg District BLM and Umpqua National Forest offices, Roseburg, Oregon). Elevations ranged from 430-610 m at Yellow Creek, 610-700 m at Boulder Ridge, and 480-670 m at Taft Creek. Climate on all three sites was characterized by cool wet winters and warm, dry summers. Mean annual precipitation was 86 cm at Yellow Creek, 97 cm at Boulder Ridge, and 137 cm at Taft Creek (Loy et al. 2001).

Methods

We located tree voles by visually searching for arboreal nests as we walked through forests. We climbed to all potential nests to determine if they were occupied. We captured voles by probing their nests with a stiff piece of wire, causing them to flee the nest, at which point we captured them by hand or in dip nets, either in the nest tree (28%) or on the ground after they jumped from the nest (72%). The wire probe was especially useful in minimizing disturbance to nests, as we did not want to influence vole behavior or survival by damaging their nests.

Each captured vole was weighed and fitted with a radiocollar (Model BD-2C or BD-2NC, Holohil Systems, Carp, Ontario). We used three different radiocollar weights (0.6, 1.0, 1.5 g) depending on vole mass, in order to keep radiocollar weights $<$ 5% of body mass. Voles were categorized as adults, subadults, orjuveniles based on mass, pelage color, and external evidence of reproductive condition (Clifton 1960, Hamilton 1962, Maser and Storm 1970). Of the 50 voles captured, gender of 40 was determined based on molecular polymerase chain reaction (PCR) of a tissue sample collected from the tip of the tail (Bryja and Konecny 2003, Bellinger et a1.2005), and gender of 10 was estimated based on external characters (visible evidence of mammae or testes and distance between the urogenital vent and anus). Confirmation of gender based on PCR analysis of 24 females and 16 males indicated that our gender assignments based on morphological attributes were 92.5% accurate. The entire handling sequence from capture to release took about 20 minutes. All procedures exceeded the guidelines recommended by the

American Society of Mammalogists Animal Care and Use Committee (Gannon et al. 2007) and were conducted under Oregon State University Animal Care and Use Permit 3091.

We used hand-held radio receivers (Model R-l000, Communications Specialists, Orange, California) and H-antennas (Model RA-2AK, Telonics, Mesa, Arizona) to relocate radio collared voles every-other night. In cases when we found a vole in a different tree than its usual nest tree, we conducted a follow up visit the next day to determine if the individual was still in the new location or moved back to the previously used tree. If we could not relocate a vole, we searched > 500 m in all directions from the center of the individual's known home range to see if we could relocate it or its remains. When voles stopped moving or were radiotracked to locations on the ground or underground, we returned the following morning to locate the collar and determine the vole's fate. When voles were found dead on the ground or in trees we recorded position and condition of the remains and any other information that could be used to determine cause of death. When voles were located underground or inside rotten logs, we carefully excavated the soil or wood, searching for the body, fur, radiocollar, and evidence of other prey species that may have been eaten or cached at the same location. We then climbed to the last nest occupied by the vole to see if there was evidence of predation at the nest.

We used known-fate models in program MARK with a staggered entry design and censoring to estimate monthly and annual survival rates (Pollock et al. 1989, White and Burnham 1999). Because of small sample size we truncated the data to exclude the first and last month of data collection and estimated annual survival for the period September 2002 to August 2003. Fifteen individuals with unknown fates (e.g., transmitter failure or loss) were censored from the analysis during the time intervals when they could not be located (Pollock et al. 1989). Consequently, there was little bias in our survival estimates due to right-censoring when mortality may have been associated with transmitter failure (Murray 2006).

We used an information-theoretic approach (Burnham and Anderson 2002) to evaluate hypotheses regarding the effects of vole age, gender, mass at initial capture, time since initial capture, and forest age (young forest 22-55 yrs old, old forest 110-260 yrs old) on monthly survival. We examined a set of 24 *a priori* models and one *a posteriori* model using Program MARK (White and Burnham 1999). Each model included a suite of independent variables and amounted to a unique hypothesis regarding variables that may have influenced survival. To identify the most parsimonious model, we ranked models using Akaike's Information Criterion corrected for small sample size (AIC_c) and computed AIC weights (w_i) as a relative measure of support for all models. To evaluate the relative importance of each parameter, we summed AIC weights across all models in which a selected parameter occurred and standardized these by dividing by the number of times the parameter occurred in various models ($Ew_i/$ occurrence). We considered any model with ^$AIC_c < 2.0$ to be competitive with the best model (Burnham and Anderson 2002). All means are expressed as X ± I SE.

Results

Of the 61 red tree voles that we radiocollared, we had enough data on 34 females (28 adults, 6 subadults) and 16 males (13 adults, 3 subadults) to use in the analysis of survival. Of these, 37 (30 females, 7 males) were in young forest and 13 (4 females, 9 males) were in old forest. On average, we radiotracked individual voles for 76 ± 8 days (range = 13 to 307) until they died or until their radiotransmitters failed or were removed by the voles, predators, or us. We radiocollared 32 of the voles one time only, whereas 18 were recaptured on 1 ($n = 13$), 2 ($n = 3$), or 3 ($n = 2$) occasions to replace transmitters that failed or were about to fail. Two voles that were recollared three times and one vole that was recollared twice were also recaptured a final time at the end of the study to remove their collars. On average, radiocollared voles were 2.4 g heavier on subsequent recaptures when compared to the initial capture (two-sample z-test, $t = 2.71$, d.f = 72, $P < 0.01$). After voles were released, 90% continued to use the same nest in which they were captured. Thus, it appeared that our capture methods had little effect on the behavior or survival of most individuals.

Of the 50 voles included in the analysis, 25 (50%) were killed by predators, 3 (6%) died from unknown causes, 1 (2%) died when its foot became entangled in its radiocollar, 8 (16%) either removed their radiocollars or had them removed by unknown predators, 3 (6%) were still alive when their radiocollars were removed at the end of the study, 8 (16%) disappeared from unknown causes or transmitter failure, and 2 (4%) were still alive when they were last seen with failed transmitters during unsuccessful recapture attempts. Of the 25 voles killed by predators, evidence at the scene suggested that 15 (60%) were killed by weasels *(Mustela erminea* or *M. frenata),* 3 (12%) were killed by owls, 1 (4%) was killed by a gopher snake *(Pituophis catenifer),* 1 (4%) was killed by a dog *(Canis familiaris)* that was accompanying the observer at night, and 5 (20%) died of unknown causes. All three cases of predation that we attributed to owls were cases where we found intact voles that were cached face-down on tree branches.

Of the 15 mortalities attributed to weasels, 14 were females. Remains of voles killed by weasels were found in a variety of locations, including tunnels inside decayed logs (*n* = 5), subterranean nests or runways (*n* = 4), cached on tree branches (n = 2), on the ground (*n* = 3), or in tree vole nests (*n* = 1). The two voles that were cached on limbs by weasels were placed face-up and were partially eaten, including the brains and most of the internal organs. Of the 15 voles killed by weasels, 8 (53%) were mostly or entirely consumed except for bits of fur, 3 (20%) were cached intact, and 4 (27%) were mostly intact except that the brains had been eaten. In 2 cases, remains of other mammals killed by weasels were located along with the vole radiocollars, including 2 intact coast moles *(Scapanus orarius)* cached in a subterranean nest, and partial remains of a deer mouse *(Peromyscus maniculatusy* and a shrew *(Sorex* spp.) on the ground below a tree vole nest. In two cases, it was clear that weasels had climbed trees to capture voles, because there was fresh weasel scat in the vole nests. In 9 cases where we examined vole nests after voles were killed by weasels, 6 nests showed little sign of disturbance, 2 had the main entry tunnels enlarged, and 1 had most of the original nest ripped apart Weasel predation occurred throughout the year except in the months of March, May, and September. There were 2 cases where 2 voles nesting 500 m and 120 m apart, respectively, were killed by weasels on the same day. In the five cases where the predator was unknown, we recovered radiocollars on the ground below nests that had been almost entirely ripped apart.

Of 3 voles that died from unknown causes, we found 2 on the ground with minimal to moderate trauma while the third was underweight, suggesting starvation or disease. Examination of the nests of these three voles revealed no signs of disturbance. The gopher snake that ate the female vole was found in a subterranean runway approximately 20 cm below ground and 18 m from the vole nest tree. An x-ray of the snake revealed that it had swallowed the vole headfirst, with the radiocollar in place.

Of the 25 models we considered, the top survival model in program MARK was the no-effects model (S[.]). Three models were competitive with the top model (^AIC$_c$< 2), including simple univariate models of gender, vole age, or linear time SeT) effects (Table 1). There were 7 models that had less empirical support but still fit the data reasonably well (2 < ^AIC$_c$ < 4). Four of these models included linear time with the additive effects of gender, forest age, vole age, or mass at initial capture (Table 1).

The regression coefficient (beta) from the linear time model S(T) suggested that the probability of survival increased slightly during the sampling period (B_T = 0.06 ± 0.07, 95% CI = -0.07 to 0.20). There was little support for the S(gender + T) model given that 95% CI's for the beta estimates overlapped zero for both variables (B_{gender}= 0.64 ± 0.59,95% CI = -0.53 to 1.81; B_T = 0.07 ± 0.07, 95% CI = -0.06 to 0.21). We found little evidence to support our hypothesis that tree vole survival was higher in old forest compared to young forest, as the 95% confidence intervals for the betas of T and forest age in model S(forest + T overlapped zero (B_{forest} = -0.27 ± 0.30,95% CI = -0.85 to 0.31; B_T= 0.07 ± 0.07,95% CI = -0.06 to 0.21). The 95% CI's for betas also overlapped zero for univariate models offorest age S(forest) and quadratic time S(T +TT) effects (B_{forest} = 0.07 ± 0.09, 95% CI = -0.09 to 0.25 and B_T = 0.01 ± 0.30,95% CI = -0.58 to 0.59; B_{TT} = 0.01 ± 0.02, 95% CI = -0.04 to 0.05). The estimate of beta for mass at initial capture suggested that bigger tree voles had a higher probability of survival, as the 95% CI barely overlapped zero (B_{mass} = 0.14 ± 0.08, 95% CI = -0.02 to 0.30). Akaike weights summed across models and standardized by occurrence in models ($E^{W}{}_{i}$ / occurrence) indicated that a linear time effect made the largest contribution to model fit (0.048), compared to gender (0.032), vole age

TABLE 1. Model selection results from analysis of annual survival of 50 radiocollared red tree voles (*Arborimus longicaudus*) in Douglas County, Oregon, September 2002 to August 2003. Models are listed in order of increasing AIC_c values. All models shown were *a priori* except for the second model, which was developed *a posteriori*.

Model structure[1]	AIC_c	ΔAICc	w_i[2]	Model likelihood	*K*[3]	Deviance
S(.)	126.77	0.00	0.20	1.00	1	124.75
S(adult males * others)	127.47	0.69	0.14	0.71	2	123.38
S(gender)	127.92	1.14	0.11	0.56	2	123.84
S(T)	128.02	1.25	0.10	0.54	2	123.94
S(age)	128.62	1.84	0.08	0.40	2	124.53
S(gender + T)	128.83	2.06	0.07	0.36	3	122.67
S(forest + T)	129.21	2.43	0.06	0.30	3	123.04
S(gender + forest)	129.93	3.16	0.04	0.21	3	123.76
S(age + T)	129.96	3.18	0.04	0.20	3	123.79
S(T + TT)	130.07	3.29	0.04	0.19	3	123.90
S(mass + T)	130.10	3.33	0.04	0.19	3	123.94
S(age + mass)	130.68	3.91	0.03	0.14	3	124.52
S(gender * forest)	131.54	4.77	0.02	0.09	5	121.13
S(gender * age)	131.59	4.82	0.02	0.09	5	123.31
S(gender * T)	132.79	6.02	0.01	0.05	5	122.37
S(gender + T + TT)	132.98	6.21	0.01	0.04	5	122.56
S(age * T)	133.67	6.90	0.01	0.03	5	123.25
S(t)	138.97	12.20	0.00	0.00	12	112.68
S(gender + t)	139.23	12.46	0.00	0.00	13	110.53
S(gender * t)	157.82	31.05	0.00	0.00	24	100.15
S(age * t)	161.40	34.63	0.00	0.00	24	103.72
S(mass)	205.82	79.04	0.00	0.00	2	203.79
S(mass + forest)	207.71	80.93	0.00	0.00	4	203.62
S(forest)	207.83	81.06	0.00	0.00	2	205.80
S(gender * age * t)	228.81	102.03	0.00	0.00	48	85.77

[1] Covariates indicate model structure for variable time effects (t), linear time effects (T), quadratic time effects (T + TT), forest age (forest), and age, gender or mass of the vole at initial capture. The no-effects model included no effects of vole age, gender, mass, forest age or time on survival.

[2] Model weight.

[3] Number of parameters in model.

(0.028), forest age (0.027), a quadratic time effect (0.027), mass at initial capture (0.019), and variable time (0.00]). The comparatively low model. weights and the 95% confidence intervals for the effects of mass at initial capture and variable time (t) provided little support for those effects.

Estimated annual survival for all 50 voles was 0.15 ± 0.06 (95% CI = 0.06 to 0.31). Contrary to our hypothesis that females would have a higher survival rate, the estimated annual survival of adult males (0.33 ± 0.21; n = 13) was almost 3 times higher than adult females (0.12 ± 0.06; n = 28). However, the 95% confidence intervals for these estimates overlapped broadly (95% CI_{males} = 0.07 to 0.76; 95% $CI_{females}$ = 0.01 to 0.31), providing little support for gender differences in survival (Table 2). Although the estimated annual survival of subadults (0.08 ± 0.12; 95% CI = 0.01

TABLE 2. Estimates of monthly s(*t*) and cumulative S(*t*) survival of 50 radiocollared red tree voles (*Arborimus longicaudus*) in western Oregon, 2002 to 2003. The number at risk is r(*t*) and number of deaths is d(*t*). C is the number censored from the analysis due to loss of signal.

	Males						Females					
	r(*t*)	d(*t*)	C	s(*t*)	S(*t*)	var.	r(*t*)	d(*t*)	C	s(*t*)	S(*t*)	var.
Sep	2	1	1	0.50	0.50	0.25	11	0	1	1.00	1.00	0.00
Oct	3	0	0	1.00	0.50	0.20	11	4	0	0.64	0.64	0.12
Nov	7	0	0	1.00	0.50	0.13	9	3	0	0.67	0.42	0.11
Dec	7	1	2	0.86	0.43	0.12	7	1	2	0.86	0.36	0.11
Jan	8	1	0	0.88	0.38	0.10	9	2	0	0.78	0.28	0.08
Feb	5	1	2	0.80	0.30	0.11	8	2	2	0.75	0.21	0.07
Mar	1	0	2	1.00	0.30	0.25	6	0	2	1.00	0.21	0.08
Apr	1	0	2	1.00	0.30	0.25	9	0	2	1.00	0.21	0.06
May	1	0	2	1.00	0.30	0.25	10	2	2	0.80	0.17	0.05
Jun	2	0	0	1.00	0.30	0.18	10	2	0	0.80	0.14	0.04
Jul	1	0	2	1.00	0.30	0.25	9	0	2	1.00	0.14	0.04
Aug	1	0	0	1.00	0.30	0.25	11	2	0	0.82	0.11	0.03

to 0.66; *n* = 9) was 50% lower than for adults (0.16 ± 0.07; 95% CI = 0.01 to 0.33; *n* = 41), the 95% confidence intervals for the two age groups overlapped broadly.

Discussion

Predation was the primary cause of tree vole mortality. Although many species of owls are known to feed on tree voles (Maser 1966; Forsman and Maser 1970; Reynolds 1970; Forsman et al. 2004a, b; Graham and Mires 2005), our data suggest that owls as a group were responsible for less tree vole mortality than were weasels. This was not entirely unexpected because weasels feed primarily on mice and voles (Banfield 1974), and some have suggested that mustelids may be predators of tree voles (Bailey 1936, Maser et al. 1981). Golightly et al. (2006) found *Arborimus* spp. remains in fisher *(Martes pennanti)* feces in northern California. Weasels are known to be adept climbers when pursing or caching prey (Booth 1945, Jeanne 1965, Weeks 1993, Bowman 1997), which led Smith et al. (2003) to speculate that long-tailed weasels *(MustelaJrenata)* might be predators of tree voles. We suspect that weasel predation on tree voles may be inversely proportional to nest height, but even very high nests may not entirely protect tree voles from weasels, as we found weasel scat in nests up to 31 m above ground.

We believe that short-tailed weasels *(M. erminea)* were responsible for much of the predation that we observed, but this is speculative because we could never positively confirm the species of weasel that killed our marked voles. Maser (1998) suggested that long-tailed weasels are not abundant in western Oregon and that short-tailed weasels have a greater association with forest habitats. **In** our study sites, there have been no detailed studies of the relative abundance or diets of either short- or long-tailed weasels. Wilson and Carey (1996) captured 30 short-tailed weasels and 15 long-tailed weasels in young (56--65 yrs old) Douglas-fir forests in western Washington. Of 57 weasels captured by Sullivan and Sullivan (1980) in British Columbia, 49 (86%) were in a o-year-old stand of deciduous trees and brush that was regenerating on a recent clear-cut and 8 (14%) were in a mixed successional deciduous-conifer plantation. They captured most of their weasels in late summer and early fall but did not report the relatively frequency for either species. We found that weasels preyed upon tree voles throughout the year. Because of the paucity of, and often contrasting information on weasel biology in the forests of the Pacific Northwest, there is obviously much to be learned about weasel predation on forest microtines.

The preponderance of females in the sample of tree voles killed by weasels suggests that females were more susceptible to predation by weasels than were males. Female tree voles may be easier for weasels to detect in maternal nests as was suggested by Cushing (1985) in the case of female deer mice (*Peromyscus maniculatus*). However, Yli:inen et al. (2003) reported that captive least weasels *(Mustela nivalisi* did not differentiate between odors of reproductive and non-reproductive female bank voles *(Clethrionomys glareolus)*. Norrdahl and Korpimaki (1998) found that field voles *(Microtus agrestis)* and sibling voles *(M. rossiaemeridionalis)* that moved more had a higher incidence of predation than those that moved less, and that mustelids killed more females than males. Female tree voles may be at greater risk to weasel predation than males because they live in larger and more conspicuous nests and may spend more time outside the nest while bringing cuttings back to the nest to feed their young (Swingle 2005, Forsman et al. 2009).

Although gopher snakes are known to climb trees and prey on avian nests (Rodriguez-Robles 2002), our examination of the nest of the tree vole that was predated by a gopher snake revealed no damage to the nest, so we suspect that the snake captured the tree vole on the ground or away from the nest in the forest canopy. We also believe that the single case of predation by a domestic dog that was accompanying the person who was tracking the tree vole was unusual because dogs are not normally present in forests occupied by tree voles at night. However, we know of at least two cases in which domestic cats *(Felis silvestris)* killed tree voles (Chris Maser field notes on file at the Slater Museum of Natural History, University of Puget Sound; Chris McCafferty, Oregon State University, personal communication). Because domestic cats hunt at night and are often allowed to run at large, they are undoubtedly a more significant threat to tree voles than are dogs. In the Coast Ranges of Oregon, Witmer and deCalesta (1986) found remains *of Arborimus* spp. in feces of coyotes *(Canis latrans)* and bobcats *(Felis rufus),* but did not differentiate between tree voles and white-footed voles *(Arborimus albipes)*.

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 *(Asia* otus-Reynolds 1970), barred owls *(Strix varia-Scott* Graham, Boise State University, personal communication), ringtails *tBassariscus astutus-Alexander* et al. 1994), common ravens *(Corvus* corax-Lowell Diller, Green Diamond Resource Company, personal communication), Steller's jays *(Cyallocitta stelleri-Howell* 1926, Ken Burton, USDA Forest Service, personal communication), northern pygmy-owls *(Glaucidium* gnoma-Graham and Mires 2005), and red-tailed hawks *(Buteo jamai*-censis-Graham and Mires 2005). Clifton (1960) observed a raccoon *(Procyon lotor)* sitting on top of a tree vole nest that had been torn apart and also speculated that northern flying squirrels *(Glaucomys sabrinus)* may prey upon tree voles since they are known to feed on flesh at least occasionally (Sumner and Dixon 1953, Connor 1960, McKeever 1960). We could not confirm the latter hypothesis, but we do have video of a female tree vole being chased down a tree trunk and into her nest by a flying squirrel (Eric Forsman, unpublished data).

Our data suggest that only about 15% of tree voles live longer than a year, and there was weak evidence that males live longer than females. However, we could not rule out the possibility that our radiocollars had a negative influence on survival or that survival is highly variable among years. Ideally, we should have evaluated the effects of radiocollars on survival by simultaneously sampling with alternative methods like Johannesen et al. (1997) who found that radiocollars did not affect survival in root voles *(Microtus oeconomus)*. A test of this hypothesis was not possible in our study because tree voles cannot be effectively sampled using any of the mark -recapture trapping techniques commonly used for small mammals (Swingle et al. 2004).

To compare survival of tree voles with other microtines, we computed monthly estimates of survival from data presented in mark-recapture studies (Table 3). In studies where survival was

TABLE 3. Comparison of monthly survival estimates (s) of red tree voles (*Arborimus longicaudus*) and other microtines. In studies that reported weekly, biweekly, or yearly estimates, we transformed the estimates to monthly estimates based on the product estimator functions s^4, s^2, and $s^{1/12}$, respectively, assuming constant survival over time. The low and high estimates represent the range of estimates in cases where more than one estimate was provided.

Study	Species	Low	High
This study	*Arborimus longicaudus*	na	0.85
Moorhouse et al. (2009)	*Arvicola terrestris*	0.43	0.80
Boonstra and Krebs (1979)	*Microtus californicus*	0.33	0.59
Paradis and Guédon (1993)	*Microtus duodecimcostatus*	na	0.88
Boonstra and Krebs (1979)	*Microtus pennsylvanicus*	0.48	0.85
Getz et al. (2006)	*Microtus ochrogaster*	0.43	0.64
Boonstra and Krebs (1979)	*Microtus ochrogaster*	0.48	0.82
Frase et al. (1990)	*Microtus ochrogaster*	na	0.69
Korslund and Steen (2006)	*Microtus oeconomus*	0.20	0.60
Johannesen and Ims (1996)	*Microtus oeconomus*	0.37	0.69
Boonstra and Krebs (1979)	*Microtus townsendii*	0.58	0.82
Hadley and Wilson (2004)	*Myodes gapperi*	0.27	0.37
Reed and Slade (2007)	*Peromyscus maniculatus*	0.41	0.79
Innes and Millar (1982)	*Phenacomys intermedius*	na	0.59
Reed and Slade (2007)	*Reithrodontomys megalotis*	0.63	0.80

reported in weekly, biweekly, or annual increments we transformed the estimates to monthly estimates based on the product estimator functions of *s4, s2,* and s1112, respectively, assuming constant survival over time. These comparisons indicated that our estimate of mean monthly survival of tree voles was higher than the maximum of monthly survival estimates reported in 12 of 14 studies examined (Table 3). This suggests that tree voles may have higher survival than most of their terrestrial counterparts.

Although the no-effects model was the top model in our analysis of factors influencing survival, we suspect this outcome had more to do with small sample size and low power to detect differences than anything else. lithe patterns that we observed were duplicated with slightly larger samples, many of the differences observed would almost certainly have been significant. For example, the point estimate for survival of subadults was 50% lower than for adults but we only had data on 9 subadults, resulting in comparatively large confidence intervals. Gender comparisons were also hampered by small sample size of males, which reduced the power to detect differences.

Our results did not support the hypothesis that survival of tree voles was higher in old forests than in young forests. Although this could be a result of small sample size, it does not lend support to the hypothesis that young forests are population, "sinks and barriers" for tree voles (Carey 1991:35). Tree voles had larger mean home range estimates in young forest compared to old forest but median home range size was higher in old forest because of large variation of individual home ranges (Swingle and Forsman 2009). Old forests are likely a more stable habitat than young forest for tree voles but we and others have found voles in young forest (Clifton 1960, Howell 1926, Maser 1966, Thompson and Diller 2002). Obviously, the role that young forests play in abundance and facilitating genetic and demographic connectivity between tree vole populations in old forests needs more detailed study.

Acknowledgements

Funding for this study was provided by the Oregon State Office of the USDI Bureau of Land Management and the Region 6 Office of the USDA Forest Service. Joe Lint at the Oregon State Office of the Bureau of Land Management was especially helpful in helping us secure funding and support for the study. Logistical and administrative support was provided by the Oregon Cooperative Fish and Wildlife Research Unit and the Department of Fisheries and Wildlife at Oregon State University, Umpqua National Forest, and the Roseburg District Office of the USDI Bureau of Land Management. We have benefitted from review of the manuscript by Jeffrey Dunk and one anonymous reviewer. We are especially grateful to the dedicated group of biologists who helped us capture and monitor tree voles, including Meagan Aitken- Voth, Scott Graham, Nick Hatch, Nicole Maggiuli, Mike McDonald, Jason Mowdy, Amy Price, Janice Reid, and Heather Wise. Hope Draheim at the USGS Forest and Rangeland Ecosystem Science Center in Corvallis conducted the genetic analysis of tree vole gender.

Literature Cited

Alexander, L. F, B. 1. Verts, and T P. Farrell. 1994. Diet of ringtails (*Bussariscus astutus)* in Oregon. Northwest Naturalist 75:97-101.

Aubry, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. 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 Nortbwest Research Station, Portland, Oregon. Pp. 285-294.

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

Banfield, A. W. F 1974. The Mammals of Canada. University of Toronto Press, Toronto, Ontario, Canada.

Bellinger, M. R., S. M. Haig, E, D, Forsman, and T D. Mullins. 2005. Taxonomic relationships 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 Mammalogy 12:226-233.

Boonstra, R., and C. J. Krebs. 1979. Viability of large- and small-sized adults in fluctuating vole populations. Ecology 60:567-573.

Booth, E. S. 1945. Account of a weasel in a tree. Journal of Mammalogy 26:439.

Bowman, J. C. 1997. An arboreal encounter between a long-tailed weasel, *Mustelafrenata,* and three red squirrels, *Tamiasciurus hudsonicus.* Canadian Field-Naturalist III :480-481.

Bryja, J., and A. Konecny. 2003. Fast gender identification in wild mammals 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. 1991. The biology of arboreal rodents in Douglas-fir forests. USDA Forest Service General Technical Report PNW-GTR-276. Pacific Northwest Research Station, Portland, Oregon.

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

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

Connor, P. F 1960. The small mammals of Otsego and Schoharie Counties New York. New York State Museum and Science Service Bulletin Number 382.

Com, P. S., and R. B. Bury. 1988. Distribution of the voles *Arborimus longicaudus* and *Phenacomys intermedius* in the central Oregon Cascades. Journal of Mammalogy 69:427-429.

Com, 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 Nortbwest Research Station, Portland, Oregon. Pp. 241-252.

Cushing, B. S. 1985. Estrous mice and vulnerability to weasel predation Ecology 66:1976-1978.

Dunk, J. R., and J. J. V. G. Hawley. 2009. Red-tree vole habitat suitability modeling: implications for conservation and management. Forest Ecology and Management 258:626-634.

Forsman, E. D., and C. Maser. 1970. Saw-whet owl preys on red tree mice. Murrelet 51:10.

Forsman, E. D., R. G. Anthony, E. C. Meslow, and C. J. Zabel. 2004a. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research 38:214-230.

Forsman, E. D., R. G. Antbony, and C. J. Zabel. 2004b. 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, andN. R. Hatch. 2009. Behavior of red tree voles *(Arborimus longicaudusi* based on continuous video monitoring of nests. Northwest Science 83:262-272.

Frase, B. A., T M. Pizzuto, and L. L. Getz. 1990. Survivorship of bled voles measured by recapture. Journal of Mammalogy 71: 104-105.

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

Getz, L. L., M. K. Oli, J. E. Hofmann, and B. McGuire. 2006. Vole population fluctuations: factors that initiate and determine intervals between them in *Microtus ochrogaster.* Journal of Mammalogy 87:387-393.

Golightly, R. T, T F Penland, W J. Zielinski, and J. M. Higley. 2006. Fisher diet in the Klamatb / North Coast Bioregion. Unpublished report on file at Department of Wildlife, Humboldt State University, Arcata, California.

Graham, S. A., and G. W. Mires. 2005. Predation on red tree voles by owls and diurnal raptors. Northwestem Naturalist 86:38-40.

Hadley, G. L., and K. R. Wilson. 2004. Pattems of small rnammal density and survival following ski-run development. Joumal of Mammalogy 85:97-104.

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

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, Portland, Oregon.

Innes, D. G. L., and J. S. Millar. 1982. Life-history notes on the heather vole, *Phenacomys intermedius,* in the Canadian Rocky Mountains. The Canadian Field-Naturalist 96:307-311.

Jeanne, R. L. 1965. A case of a weasel climbing trees. Joumal of Mammalogy 46:344-345.

Johannesen, E., and R. A. lms. 1996. Modelling survival rates: habitat fragmentation and destruction in root vole experimental populations. Ecology 77: 1196-1209.

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

Korslund, L., and H. Steen. 2006. Small rodent winter survival: snow conditions limit access to food resources. Joumal of Animal Ecology 75:156-166.

Loy, W G., S. Allan, A. Buckley, and J. E. Meacham. 2001. Atlas of Oregon. University of Oregon Press, Eugene.

Maser, CO. 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 Cascade. Oregon State University Press, Corvallis, Oregon.

Maser, C, B. R. Mate, J. F. Franklin, and C T. Dyrness. 1981. Natural history of Oregon Coast mammals. USDA Forest Service General Technical Report PNW-13 3. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

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

McKeever, S. 1960. Food of the northem flying squirrel in northeastem Califomia. Joumal of Mammalogy 41:270-271.

Moorhouse, T. P., M. Gelling, and D. W. Macdonald. 2009. Effects of habitat quality upon reintroduction success in water voles: evidence from a replicated experiment. Biological Conservation 142:53-60.

Murray, D. L. 2006. On improving telemetry-based survival estimation. Journal of Wildlife Management 70: 1530-1543.

Norrdahl, K., and E. Korpimaki. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology 79:226-232.

Oregon Department ofFish and Wildlife. 2008. Sensitive Species List. Salem, Oregon. Available online at www.dfw.state.or.us/wildlife/diverity/species/sensitive_species.asp (accessed 23 February 2010).

Paradis, E., and G. Guedon. 1993. Demography of a Mediterranean microtine: the Mediterranean pine vole, *Microtus duodecimcostatus.* Oecologia 95:47-53.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis, 1989. Survival analysis in telemetry studies: the staggered entry design. Joumal of Wildlife Management 53:7-15.

Reed, A. W, and N. A. Slade. 2007. Demography and environmental stochasticity: empirical estimates of survival in three grassland rodents. Journal of Zoology 272:110-115.

Reynolds, R. T. 1970. Nest observations of the long-eared owl *(Asio otuss* in Benton County, Oregon, with notes on food habits. Murrelet 51:8-9.

Rodriguez-Robles, 1. A. 2002. Feeding ecology of North American gopher snakes *iPituophis catenifer,* Colubridae). Biological Journal of Linnean Society 77: 165-183.

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

Sullivan, T. P.. and D. S. Snllivan. 1980. The use of weasels for natural control of mouse and vole populations in a coastal coniferous forest. Oecologia 47:125-129.

Sumner, L., and 1. S. Dixon. 1953. Birds and Mammals of the Sierra Nevada with Records from Sequoia and Kings Canyon National Park. University of California Press, Berkeley.

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

Swingle, J. K., and E. D. Forsman. 2009. Home range areas and activity patterns of red tree voles *(Arborirnus longicaudus)* in western Oregon. Northwest Science 83:273-286.

Taylor, W. P. 1915. Description of a new 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.

Thomas, J. W., M. G. Raphael. R. G. Anthony, E. D. Forsman, A. G. Gunderson, R. S. Holthausen, B. G. Marcot, G. H. Reeves, J. R Sedell, and D. M ..Solis. 1993. Viability Assessments and Management Considerations for Species Associated with Late-Successional and Old-Growth Forests of the Pacific Northwest USDA Forest Service, Portland, Oregon.

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

USDA Forest Service, and USDI Bureau of Land Management. 1994. Record of decision for amendments to Forest Service and Bureau of Land Management planning documents within the range of the northern spotted owl: Standards and Guidelines for management of habitat for late-successional and old-growth forest related species within the range of the northern spotted owl. USDA Forest Service and USDI Bureau of Land Management, Portland, Oregon.

USDA Forest Service, and USDI Bureau of Land Management. 2001. Record of decision and standards and guidelines for amendments to the survey and manage, protection buffer, and other mitigation measures standards and guidelines. USDA Forest Service, Pacific Northwest Region and USDI Bureau of Land Management, Portland, Oregon.

USDI Fish and Wildlife Service. 2008. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the dusky tree vole *(Arborimus longicaudus silvicola)* as threatened or endangered. Federal Register 73:63919-63926.

Weeks, H. P, Jr. 1993. Arboreal food caching by long-tailed weasels. Prairie Naturalist 25 :39-42.

White. G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120-138.

Witmer, G. W., and D. S. deCalesta. 1986. Resource use by unexploited sympatric bobcats and coyotes in Oregon. Canadian Journal of Zoology 64:2333-2338.

Wilson, T. M .. and A. B. Carey. 1996. Observations of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. Northwestern Naturalist 77:35-39.

Ylonen, H.. J. Sundell, R. TiiJikainen, J. A. Eccard, and T. Home. 2003. Weasels' *(Mustelu nivalis nivalis)* preference for olfactory cues of the vole *(Clethrionomys glareolus)*. Ecology 84:1447-1452.

Received 6 November 2009
Accepted for publication 16 May 2010