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Abstract

We used molar measurements from 136 known-age red tree voles (*Arborimus longicaudus*) to develop regression models that could estimate tree vole age from skeletonized remains. The best regression included a quadratic structure of the ratio between two measurements, crown height and anterior height, and natural log-transformed age in days. The regression predicted that molar roots begin to develop at 40 days of age and that molar crowns are worn completely away at 1,177 days of age. We used the regression to estimate the age distribution of 1,703 red tree voles found in northern spotted owl (*Strix occidentalis caurina*) pellets collected in western Oregon during 1970–2009. The age distribution of red tree voles in pellets was dominated by young individuals, with 81% younger than one year and only 0.5% older than two years. The proportion of individuals 61–120 days old was particularly high relative to other age classes. The proportion of subadult (52–120 days old) individuals exhibited regional variation between the Oregon Cascades and the Coast Range. Localized annual variation in age distribution was low, exhibited no evidence of cyclic variation, and was positively associated with local precipitation rates during the spotted owl nesting season (March–June). We hypothesize that the age distribution of tree voles in owl pellets may be similar to the age structure of tree vole populations in the wild, but acknowledge that this is virtually impossible to test because tree voles cannot be adequately sampled using conventional small mammal capture methods.

Keywords: *Arborimus longicaudus*, age structure, northern spotted owl, owl pellet, red tree vole

Introduction

Although red tree voles (*Arborimus longicaudus*) were first described as a unique species over a century ago, relatively little is known about their population ecology or long-term population trends (Verts and Carraway 1998, Forsman et al. 2016). Recent research has increased our understanding of tree vole taxonomy (Murray 1995, Bellinger et al. 2005) and geographic distribution (Forsman et al. 2004a, 2016). However, demographic parameters remain poorly understood because conventional small mammal sampling methods

are largely precluded by the unique biological and behavioral characteristics of the species (Gomez and Anthony 1998, Smith et al. 2003, Swingle et al. 2004). Red tree voles are primarily arboreal and subsist on a specialized diet of conifer needles (Howell 1926, Hamilton 1962, Maser 1966). Their distribution is limited to coniferous forests in western Oregon and northwestern California north of the Klamath River (Forsman et al. 2004a, 2016). In addition, adult red tree voles are solitary (Clifton 1960, Swingle and Forsman 2009, Forsman et al. 2016) and occur at low densities relative to other North American arvicoline (microtine) rodents (Maser 1966, Verts and Carraway 1998, Marks-Fife 2016). As a result, field sampling of tree voles is typically opportunistic (Forsman and Swingle 2010), detection-biased (Maser 1966, Swingle 2005), and labor-intensive (Swingle and

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Forsman 2009). Attempts to capture tree voles in traps have been unsuccessful except for rare captures in pitfall traps (Corn and Bury 1986, Johnson 1973, Gilbert and Allwine 1991) and traps placed in arboreal nests (Wight 1925, Swingle et al. 2004). Thus, there are no randomly-sampled collections of red tree vole specimens available for studies of population ecology.

The population dynamics of arvicoline rodents has long been a topic of interest to ecologists, due in part to frequent occurrence of multiannual fluctuations in population structure and density (Boonstra et al. 1998, Tkadlec and Zejda 1998a, Korpimäki et al. 2005). Fluctuations in some species have been described as cyclic, generally observed as a season of peak density followed by a decline phase with regular periodicity of 3–5 years, and have been associated with a suite of density-dependent changes in life history traits (Tkadlec and Zejda 1998b, Boonstra and Krebs 2012). Many other arvicoline species exhibit irregular outbreaks, and still others are relatively stable among years (Korpimäki et al. 2005). Annual variation in population structure is most commonly associated with trophic interactions that influence annual survival and reproduction (Boonstra et al. 1998, Norrdahl and Korpimäki 2002, Boonstra and Krebs 2012), particularly predation rates (Henttonen et al. 1985, Klemola et al. 2003, Korpimäki et al. 2005), and in some species has been observed as changes in population age structure (Leslie and Ranson 1940, Tkadlec and Zejda 1998a, Boonstra et al. 1998). Estimation of population age structure in red tree voles is undescribed.

In the Pacific Northwest, the northern spotted owl (*Strix occidentalis caurina*) is a major predator of red tree voles (Forsman et al. 2004a, 2004b, 2016). During the last 50 years there have been numerous studies of spotted owl natural history and demography in western Oregon and northwestern California (Forsman et al. 1984, Anthony et al. 2006, Dugger et al. 2016), many of which included collection of egested pellets that were used to describe prey items consumed by spotted owls (Barrows 1980, Zabel et al. 1995, Forsman et al. 2004b). Collectively, remains from approximately

4,000 red tree voles have been recovered and catalogued from owl pellets dating back to 1970 (Forsman et al. 2016). Although these data cannot be considered a random sample and inferences to wild red tree vole populations are limited, they can be used to describe the age distribution of red tree voles predated by spotted owls.

Estimating the age distribution of red tree vole remains in owl pellets requires a method to estimate the age of individuals. Age determination methods for arvicoline rodents generally utilize eye lens mass (Askaner and Hansson 1967, Kozakiewicz 1976, Janova et al. 2003) or molar tooth development (Zejda 1961, Tupikova et al. 1968, Lowe 1971), but no such methods currently exist to estimate age of red tree voles on a continuous scale. Because recovering teeth from owl pellets is far more successful than recovering eye lenses, we examined age-dependent dental changes (i.e., molar development; Olenov 2009) as an indicator of red tree vole age.

Our primary objective was to develop a regression to estimate red tree vole age as a function of molar tooth development. Our second objective was to use the molar-age regression to estimate the age distribution of red tree vole remains in northern spotted owl pellets collected in western Oregon during 1970–2009 (Forsman et al. 2004b), and to examine the data for regional and annual variation and correlations with local climate and weather factors. If owls are foraging optimally on the individuals that are most available for predation, then the age distribution of red tree voles predated by owls might provide insights into the age structure of wild populations. Climate and weather conditions might also be expected to have measurable effects on the age distribution of red tree voles predated by spotted owls, whether attributable to red tree vole population dynamics, spotted owl population dynamics, or predator-prey interactions.

Methods

Molar-Age Regression

To estimate the age distribution of red tree voles in spotted owl pellets we developed a regression

model that quantified the relationship between red tree vole age in days and measurements from first mandibular molars (M1), which are frequently utilized in arvicoline age determination studies (Lowe 1971, Tkadlec and Zejda 1998a, Meri et al. 2008). We obtained molar measurements from known-age red tree vole specimens in natural history museums (collected 1957–1985) and from a captive colony at Oregon State University (OSU), Corvallis, OR (collected 2013–2014). All references to tree voles and spotted owls in this study refer to red tree voles and northern spotted owls, no other species or subspecies were examined.

We recorded molar measurements by photographing molars with a Leica DFC425 digital camera (Leica Microsystems, Buffalo Grove, Illinois) mounted on a Leica S6D binocular scope. We recorded measurements of the buccal aspect of each molar to the nearest micrometer using Image-Pro Plus (Media Cybernetics, Rockville, Maryland). *Arborimus* is one the few arvicoline genera that possess rooted hypsodont molars (True 1890, Johnson 1973). The roots are absent at birth, begin to appear during early development, and elongate with age while the molar crown simultaneously wears down (Figure 1). Thus, “molar development” in this study refers to an increase in root length and a concomitant decrease in crown height. We recorded four primary measurements for each molar (Figure 1). Anterior height (AH) was measured as the vertical distance along the 2nd columnar cusp from the top of the occlusal surface down to the tip of the anterior (aboral) root. This measurement was equivalent to “length/height of the entire tooth” used in other studies of arvicoline age determination from molar development (Koshkina 1955, Tupikova et al. 1968, Viitala 1971). Posterior height (PH) was measured as the vertical distance along the 5th columnar cusp from the top of the occlusal surface down to the tip of the posterior (oral) root. Crown height (CH) was measured as the vertical distance along the 4th columnar cusp from the top of the occlusal surface down to the peak of the crutch between the roots or the anticipated location of the peak in very young individuals prior to molar root development. We measured crown length (CL) as the horizontal distance between the anterior and

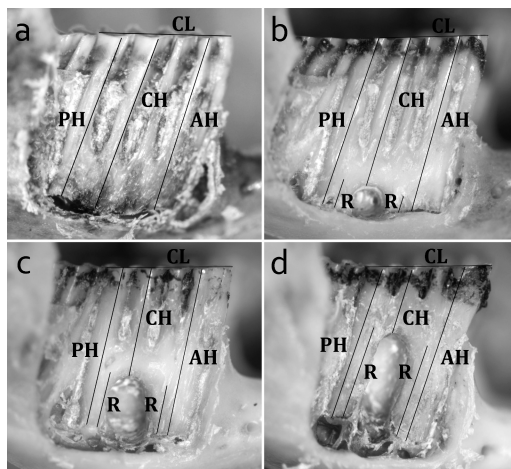


Figure 1. Measurements recorded from the buccal aspect of right-side first lower molars (M1) of red tree voles: anterior height (AH), posterior height (PH), crown height (CH) and crown length (CL). Examples include molars from individuals at ages a) 38 days, b) 60 days, c) 240 days, and d) 480 days. Note the increase in root length (R) and decrease in crown height with increasing age.

posterior occlusal edges of the crown. Sampling priority was given to the M1 molar in the right jaw. In rare cases we measured the left M1 in place of a damaged or missing right M1.

Although molar roots did not begin to appear until tree voles were several weeks old, early development of the molar base began immediately after birth. During the first two weeks, the molar consisted of a developed crown with the base still open and unformed. At this stage the vertical reentrant grooves (i.e., crenulations; Howell 1926) essentially ran the full height of the molar from the top of the occlusal surface down to the open dentine base. As age increased, the molar base closed and expanded downward to create a smooth cementum neck below the reentrant grooves (Figure 2; Tupikova et al. 1968, Gustafsson et al. 1982, Meri et al. 2008). Development of the molar neck eventually concluded at the crutch peak when roots began to form on either side. We hypothesized that measurements of the molar neck could be used to estimate ages of very young individuals prior to molar root development, as in other arvicoline species (Viitala 1971, Gustafsson et al. 1982). For this reason we recorded neck height (NH),

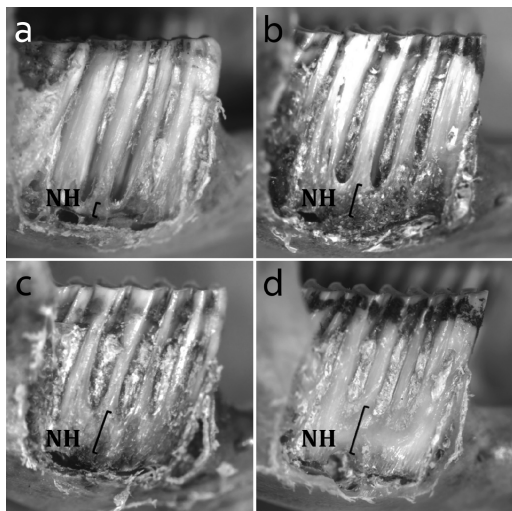


Figure 2. Development of the molar neck (neck height [NH]) from the buccal aspect of right-side first lower molars (M1) of red tree voles at ages a) 12 days, b) 19 days, c) 38 days, and d) 60 days. The crutch peak and early root development are evident at 60 days.

measured as the vertical distance along the 4th columnar cusp from the bottom of the reentrant grooves down to the peak of the crutch between the roots or the anticipated location of the peak in very young individuals prior to root development (Figure 2). Thus, NH is a sub-measurement of the CH measurement.

In 2012, we recorded molar measurements from known-age tree vole specimens at the Burke Museum of Natural History, University of Washington, Seattle WA ($n = 23$), and the Slater Natural History Museum, University of Puget Sound, Tacoma WA ($n = 73$). The majority of museum specimens were captive-reared tree voles from studies conducted by Clifton (1960), and Hamilton (1962), and M. L. Johnson (unpublished field and lab notes from 1957–1985, on file at the Burke Museum of Natural History, University of Washington, Seattle). With museum permissions, we examined the M1 molar in each right mandible by using a diamond-tipped Dremel Tool (Robert Bosch Tool Corporation, Racine, Wisconsin) to remove bone from around the buccal surface and expose the roots. This method allowed us to record measurements without removing molars

from mandibles, avoiding accidental root breakage and leaving specimens intact.

Preliminary analyses of the museum specimens suggested strong associations between molar development and age but indicated a need for additional data, particularly during the first year of life. We augmented the museum dataset by rearing a colony of known-age tree voles at OSU. Our objective was to produce 5–7 individuals in each of eight age classes representing 60-day increments from 60–480 days (i.e., 60 days old, 120 days old, etc.). Protocols for care, maintenance, and euthanasia in the OSU colony conformed to American Society of Mammalogists guidelines (Sikes et al. 2011) and were approved in an Animal Care and Use Proposal by OSU's Institutional Animal Care and Use Committee.

We housed the OSU colony of tree voles during February 2013–July 2014. The founder population included nine adult females and one adult male that were captured in forests near Harlan, Benton County, Oregon, during February–July 2013. Eight of the females were pregnant at the time of capture and seven had pre-dispersal age young in their nests, all of which were imported into the OSU colony. We used regressions of mass to estimate the ages of 10 pre-dispersal young (Clifton 1960, Hamilton 1962, Maser and Storm 1970). The breeding population included the 10 founder tree voles and three of the imported young, one female and two males, when they reached adult age. Descriptions of our husbandry and captive breeding methods are available in Marks-Fife (2016). Birth dates of captive-born individuals were considered accurate to within two days. To simulate natural dispersal timing, we moved young tree voles from their natal nests to private enclosures at 56 ± 4 days of age (Swingle 2005, Forsman et al. 2009).

To achieve our age class sample objectives, each known-age tree vole in the colony was assigned an age to be euthanized for molar collection. We mixed the parentage of individuals in each age class to reduce the possibility of genetic effects on the molar-age regression. At the time of euthanasia, we determined sex, recorded standard body measurements (Nagorsen and Peterson 1980), and

donated various tissue samples to collaborating laboratories (Kitanovic et al. 2018). We prepared skeletons by cleaning them in a dermestid beetle colony, degreasing in 1% ammonia, and rinsing in fresh water.

Methods used to measure tree vole molars in the OSU colony were identical to the methods for measuring museum specimens, with the exception that NH measurements were recorded only in specimens from the OSU colony. Specimens were prepared as museum skins and donated, along with skeletons, genetic samples, and body measurements, to the OSU Fisheries and Wildlife mammal collection and the Burke Museum of Natural History.

The methods we used to measure tree vole molars in the museum, OSU, and owl pellet specimens differed in one important regard. Molars from owl pellets were separated from the mandibles and placed directly on the microscope stage plate during measuring, whereas molars from museums and the OSU colony were measured *in situ*, and therefore elevated several millimeters (mm) above the stage plate. No correction factor was available to compensate for this potential calibration bias. For this reason, we developed regression models based on ratios generated from the four primary molar measurements, as opposed to individual molar measurements. Molar measurement ratios have previously been utilized in arvicoline age determination studies (Koshkina 1955, Tupikova et al. 1968), and their application in our study standardized the three datasets. In several very young individuals there was no measurable root development and the bottom of the molar was convexly rounded, creating a scenario where the crown height was equal to or greater than the anterior height ($CH \geq AH$). Molars from these individuals were excluded from the analysis. We also excluded molars of museum specimens that were broken or maloccluded. No malformed molars were observed in the OSU specimens.

We pooled the data from the museum and OSU specimens for analyses (R 3.2.1 software; R Core Team 2015) and coded the data sources using a binary variable. We analyzed the data using mixed effects general linear models to

evaluate 14 molar measurement ratios as fixed effects and data source as a random effect to account for potential variation in regression equations between the museum and OSU datasets (R package “lme4”; Bates et al. 2015). We used an information-theoretic approach to develop an *a priori* model set (Table 1) to determine which molar measurement ratio most accurately predicted tree vole age in days. Residual scatterplots (R package “ggplot2”; Wickham 2016) revealed that the data were not normally distributed, so we performed a natural log (ln) transformation of the response variable (age). We evaluated model likelihood using Akaike’s Information Criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i). Models with $\Delta AIC_c < 2$ were considered competitive with the top model (Burnham and Anderson 2002). We used R-squared (R^2) values to determine how well each model explained variation in the molar-age relationship. We conducted 10-fold cross-validation (R package “dismo”; Hijmans et al. 2017) on the highest-ranked model using root mean square error (RMSE) as a measure of prediction error.

We performed an additional analysis using a single fixed effects general linear model to relate the ratio of molar neck height over crown height (NH/CH) on tree vole age (not transformed) using young specimens prior to molar root development. We hypothesized that this regression could be used to predict age in very young tree voles for which regressions that incorporated molar root measurements would not apply. All molars came from the OSU colony so no random effect of data source was included.

We used fixed effects logistic regression models to evaluate whether molar measurement ratios also predicted tree vole sex. Adult tree voles exhibit sexual dimorphism in body size and behavior (Clifton 1960, Hamilton 1962, Swingle and Forsman 2009), and intraspecific variation in arvicoline vulnerability to owl predation is often attributed to sexually-dimorphic traits (Boonstra 1977, Longland and Jenkins 1987, Lyman et al. 2016). In addition to age, sex was a factor we hypothesized would affect individual vulnerability to owl predation, so we tested whether we

TABLE 1. Model selection results from the mixed-model regression analysis of molar measurement ratios on age of red tree voles [ln(age)]. All models included a random effect of data source (i.e., museums or OSU colony). Results included an *a posteriori* model* using a quadratic structure of the best *a priori* model.^a

Model ^b	ΔAIC_c	W_i	R^2
(CH / AH) + (CH / AH) ² *	0.00	0.99	0.91
CH / AH	10.92	0.01	0.90
CH / CL	11.31	0.00	0.89
CH / [(AH + PH) / 2]	13.14	0.00	0.89
CH / PH	28.03	0.00	0.87
CH / [(AH + PH) / 2] / CL	42.53	0.00	0.87
CH / AH / CL	44.92	0.00	0.87
CH / PH / CL	47.04	0.00	0.86
(AH – CH) / CL	77.36	0.00	0.83
(PH – CH) / CL	83.98	0.00	0.82
PH / CL	262.35	0.00	0.33
CH / (PH – CH)	294.59	0.00	0.21
AH / CL	295.52	0.00	0.15
CH / (AH – CH)	295.66	0.00	0.20
CH / [(AH – CH) + (PH – CH)] / 2	302.59	0.00	0.16
Intercept-only model	311.43	0.00	NA

^aColumn headings indicate differences in AIC_c values relative to the best model (ΔAIC_c), Akaike weights (w_i), and R^2 . Lowest $AIC_c = -10.67$.

^bCodes for molar measurements indicate: anterior height (AH), posterior height (PH), crown height (CH), and crown length (CL).

could distinguish females from males using molar measurements. We evaluated model likelihood using an information-theoretic approach which included an *a priori* model set and associated Akaike's Information Criteria statistics to evaluate models (i.e., AIC_c , AIC_c weights, etc.; Burnham and Anderson 2002). We used R^2 to determine how much of the amount of variation in sex could be accounted for by molar measurement ratios.

Red Tree Voles in Spotted Owl Pellets

We used the best molar-age regression model to estimate ages of 1,703 tree voles for which at least one lower M1 was recovered from spotted owl pellets collected in western Oregon during 1970–2009. We binned age estimates into 60-day age classes

to examine the data on a continuous scale, and into four categorical age groups since relative abundance of age groups is a common variable in age distribution analyses of rodent populations (Zejda 1961, Haitlinger 1965, Perrin 1982). The age groups included pre-dispersal young (< 52 days; Forsman et al. 2009), post-dispersal subadults (52–120 days), 1st-year adults (121–360 days), and 2nd-year adults (> 360 days). We defined one year as 360 days for the purpose of data comparison between the binning methods. Individuals older than two years (720 days) were rare and so were included with 2nd-year adults. Although 52–120 days old is not an absolute biological definition of the tree vole subadult stage, tree voles are known to reach adult size, adult pelage, and sexual maturity by 120 days of age (Clifton 1960, Hamilton 1962, Maser and Storm 1970). All references to subadults in this study refer to the post-dispersal subadult age group. The proportion of subadult individuals relative to total individuals in a sample, hereafter referred to as the subadult age ratio (SAR), was used to index tree vole age distribution in spotted owl pellets.

We examined regional, annual, and climate-related variation in the age distribution of tree voles in spotted owl pellets. Pellets containing tree vole remains were associated with the collection year and owl territory in which they were collected. We assumed that pellets were egested in the same season they were collected because most were collected below spotted owl roosts during multiple-visit monitoring studies in the spring and summer (Forsman et al. 2004b). Pellets left overwinter deteriorated rapidly and were rarely available for collection in subsequent years. Pellet collection locations were categorized by geographic subregions corresponding to major mountain ranges or subdivisions of major mountain ranges within the distribution of spotted owls in western Oregon (Forsman et al. 2004a, 2004b, 2016). All regional analyses in this study were limited to the Central Coast, South Coast, and Central Cascades subregions since only these three included sufficient sample sizes.

Several of our methods for conducting regional analyses of tree vole age distribution in spotted owl pellets (e.g., sample size requirements) followed methods previously used to describe prey species abundance in the same pellet data (Forsman et al. 2004a). Individual owl pellets generally contained multiple prey items and we pooled tree vole age data from all pellets collected at each spotted owl territory (i.e., sample unit = territory). We calculated SAR across years for owl territories that included the remains of ≥ 10 individual tree voles, then averaged the territorial estimates within subregions and compared regional mean SAR using Student's *t*-tests ($\alpha = 0.05$). We also estimated regional mean numbers of subadult tree voles predated per spotted owl territory per year by multiplying our SAR estimates by regionally-corresponding estimates of mean numbers of tree voles (all ages) predated per spotted owl territory per year (Forsman et al. 2004a). We categorized the estimates based on the reproductive status of owls at each territory (i.e., individual owls, non-nesting pairs, nesting pairs with two young) following Forsman et al. (2004a). We calculated combined variance using the delta method (Powell 2007) and Satterthwaite's approximation of the standard error.

We examined annual variation in tree vole age distribution in spotted owl pellets using data collected during 2000–2009 in the Tyee Northern Spotted Owl Demographic study area, one of eight long-term study areas included in the Northern Spotted Owl Effectiveness Monitoring program (Lint et al. 1999, Dugger et al. 2016). The Tyee study area was the only study area with ≥ 10 consecutive sampling years that included ≥ 10 tree voles in pellets each year. We calculated annual SAR estimates from all spotted owl pellets collected on the Tyee study area regardless of owl territory (i.e., sample unit = year). To examine the data for evidence of cyclic variation, we used Pearson's chi-square (X^2) test to compare frequency counts of the four tree vole age groups between the two years that represented the maximum and minimum SAR estimates, reasoning that these were the extreme peak and decline years in the sample. Demonstrating a difference in age distribution between these two years would not provide

evidence of cyclic variation, but a finding of no difference would indicate that there was too little annual variation in the 10-year sample to justify further analysis of the data for evidence of cyclicity.

We used an information-theoretic approach to evaluate relationships between SAR and annual climate and weather variables calculated regionally or locally for the Tyee study area during 2000–2009 and previously found to be associated with northern spotted owl demographics (Forsman et al. 2011, Dugger et al. 2016). We obtained mean monthly minimum temperature and total precipitation data from PRISM (Parameter-elevation Regression on Independent Slopes Model) maps produced by the Oregon Climate Service (2015). We subdivided the PRISM data into annual (01 July–30 June) and seasonal periods based on the northern spotted owl reproductive cycle: early nesting (March–April), late nesting (May–June), and winter (November–February). Other variables used in the climate analysis included the Southern Oscillation/el Niño Index (SOI), Pacific Decadal Oscillation (PDO), and Palmer Drought Severity Index (PDSI). The SOI (NOAA 2015a) and PDO (University of Washington 2015) represented annual measures of region-wide climate patterns, while the PDSI represented the annual deviation of moisture conditions from the 30-year mean of 1970–2000 (NOAA 2015b). We used an information theoretic approach to develop an *a priori* model set and evaluated the models using AIC_c (Burnham and Anderson 2002). We examined covariate coefficients (β) to evaluate the direction of relationships and the strength of the effect within each model (Dugger et al. 2016). We used R^2 to determine how much of the annual variation in SAR was explained by the best model.

Results

Molar-Age Regression

Our sample of known-age tree voles included 84 specimens from museums (age range = 39–1,052 days) and 52 from the OSU colony (age range = 39–480 days), with 6–7 individuals in each of the target 60-day age classes ($n_{\text{pooled}} = 136$). The sex ratio of tree voles born in the OSU colony was exactly 1:1. Adult (> 120 days) males and

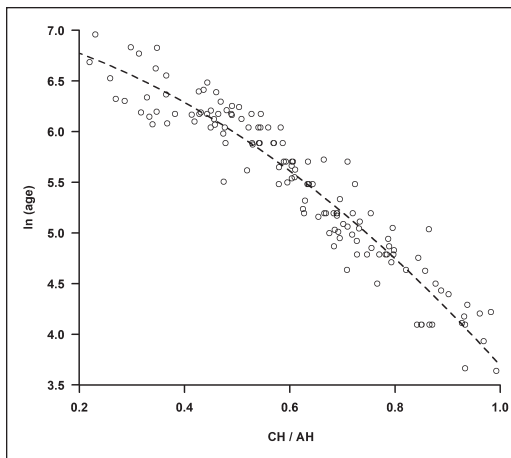


Figure 3. Relationship between the best molar measurement ratio (crown height over anterior height [CH/AH]) and age [ln(age)] of red tree voles. Dashed line represents the quadratic form of CH/AH.

non-pregnant adult females, including known-age individuals and individuals from the founder population, had mean masses = 26.1 g (SD = 1.9, $n = 23$) and 28.3 g (SD = 2.3, $n = 32$), respectively. Non-pregnant adult females were subdivided into non-breeding individuals and breeding individuals during periods of non-pregnancy, with mean masses = 27.4 g (SD = 2.4, $n = 23$) and 30.8 g (SD = 1.8, $n = 9$), respectively. Standard body measurements are listed in Supplemental Table S1 (available online).

The best model relating molar measurements and tree vole age in days [ln(age)] included the ratio of crown height over anterior height (CH/AH; Table 1). There was one other competitive model, which included crown height over crown length (CH/CL). A scatterplot of the data with a locally weighted smoothing (LOESS) curve suggested a quadratic rate of change in the best *a priori* model, so we fit an *a posteriori* model using a quadratic form of CH/AH on ln(age) (Table 1; Figure 3). No quadratic shape was observed in the CH/CL model so the quadratic form was not considered. The quadratic CH/AH model was strongly supported, receiving approximately 99% of the Akaike weight (Table 1). The amount of variation in the molar-age relationship explained by the quadratic model was high ($R^2 = 0.91$) and

the prediction RMSE from cross-validation was low (1.262 days). The exponentiated form of the regression (Equation 1) was:

$$\text{age (days)} = 1176.62 \times \exp\left(-1.01 \times \left[\frac{CH}{AH}\right]\right) \times \exp\left(-2.37 \times \left[\frac{CH}{AH}\right]^2\right) \quad (\text{Eqn 1})$$

The CH/AH ratio had a possible range = 1–0, where CH/AH = 1 (i.e., CH = AH) represented a young individual prior to molar root development and CH/AH = 0 represented an extremely old individual with the crown and molar neck worn completely away. The predicted intercept for CH/AH = 1 (i.e., onset of root development) occurred at 40 days of age, which was consistent with our observations since the earliest root development in the pooled sample of known-age tree voles was observed at approximately 39 days. The predicted intercept for CH/AH = 0 occurred at 1,177 days of age, which may be an underestimate because some tree voles in captivity have survived beyond that age without their crowns wearing completely away, the oldest being a female that lived 1,683 days (Clifton 1960; Eric D. Forsman, US Forest Service, personal communication).

Ten of the models in our model set exhibited $R^2 \geq 0.82$ (Table 1), indicating that while these models were less efficient at explaining variance than the top model, they did predict tree vole age reasonably well. The model representing the ratio of crown height over crown length (CH/CL) exhibited relatively high prediction strength ($R^2 = 0.89$) and did not incorporate molar root measurements. This model (Equation 2) may be useful for predicting age in tree vole specimens where molar root measurements are confounded by breakage or other factors:

$$\text{age (days)} = 2469.42 \times \exp\left(-2.89 \times \left[\frac{CH}{CL}\right]\right) \quad (\text{Eqn 2})$$

Our sample included nine very young known-age tree voles in which no molar root development was yet visible (CH \geq AH). Presence of a measurable molar neck in these individuals was first observed at approximately 12 days of age and development of molar roots was first observed at approximately 39 days old. Mean NH at 12 days = 0.22 mm (SD = 0.03, $n = 2$), at 60 days = 0.81 mm (SD = 0.10, $n = 6$), and at 60–480 days = 0.91 mm (SD = 0.14, $n = 52$). Mean NH/CH

at 12 days = 0.07 (SD = 0.01) and at 60 days = 0.25 (SD = 0.01). The small availability of very young specimens precluded our ability to derive a strong linear regression of NH/CH on tree vole age ($t_7 = 1.845$, $P = 0.11$, $R^2 = 0.30$). Regardless, this regression (Equation 3) may be helpful for estimating ages of young tree voles prior to molar root development:

$$\text{age (days)} = 16.15 + \left(44.63 \times \left[\frac{NH}{CH}\right]\right) \text{ (Eqn 3)}$$

The model that best represented the relationship between molar measurement ratios and tree vole sex included crown height over posterior height over crown length (CH/PH/CL). However, the R^2 for this model was very low ($R^2 = 0.06$), suggesting that tree vole sex could not be predicted using molar measurements.

Red Tree Voles in Spotted Owl Pellets

Of the 1,703 tree voles identified in spotted owl pellets, we estimated that 3% were pre-dispersal young, 35% were post-dispersal subadults, 43% were 1st-year adults, and 19% were 2nd-year adults (Figure 4). Only 0.5% of tree voles in owl pellets were older than two years. The estimated age of the oldest individual in the sample was almost exactly three years (1,088 days). Only 0.8% of individuals had not yet begun to develop molar roots ($AH \leq CH$), indicating that spotted owl predation on tree voles < 40 days old was rare. This was not surprising given that young tree voles do not normally venture outside their natal nests until they are 30–35 days old and are likely much less available for owl predation before that age (Forsman et al. 2009).

Subadult age ratios of tree voles in spotted owl pellets (Table 2) did not differ between the Central Coast ($n_{\text{territories}} = 8$) and South Coast ($n_{\text{territories}} = 14$) subregions ($t_{12,97} = 0.59$, $P > 0.1$), but were lower in the Central Cascades ($n_{\text{territories}} = 8$) sub-region ($t_{10,38} = -3.30$, $P < 0.01$). Estimates of the total number of subadult tree voles predated per year at individual owl territories varied (range = 5–42) depending on owl reproductive status and subregion (Table 3).

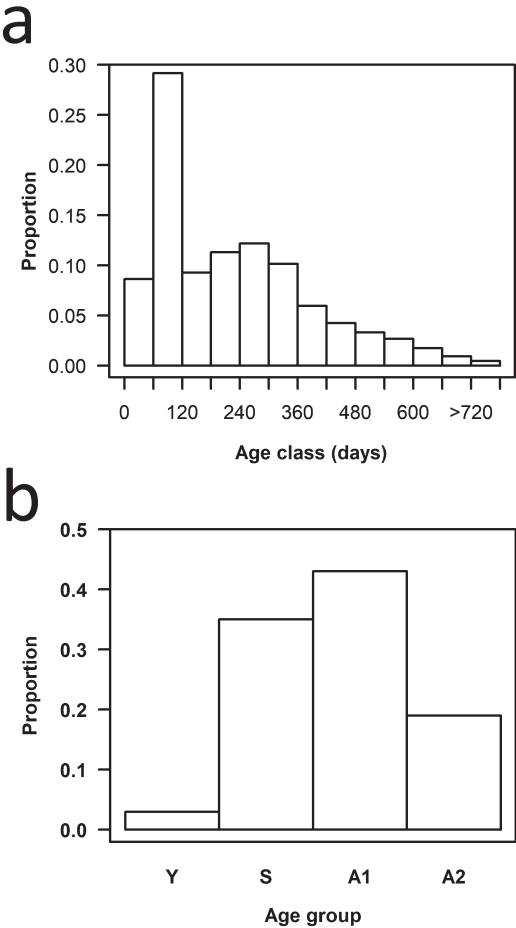


Figure 4. Estimated age distribution of 1,703 red tree voles identified in northern spotted owl pellets in western Oregon during 1970–2009, binned by a) 60-day age classes, and b) age groups. Age groups included pre-dispersal young (Y), post-dispersal subadults (S), 1st-year adults (A1), and 2nd-year adults (A2).

The mean annual SAR of tree voles in owl pellets collected during 2000–2009 in the Tyee study area was 0.36 (SE = 0.02, 95% CI = 0.33–0.39, CV = 14.4%). Pearson’s chi-square test provided no evidence that age group distributions differed between the two sample years representing the maximum ($n = 39$) and minimum ($n = 48$) SAR estimates ($X^2_3 = 4.48$, $P > 0.1$). The model set describing relationships between annual SAR and climate and weather variables included two competitive models ($\Delta AIC_c < 2$, $R^2 = 0.47$ –0.53) that included effects of precipitation during both

TABLE 2. Mean estimates ($\bar{X} \pm \text{SE}$) of subadult age ratios (SAR) of red tree voles in northern spotted owl pellets from three geographic subregions in western Oregon, 1970–2009.

Geographic Subregion	$\bar{X} \pm \text{SE}$	95% CI	CV (%)	n^a
Central Coast	0.40 ± 0.04	0.32–0.49	30.7	8
South Coast	0.37 ± 0.03	0.32–0.43	28.7	14
Central Cascades	0.20 ± 0.05	0.10–0.30	70.0	8

^aNumber of owl territories sampled. Estimates were based on owl territories with ≥ 10 tree voles in pellets (range = 10–29).

TABLE 3. Mean estimates ($\bar{X} \pm \text{SE}$) of subadult red tree voles predated per northern spotted owl territory per year in three geographic subregions in western Oregon, 1970–2009. Estimates were subdivided based on breeding status of owls.

Geographic Subregion	Non-Breeding Individual	Non-Nesting Pair	Pair With 2 Young	CV (%)
Central Coast	15.6 ± 4.9	31.1 ± 9.7	40.4 ± 12.7	91.3
South Coast	16.1 ± 2.8	32.2 ± 5.6	41.9 ± 7.2	75.4
Central Cascades	4.5 ± 2.9	8.9 ± 5.7	11.6 ± 7.4	150.1

the early and late spotted owl nesting periods (Table 4). The only other model that ranked above the intercept-only model included an effect of temperature during the early spotted owl nesting period ($R^2 = 0.40$).

Discussion

Molar-Age Regression

The best model describing associations between lower M1 measurements and tree vole age was based on the ratio of crown height over anterior height. This result was the reciprocal form of the molar measurement ratio used by Tupikova et al. (1968) to estimate age in *Myodes* (formerly *Clethrionomys*; Carleton et al. 2014), an arvicoline genus that also has rooted molars. However, the estimated age at which molar roots began to develop in tree voles was 40 days, considerably earlier than has been reported for North American *Myodes* spp. (range = 80–90 days; Tupikova et al. 1968, Perrin 1978). Models in our analysis that utilized the anterior height measurement consistently ranked higher than equivalent models that utilized posterior height or the anterior-posterior average, suggesting that anterior root development

was a more reliable indicator of tree vole age than posterior root development. The best regression model (Equation 1) could only be used to estimate ages of tree voles with measurable anterior molar roots (≥ 40 days old). Equation 2 could be used for estimating ages of specimens with broken or otherwise unavailable molar roots. We do not recommend using Equation 2 to estimate ages of young tree voles prior to root development. The best method to estimate the age of young tree vole molars prior to development of anterior roots was to use molar neck measurements (Equation 3; Figure 2). We found no evidence of sexual

differences in molar measurement ratios, but it is possible that other skeletal measurements could be used to predict the sex of tree voles in owl pellets (Longland and Jenkins 1987).

All of the known-age tree voles from the OSU colony and most of the known-age specimens from museums were products of captive rearing, and we could not discount the possibility that rates of root development or crown wear differed between captive and wild tree voles. We suspect that these differences, if they existed, were small because the majority of captive tree voles were fed a natural diet of fresh conifer cuttings (Clifton 1960, Hamilton 1962), which should have resulted in comparable rates of molar development. Tree voles rarely gnaw on cages, so we do not believe that crown wear was affected by captivity. We also have no evidence that captivity affected the rate or timing of root development. In addition, we considered the possibility of temporal effects on molar development between the OSU colony and museum specimens since the two datasets represented captive offspring of wild voles that were collected during non-overlapping periods, but found no evidence to suggest that such effects existed.

TABLE 4. Model selection results from the analysis of effects of local climate and weather variables on the annual subadult age ratio (SAR) of red tree voles in northern spotted owl pellets in the Tyee study area in western Oregon, 2000–2009.^a

Climate or weather variable	ΔAIC_c	W_i	R^2	$\beta \pm SE$	β 95% CI
Precipitation (early nesting)	0.00	0.41	0.53	0.04 ± 0.01	0.01–0.06
Precipitation (late nesting)	1.16	0.23	0.47	0.04 ± 0.01	0.01–0.06
Temperature (early nesting)	2.44	0.12	0.40	0.03 ± 0.01	0.01–0.06
Intercept-only model	3.82	0.06	NA	NA	NA
Temperature (winter)	3.84	0.06	0.32	0.03 ± 0.02	-0.01–0.06
Pacific Decadal Oscillation	4.90	0.04	0.25	0.03 ± 0.02	-0.01–0.06
Precipitation (winter)	5.72	0.02	0.19	-0.02 ± 0.02	-0.06–0.01
Southern Oscillation / El Niño Index	5.94	0.02	0.18	-0.02 ± 0.02	-0.05–0.01
Precipitation (annual)	6.30	0.02	0.15	0.02 ± 0.02	-0.01–0.05
Temperature (late nesting)	7.23	0.01	0.07	-0.02 ± 0.02	-0.05–0.02
Palmer Drought Severity Index	7.31	0.01	0.07	-0.01 ± 0.02	-0.05–0.02

^aColumn headings indicate differences in AIC_c values relative to the best model (ΔAIC_c), Akaike weights (w_i), R^2 , and standardized beta coefficients (β). Lowest $AIC_c = -30.05$. The number of tree voles in Tyee owl pellets per year had range = 26–64.

Red Tree Voles in Spotted Owl Pellets

The percentage of tree voles in spotted owl pellets was low for the 0–60 day age class and highest for the 61–120 day age class (Figure 4a). The proportion of tree voles > 120 days old in spotted owl pellets decreased relative to the 61–120 day age class, but remained relatively stable among 60-day age classes from 121–360 days, then declined steadily to nearly zero by two years. The fact that so few individuals survived beyond two years old was not surprising given that voles in general tend to be short-lived (Boonstra 1994, Tkadlec and Zejda 1998a, Boonstra and Krebs 2012), and that few tree voles in captivity have lived longer than two years (Clifton 1960; Eric D. Forsman, US Forest Service, personal communication). Low predation rates on the youngest age class (i.e., 0–60 days) by non-nest predators is common in prey species with altricial young that stay in their natal area for a period following birth (Perrin 1982). This describes tree voles, whose young rarely venture outside the natal nest during the first month of life and do not permanently disperse until they are nearly two months old (Forsman et al. 2009). The high percentage of dispersal-age tree voles in owl pellets suggests that individuals in this age class were either more abundant than older age classes in wild popula-

tions, or exhibited characteristics that made them more vulnerable to owl predation, or both. High predation rates immediately following dispersal are not uncommon in arvicoline rodents (Longland and Jenkins 1987). Elevated vulnerability of recently-dispersed tree voles to owl predation may be attributable to limited agility, poorly-developed predator avoidance skills, or high exposure rates during the process of establishing home ranges and building nests.

Interestingly, one female in the OSU colony became pregnant at approximately 64 days old after copulating with a male of similar age. This was the youngest age of successful red tree vole copulation on record. In wild populations, the proximal factors that influence dispersal timing are not well understood. Brooding adult females have been observed becoming aggressive toward their young when the young reach dispersal age (range = 47–57 days; Forsman et al. 2009), and it has been suggested that dispersal is a function of mothers driving their older offspring out of the nest to secure limited resources for younger litters (Forsman et al. 2009). Based on our observations, another possible explanation is that mothers drive their offspring from the nest during the early onset of sexual development, most likely as a biological

defense against inbreeding or simply as territorial behavior toward perceived “adults”.

We found no evidence that age distributions of tree voles in owl pellets varied between the Central Coast and South Coast subregions, but strong evidence of differences between those subregions and the Central Cascades subregion. One possible explanation for this difference is that spotted owls in the Cascade Range occur at higher elevations where colder temperatures and increased snow cover during the winter reduce their access to many prey species. This could produce seasonal differences in predation rates on tree voles between owls in the Oregon Cascades and Coast Ranges.

Annual variation in tree vole subadult age ratios in the Tyee study area was most strongly associated with variation in precipitation during the spotted owl nesting season (March–June), with a positive correlation. While the time series for this analysis was relatively short (10 years) and annual variation in the age distribution was low ($CV = 14.4\%$), the amount of variation explained by seasonal precipitation models was relatively high ($R^2 = 0.47\text{--}0.53$), suggesting that seasonal weather patterns may be primary drivers of annual variation in the age distribution of red tree voles predated by spotted owls. One possible explanation is that higher levels of spring precipitation might increase tree vole productivity by increasing the water content of conifer needles, red tree voles’ primary food and water source (Howell 1926, Maser 1966, Forsman and Price 2011), thereby increasing the abundance of dispersal-age individuals available for predation. Weather patterns and environmental moisture levels are known to be primary drivers of annual variation in the population structure of North American *Myodes* spp. via food abundance and quality (Boonstra and Krebs 2012).

Annual variation in arvicoline populations is often principally attributed to predation (Henttonen et al. 1987, Klemola et al. 2003, Korpimäki et al. 2005), and tree voles are a short-lived species seemingly as a direct result of intense predation by owls, weasels (*Mustela* spp.), and other predators (Forsman et al. 2004a, Swingle

et al. 2010). Our data suggest that there may be associations between annual variation in tree vole age distribution in owl pellets and local climate and weather patterns. We found no evidence that tree vole age distribution in a localized sample of owl pellets differed among years, and thus no evidence of cyclic variation, though this cannot be extrapolated to wild tree vole populations. The majority of forest-associated *Myodes* populations in North America tend to fluctuate in irregular, non-cyclic patterns primarily because densities in the early breeding season are too low to support the necessary density-dependent social inhibition (Boonstra and Krebs 2012). Given the evidence that tree voles occur at low population densities with little social interaction (Maser 1966, Marks-Fife 2016, Forsman et al. 2016), the relatively constant abundance of conifer needles as a primary food source (Hamilton 1962, Maser 1966, Verts and Carraway 1998), relatively constant and intense predation pressure (Forsman et al. 2004a, Swingle et al. 2010), and our suggested associations between red tree vole age distribution in spotted owl pellets and local climate and weather variables, we see no reason to believe that multiannual fluctuations in tree vole population structure and density are cyclic.

Previous studies that used owl pellet data to describe age structure in prey populations generally incorporated a concurrent prey species trapping component and utilized pellets that were collected randomly over an annual cycle (Davis 1959, Dean 1972, Perrin 1982). Since it is not possible to study tree voles using conventional small mammal sampling methods (Gomez and Anthony 1998, Smith et al. 2003, Swingle et al. 2004), we could not incorporate a control group of trapped individuals in our study. In addition, owl pellets in this study were not collected randomly over an annual cycle. The majority were collected opportunistically during the period when spotted owls were roosting at nest sites (March–August), which corresponded closely with the peak reproductive period of red tree voles (February–September; Swingle 2005). Thus, the age distribution of tree voles in spotted owl pellets primarily reflected predation during a seven-month period each year and was based on sampling methods that included

an undetermined amount of sampling bias by owls and by surveyors. A more standardized method of pellet collection could possibly describe tree vole population structure with fewer seasonal effects. Considering behavioral differences among the four tree vole age groups as they likely relate to vulnerability to predation by owls, we hypothesize that the age distribution of tree voles in the pellet data may be roughly similar to the age structure in wild populations, at least among individuals ≥ 52 days old since pre-dispersal young are likely under-represented. This is particularly true of tree voles > 120 days old, since physical and behavioral characteristics become relatively static in adulthood, sexual dimorphism notwithstanding. It is also notable that although the tree vole age distribution data from owl pellets cannot be used to directly estimate survival rates in wild populations, the percentage of individuals older than one year (19%) was similar to the estimate of annual survival from radio-telemetry data (15%; 95% CI = 6–31%; Swingle et al. 2010), supporting the hypothesis that the age distribution of tree voles in spotted owl pellets may be similar to age structure in wild populations. At present, we know of no alternate methods that are likely to more accurately approximate age structure in

tree vole populations than the methods presented in this study. All other methods attempted to date had more serious methodological biases (Forsman et al. 2016).

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