

SIZE-ASSOCIATED MORPHOLOGICAL VARIATION IN THE RED  
TREE VOLE (*ARBORIMUS LONGICAUDUS*)

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**ABSTRACT**—We examined patterns of size-associated morphological variation within the Red Tree Vole (*Arborimus longicaudus*) for the purposes of 1) identifying differences between the Red Tree Vole and the Dusky Tree Vole (*A. l. silvicola*), a putative subspecies of the Red Tree Vole; and 2) examining spatial patterns of morphological variation across the species' range. Our results illustrate subtle, but significant, morphological differences across the boundary that has been proposed to delimit the ranges of the Dusky Tree Vole and Red Tree Vole. However, the morphological characters examined have virtually no diagnostic utility for distinguishing between subspecies. We also performed a series of linear regressions that revealed correlations between morphological variation and latitude. Ultimately, these findings indicated that morphological variation in Red Tree Voles is in good agreement with Bergmann's Rule and Allen's Rule, 2 well-established ecographic principles that dictate relationships between environmental temperatures and morphological attributes. Because our analyses do not demonstrate strong differences between tree vole subspecies, we encourage future analyses of variation in pelage coloration and genetic structure to unequivocally determine the Dusky Tree Vole's status.

**Key words:** Allen's Rule, *Arborimus longicaudus*, *Arborimus longicaudus silvicola*, Bergmann's Rule, Dusky Tree Vole, latitude, morphology, Oregon Red Tree Vole, subspecies

Red Tree Voles (*Arborimus longicaudus*) possess unique ecological and life history attributes that place them among the most specialized mammals in North America. Endemic to Douglas-fir (*Pseudotsuga menziesii*), Sitka Spruce (*Picea sitchensis*), Western Hemlock (*Tsuga heterophylla*), and Grand Fir (*Abies grandis*) forests of western Oregon and coastal California north of the Klamath River, they live an almost exclu-

sively arboreal existence, constructing nests within the forest canopy and relying solely on a diet of conifer needles and twig bark (Taylor 1915; Howell 1926; Benson and Borell 1931; Swingle and Forsman 2009). Red Tree Voles primarily are nocturnal and solitary except for brief periods when males visit nests of females to breed (Howell 1926; Forsman and others 2009; Swingle and Forsman 2009). Compared to

other microtines, they have small litters (1 to 4 offspring), a long gestation period (28 d), and a long period of juvenile dependence on the female before dispersing (47 to 60 d: Clifton 1960; Hamilton 1962; Forsman and others 2009; Swingle and Forsman 2009). Females often breed within a few days after giving birth (post-partum mating). Because of the long period of juvenile dependency, it is common to find females with overlapping litters of large and small juveniles in the nest at the same time (Clifton 1960; Hamilton 1962; Forsman and others 2009).

Although Red Tree Voles occur in a broad range of forest age classes, they appear to be most common in old forests (Corn and Bury 1986; Meiselman and Doyle 1996; Dunk and Hawley 2009). Tree voles are considered to be extremely vulnerable to timber harvest because of their intimate association with the forest canopy and their comparatively low reproductive rate (Maser 1966; Carey 1989; Huff and others 1992; Verts and Carraway 1998). This fact, coupled with their importance as a food source for the threatened Northern Spotted Owl (*Strix occidentalis caurina*; Forsman and others 2004a), is the main reason that Red Tree Voles were identified as a species of concern in the Northwest Forest Plan (USDA FS and USDI BLM 1994), and were included in the list of species that federal agencies were required to survey before conducting timber management activities in potential Tree Vole habitat (USDA FS and USDI BLM 2000).

Attributes of the Red Tree Vole that make them unique also make them difficult to investigate and monitor. They are difficult to capture by use of conventional small mammal sampling techniques, and although they occasionally stumble into snap traps or live traps placed upon their nests (Wight 1925; Swingle and others 2004), or terrestrial pitfall traps (Corn and Bury 1986, 1991; Gomez and Anthony 1998; Martin and McComb 2002), capture rates using these methods are so low as to be useless for population estimates. As a result, manual extraction of individuals from nests has always been the most efficient, albeit labor intensive capture and collection method (Howell 1926; Maser 1966; Swingle and others 2004; Swingle 2005). For this reason, the population ecology of Red Tree Voles is poorly understood,

and what little is known is often surmised indirectly from visual nest counts (Meiselman and Doyle 1996; Thompson and Diller 2002; Dunk and Hawley 2009) or their prevalence in owl diets (Forsman and others 2004b).

Just as their elusiveness has limited ecological research and monitoring efforts, a paucity of specimens for morphological examination has also constrained systematic investigations and taxonomy (Johnson 1973). Red Tree Voles were first described and placed in the genus *Phenacomys* (as *P. longicaudus*) based on examination of a single specimen (True 1890; Todd 1891). Taylor (1915:114), commenting on "... the poverty of material representative of it [*P. longicaudus*] ...", later proposed the subgenus *Arborimus* for *P. longicaudus* based on unique characters and differences between tree voles and other *Phenacomys* species. Johnson (1968, 1973) later conclusively raised *Arborimus* to full generic rank using morphological, ecological, and blood protein data as evidence.

Although higher-level taxonomic issues appear to be resolved (Bellinger and others 2005), there is no consensus regarding the significance of geographic variation noted within Red Tree Voles. Based on examination of a single specimen from Tillamook County, Oregon, Howell (1921) described the "Forest Tree-Lemming" (*P. silvieolus*) as a new species that is distinct from the Red Tree Vole. Miller (1923) subsequently corrected the specific epithet to *P. silvicola*, and Bailey (1936:198) provided the alternate common name of "Dusky Tree Mouse". After analyses of 3 additional specimens, Howell (1926) retained full specific status for *P. silvieola*, but acknowledged that it might only be a subspecies of the then-classified *P. longicaudus*. Based on protein electrophoresis patterns, Johnson (1968) suggested that tree voles be placed in the genus *Arborimus* and that *silvicola* be formally relegated to a subspecies of *A. longicaudus* (*A. l. silvicola*). Although Hall (1981) considered the subspecific designation to be "provisional", others appear to have endorsed subspecific ranks (Johnson and George 1991; Verts and Carraway 1998) and placed the Dusky Tree Vole on the western slopes of the Coast Range in Tillamook and Lincoln counties, Oregon. Citing Hall (1981), Johnson and George (1991) suggested that color (noting the Dusky Tree Vole's darker dorsal pelage) and geography are primary factors that

distinguish between the 2 subspecies. However, no formal analyses of color patterns have yet been performed. Note that Maser (1998) mentioned geographical variation in pelage color of the Red Tree Vole, but made no reference to the existence of different subspecies in *A. longicaudus*.

In this study, we analyzed a series of size-associated morphological characters from Red Tree Voles. Because only a few specimens were initially used to describe the Dusky Tree Vole taxon (Howell 1921, 1926), a complete understanding of the realm of possible differences between putative subspecies is lacking. Therefore, we performed a series of analyses designed to determine if morphological variation corresponded to the strict definition of the range of the Dusky Tree Vole (Tillamook and Lincoln counties) suggested in Johnson and George (1991). We performed analyses using a reasonably comprehensive set of size-associated morphological data obtained from throughout the range of the species. Though our data did not include pelage color information, our analyses nonetheless allowed us to determine if other morphological characters can distinguish and diagnose putative subspecies. As an alternative to determining if variation is distributed between subspecies, we also examined latitudinal patterns of morphological variation across the range of the Red Tree Vole to determine if morphological gradients exist instead.

METHODS

*Data Collection*

Museum collections known to house Red Tree Vole specimens and records were visited between 2004 and 2009 to obtain morphological data. For each specimen, we recorded county of collection, specific collection locality, sex, body length, tail length, hind foot length, ear length, and mass. All data were obtained from specimen tags or original field notes rather than through new measurements to better encapsulate specimen condition at the original time of collection. Our data set contained records for 154 males and 218 females collected from across the species' range (Fig. 1). However, records were incomplete in many instances, which resulted in reduced sample sizes for all measurements (Table 1). Furthermore, we excluded

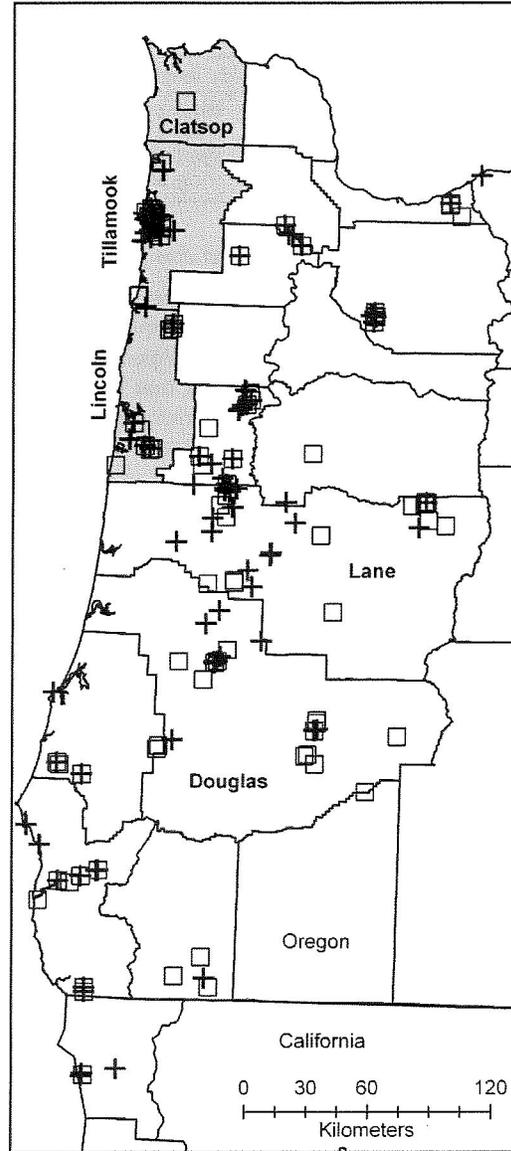


FIGURE 1. Collection locations of specimens analyzed in this study. Squares and crosses indicate males and females, respectively. The putative geographic range of the Dusky Tree Vole is highlighted in grey. Specific counties mentioned by name in the manuscript text are indicated.

mass estimates from specimens captured in pitfall traps or held in captivity for long periods, because many of these individuals were emaciated at death. Complete data sets with no missing data were available for 96 males and 137 females.

TABLE 1. Mean estimates ( $\bar{X} \pm s$ ) and sample sizes of morphological measurements of Red Tree Voles examined in this study. Ninety-six males and 137 females had records for all 5 characters.

	Mass (g)	Body length (mm)	Tail length (mm)	Hind foot length (mm)	Ear length (mm)
Males	26.8 $\pm$ 3.0 <i>n</i> = 100	101.6 $\pm$ 5.1 <i>n</i> = 129	69.3 $\pm$ 5.4 <i>n</i> = 136	21.3 $\pm$ 1.1 <i>n</i> = 136	11.9 $\pm$ 1.4 <i>n</i> = 116
Females	30.4 $\pm$ 5.4 <i>n</i> = 153	106.4 $\pm$ 7.3 <i>n</i> = 191	75.8 $\pm$ 7.2 <i>n</i> = 190	21.6 $\pm$ 1.3 <i>n</i> = 193	12.0 $\pm$ 1.6 <i>n</i> = 158

#### Statistical Approach and Data Analysis

We used univariate *t*-tests (SASInstitute Inc, Cary, NC) to determine if morphological traits differed between putative subspecies. Johnson and George (1991) suggested that the range of the Dusky Tree Vole was restricted to the Pacific slope of the Oregon Coast Range in Lincoln and Tillamook Counties. However, 1 additional record to the north of Tillamook in Clatsop County was also in our data set (Fig. 1). We considered that specimen to be a Dusky Tree Vole for the purposes of our analyses. Males and females were analyzed separately to account for sexual dimorphism (Howell 1926). Natural logarithmic transformations of mass, ear length, and hind foot length were used to obtain approximately normal distributions. For similar reasons, a cube-root transformation was used for body length. Pooled-variance estimates (for homogeneous variances) or Satterwaite estimates (for heteroscedastic variances) were used based on the outcome of initial tests for homogeneity of variances.

The univariate comparisons described above were subsequently quantified and evaluated in the context of the "75% rule" (Amadon 1949). The 75% rule states that, for valid subspecies, 75% or more of individuals from 1 group must be diagnosable from 99% or more of a 2nd group. Rather than focusing on statistical differences between putative subspecies, the 75% rule is a generalized framework emphasizing diagnosability of groups based on the set of characters examined. Initially, we used the 75% rule in a strict context by calculating the diagnosability index ( $D_{ij}$ ) of Patten and Unitt (2002; p. 30).  $D_{ij}$  can be expressed as

$$D_{ij} = u_2 - \sigma_2(t_{\alpha=0.25, df2}) - u_1 - \sigma_1(t_{\alpha=0.01, df1})$$

where  $u_1$  and  $u_2$  are the mean character values for groups 1 and 2,  $\sigma_1$  and  $\sigma_2$  are the respective standard deviations, and  $t_{\alpha=0.01, df1}$  and  $t_{\alpha=0.25, df2}$  correspond to critical values of the

*t* distribution at the specified levels of  $\alpha$  and degrees of freedom associated with groups 1 and 2. When  $u_2 > u_1$ ,  $D_{ij}$  will be  $>0$  if conditions of the 75% rule are explicitly met or exceeded. The test is performed reciprocally (through calculation of  $D_{ji}$ ) by swapping values of  $\alpha$  associated with the critical *t* values (Patten and Unitt 2002). In our analyses, we determined the reciprocal diagnosability of groups *i* and *j* ( $D_{ij}$  and  $D_{ji}$ ) under the 75% rule, where putative Dusky Tree Voles (as defined above; group *i*) and specimens from the remainder of the range (group *j*) were treated as the operational units of interest.

We further extended the framework of Patten and Unitt (2002) to infer the actual degree of diagnosability of putative Dusky Tree Voles and Red Tree Voles using the set of characters examined here. In this case, we ask a more general question: "What proportion of Dusky Tree Voles can be discerned from 99% of Red Tree Voles in the remainder of the species' range?" To answer this question, we fixed  $\alpha$  associated with the *r*-value from Red Tree Voles at  $\alpha = 0.01$ . Next, we allowed  $\alpha$  (and the associated value of *t* given the degrees of freedom) for Dusky Tree Voles to vary and iterated over the interval from  $\alpha = 0$  to  $\alpha = 1$  in steps of  $10^{-4}$ . We then identified the lowest value of  $\alpha$  that yields  $D_{ij} > 0$ , and then inferred  $1 - \alpha$  to be an estimate of the proportion of Dusky Tree Voles that can be diagnosed from 99% of Red Tree Voles. Note that  $\alpha$  in this context can be interpreted as the proportion of Dusky Tree Voles that do not differ from 99% of Red Tree Voles.

As an alternative to identifying distinct morphological clusters (and nominally, different subspecies), we performed an additional series of analyses designed to consider the plausibility of clinal geographic variation in morphology. We used linear regression (SAS Institute Inc, Cary, NC) to explore relationships between each morphological character and

TABLE 2. Results of analyses comparing female Dusky Tree Voles with specimens from the remainder of the range of Red Tree Voles. Mean character values  $\pm$  SE (in transformed units as described in the Methods) and *P*-values from analyses are provided. Mean differences between groups  $\pm$  SE in untransformed units also are provided. Reciprocal diagnosability indices ( $D_{ij}$  and  $D_{ji}$ ) and the percent of Dusky Tree Voles that can be distinguished from Red Tree Voles also are provided.

Variable	Dusky Tree Voles	Remainder of range	Difference	<i>P</i>	$D_{ij}$	$D_{ji}$	Percent distinguishable
Ln (Mass)	3.42 $\pm$ 0.028	3.40 $\pm$ 0.016	0.907 $\pm$ 0.96	0.3974	-0.4915	-0.5354	2.8
(Body length) <sup>1/3</sup>	4.703 $\pm$ 0.013	4.65 $\pm$ 0.104	4.046 $\pm$ 1.10	0.0004	-0.2601	-0.2587	3.5
Tail length	74.25 $\pm$ 0.886	76.39 $\pm$ 0.631	-2.149 $\pm$ 1.12	0.0576	-19.524	-18.787	1.5
Ln (Hind foot length)	3.095 $\pm$ 0.006	3.058 $\pm$ 0.006	0.788 $\pm$ 0.20	<0.0001	-0.1488	-0.1167	0.6
Ln (ear length)	2.451 $\pm$ 0.011	2.494 $\pm$ 0.012	-0.809 $\pm$ 0.28	0.0078	-0.2939	-0.2166	0.1

geography as reflected by latitude (UTM North-ing). Analyses were performed separately for each sex, and separate analyses also were performed where putative Dusky Tree Vole specimens were excluded from the data set. For all analyses, appropriate transformations were used to normalize data as previously described.

RESULTS

*Univariate Comparisons of Dusky Tree Voles and Red Tree Voles*

Our analyses revealed the presence of slight, but in some instances significant, differences in morphology between putative Dusky Tree Voles and Red Tree Voles. Based on the female data set, body length, hind foot length, and ear length measurements were significantly different between putative subspecies (Table 2). Approximately significant results (*P* = 0.058) were noted for tail length. Males showed comparable, highly significant patterns (Table 3). Of the 5 characters examined, only body mass revealed no clear differences between putative subspecies.

Despite detection of significant differences between groups, our analyses suggested that the characters examined have little diagnostic utility (Tables 2,3). For all characters examined, no positive values of  $D_{ij}$  were obtained for data derived from either sex. Indeed, based on our extension of the Patten and Unitt (2002) framework, our data suggest that we may only be able to diagnose in the range of 0.1 to 5.1% of Dusky Tree Voles from Red Tree Voles based on the characters analyzed here (Tables 2, 3).

*Regression Analyses*

In most situations, regression analyses revealed slight, but significant, associations between geography (latitude) and different morphological variables. For females (Fig. 2), mass ( $r^2$  = 0.048, *P* = 0.007), body length ( $r^2$  = 0.094, *P* < 0.001), and hind foot length ( $r^2$  = 0.108, *P* < 0.001) all increased with increasing latitude. However, no significant latitudinal patterns were observed for tail length ( $r^2$  = 0.0004, *P* = 0.776) or ear length ( $r^2$  < 0.001, *P* = 0.7348). Qualitatively similar patterns were observed for

TABLE 3. Results of analyses comparing male Dusky Tree Voles with specimens from the remainder of the range of Red Tree Voles. Mean character values  $\pm$  SE (in transformed units as described in the Methods) and *P*-values from analyses are provided. Mean differences between groups  $\pm$  SE in untransformed units also are provided. Reciprocal diagnosability indices ( $D_{ij}$  and  $D_{ji}$ ) and the percent of Dusky Tree Voles that can be distinguished from Red Tree Voles also are provided.

Variable	Dusky Tree Voles	Remainder of range	Difference	<i>P</i>	$D_{ij}$	$D_{ji}$	Percent distinguishable
Ln (Mass)	3.273 $\pm$ 0.017	3.288 $\pm$ 0.015	-0.415 $\pm$ 0.61	0.5067	-0.3303	-0.3291	1.2
(Body length) <sup>1/3</sup>	4.620 $\pm$ 0.009	4.573 $\pm$ 0.009	3.158 $\pm$ 0.87	0.0004	-0.1893	-0.1699	2.1
Tail length	67.310 $\pm$ 0.702	70.859 $\pm$ 0.557	-3.549 $\pm$ 0.89	0.0001	-12.366	-12.808	5.1
Ln (Hind foot length)	3.079 $\pm$ 0.0054	3.043 $\pm$ 0.0064	0.765 $\pm$ 0.18	<0.0001	-0.1254	-0.1003	1.1
Ln (ear length)	2.413 $\pm$ 0.013	2.515 $\pm$ 0.015	-1.254 $\pm$ 0.25	<0.0001	-0.2536	-0.1933	1.4

## Females

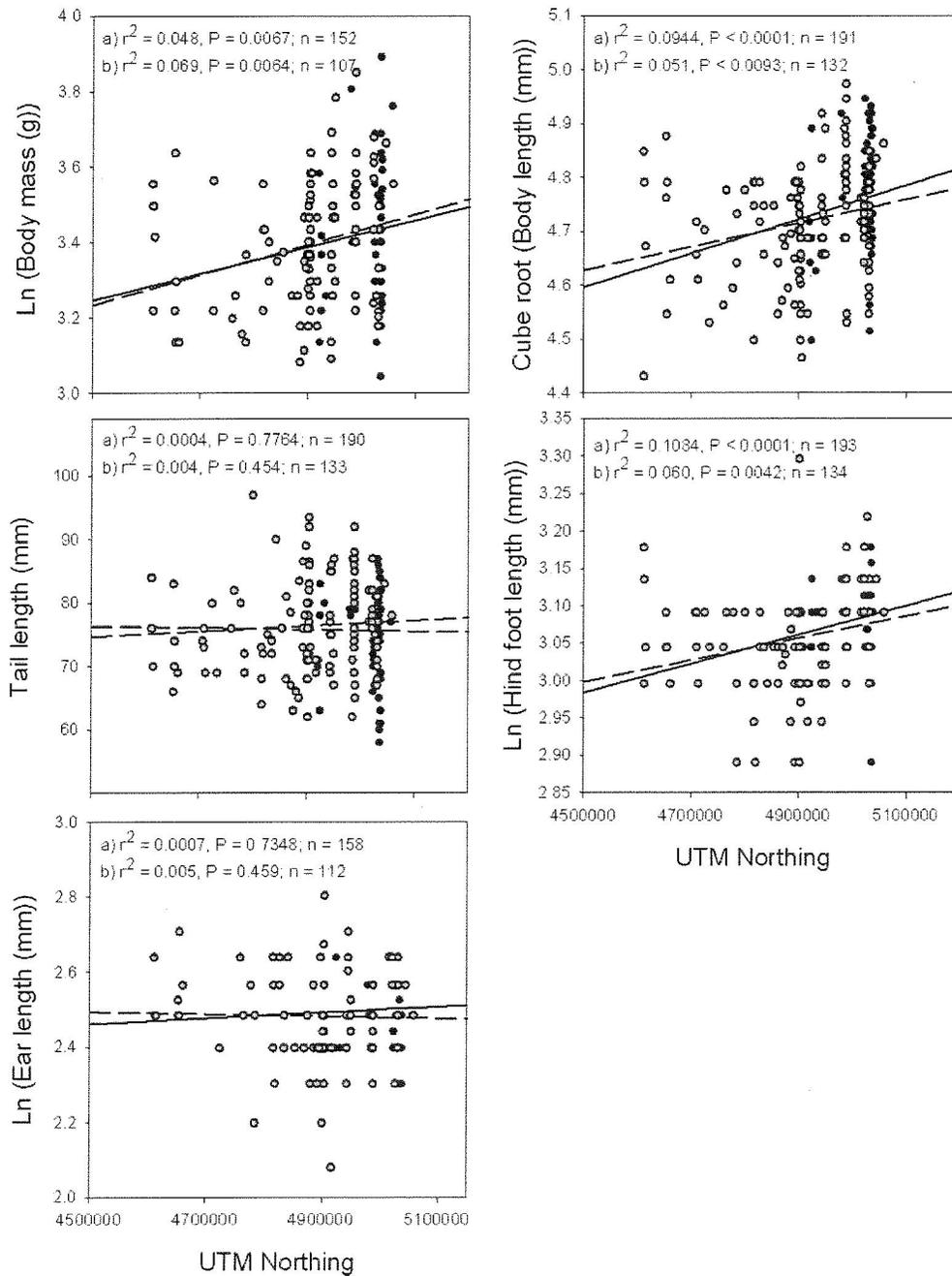


FIGURE 2. Results of univariate linear regressions of morphometric data for female tree vole specimens against latitude (expressed as UTM Northing). Results of analyses based on all data (results "a" and solid regression line) are provided, as are results of analyses that excluded putative Dusky Tree Voles (results "b", dashed regression line, gray symbols only).

each character when putative Dusky Tree Voles were excluded from these analyses (Fig. 2).

Males (Fig. 3) demonstrated slightly different trends. Body length ( $r = 0.115, P < 0.001$ ) and hind foot length ( $r = 0.117, P < 0.001$ ) increased with latitude, whereas tail length showed an inverse relationship with latitude ( $r = 0.031, P = 0.042$ ). Ear length ( $r = 0.023, P = 0.114$ ) and mass ( $r = 0.001, P = 0.755$ ) showed no significant latitudinal patterns. When putative Dusky Tree Voles were excluded from analyses, only hind foot length ( $r = 0.050, P = 0.049$ ) continued to demonstrate significant patterns at the  $\alpha = 0.05$  level. However, P-values associated with the body length regression were nonetheless approximately significant ( $r = 0.042, P = 0.086$ ).

## DISCUSSION

### *Morphological Variation in the Red Tree Vole*

When using the geographic criteria suggested by Johnson and George (1991), our analyses identified significant morphological differences between putative Dusky Tree Voles and Red Tree Voles (Tables 2, 3). Subspecies definitions range in complexity from simple, logically intuitive statements (Mayr 1963) to more formal quantitative standards (Amadon 1949; Haig and others 2006). However, all tend to encapsulate similar concepts: members of a subspecies differ in a marked manner from the remainder of the species. Thus, although our analyses revealed significant differences between groups, we also must recognize that the differences are extremely subtle: based on available information, the sets of characters examined hold little diagnostic utility (Tables 2, 3) and cannot be used to readily discern between putative subspecies groups.

Our latitudinal analyses of morphology appeared to provide the best explanations for size-associated variation within Red Tree Voles (Figs. 2, 3). In general, characters associated with gross body size (body length, hind foot length, and female body mass) were clinal and revealed significant positive associations with latitude. These patterns are coincident with Bergmann's Rule (Bergmann 1847), the well-known ecographic principle stating that larger forms of species tend to be more commonly associated with cooler climate and higher latitude (Mayr 1956). Bergmann's Rule appears to be well-established in the mammalian literature (Ashton and others 2000; Blackburn and

Hawkins 2004). Although debate continues, the underlying mechanism for this relationship may be attributable to increased heat retention of larger animal forms and its advantage in colder regions (Brown and Lee 1969).

Highly coincident latitudinal patterns were observed in females regardless of whether or not Dusky Tree Voles were included in analyses (Fig. 2). From this we can conclude that size-associated variation between subspecies (where 1 subspecies occupies a large part of the northern range of the species in general) is not the underlying driver for the observed statistical pattern. Statistical trends of males mainly differed for tail length when putative Dusky Tree Voles were excluded. In this case, the much smaller sample size of the reduced data set may not have provided sufficient statistical power to detect the otherwise weak but significant signal observed when all data were considered (Fig. 3).

If a need for heat retention is the primary factor influencing the observed intraspecific variation, it also may explain why only slight latitudinal associations were observed in our study (Figs. 2, 3). Our specimens were collected over a range of elevations and microclimates within the region. Consequently, our use of latitude in analyses may be only a rough surrogate for the actual local temperatures that individuals experience. Likewise, the full range of the Red Tree Vole comprises a relatively small geographical region that generally is not considered to encompass substantial climatic variation. Given subtle climatic variation, we should expect only subtle morphological variation in response.

Although not apparent in the female data set, our analyses also identified a significant negative association between latitude and tail length of males (Fig. 3). This pattern appears to reflect Allen's Rule (Allen 1877), which states that appendages are also likely to be reduced in cooler climates in response to the need for heat retention. Although additional data are needed to corroborate, the absence of these patterns in females may reflect behavioral differences of the 2 sexes. For example, video monitoring studies suggest that females spend the majority of their time inside their nests (Forsman and others 2009), which provide insulation from cold temperatures. In contrast, males may be exposed to cold temperatures more often and for longer periods than females because they

### Males

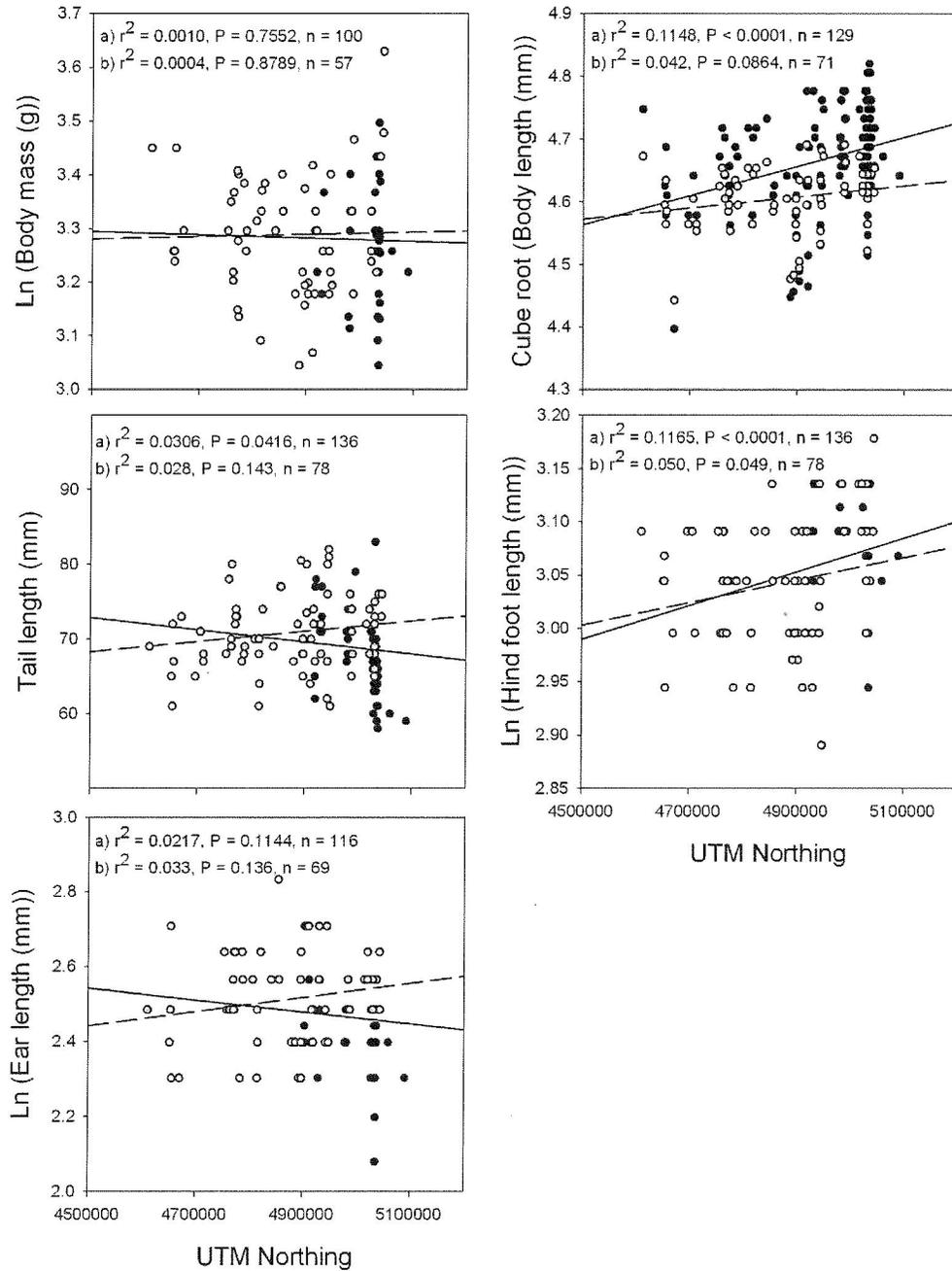


FIGURE 3. Results of univariate linear regressions of morphometric data for male tree vole specimens against latitude (expressed as UTM Northing). Results of analyses based on all data (results "a" and solid regression line) are provided, as are results of analyses that excluded putative Dusky Tree Voles (results "b", dashed regression line, gray symbols only).

occupy more nests and travel between nest sites more frequently than females (Swingle and Forsman 2009). Males also have larger home ranges than females during the breeding season (late winter and spring) as they actively visit nests of females to see if females are reproductively receptive (Forsman and others 2009; Swingle and Forsman 2009). These behaviors ultimately may result in greater exposure of males to ambient environmental conditions.

*Geographical Patterns of Morphological vs. Genetic Variation in the Red Tree Vole*

The latitudinal gradients of morphological variation observed in this study are in stark contrast to prior genetic analyses of Red Tree Voles (Miller and others 2006), where genetic discontinuities were detected across the range of the species. Using DNA sequences from the mitochondrial control region, a primary discontinuity was observed that divided northern and southern regions. Although some overlap of groups existed, Red Tree Voles north of Douglas County and southeastern Lane County in Oregon differed from individuals to the south. Likewise, a secondary discontinuity coincided with the Willamette Valley, which separated individuals from the northern Oregon Coast Range and the Oregon Cascade Range. The latter discontinuity likely reflects a barrier to gene flow across the largely non-forested Willamette Valley. However, the primary north-south genetic discontinuity does not appear to coincide with any notable geological or geographic feature, and may instead reflect historical range expansion events or vicariance associated with past glacial cycles (Miller and others 2006).

Reconciliation of the morphological and genetic data is possible. For example, if the observed size-associated variation is a phenotypically plastic response to environmental conditions, then there is no reasonable expectation for morphology to correspond with genetics. Indeed, evidence from *Mus musculus* (House Mouse) suggests that exposure to colder temperatures can reduce appendage development (Harrison and others 1959; Barnett 1965; Serrat and others 2008), which may be caused by temperature-induced changes in growth rates of cartilaginous tissues (Serrat and others 2008). In contrast, if body size has a genetic basis and affords a selective advantage in appropriate

environmental settings, then basic population genetic principles apply. Traits under selection logically will coincide with the environmentally-imposed selection gradient to produce patterns that differ from patterns observed in the neutral mitochondrial DNA sequence data. For Red Tree Voles, discordant patterns will be especially pronounced if size-associated genes reside in the biparentally inherited nuclear genome rather than in the smaller, maternally inherited mitochondrial genome that was the focus of Miller and others (2006).

*Conservation Implications*

Assessments of intraspecific variation in the Red Tree Vole, though of interest from an academic perspective, nonetheless also have applications for conservation and management. Because of its small geographic range, apparent rarity, and sensitivity to timber harvest, the Dusky Tree Vole has been petitioned for listing as either threatened or endangered under the US Endangered Species Act (USFWS 2008). Although our analyses detected geographical variation among the set of morphological characters examined, that variation cannot be used to diagnose putative Dusky Tree Voles from Red Tree Voles collected in other areas. Additional data will therefore be required to unequivocally evaluate the Dusky Tree Vole's taxonomic status. For example, pelage color is considered to be the main character that distinguishes Red Tree Voles and Dusky Tree Voles (Johnson and George 1991). However, no rigorous quantitative analyses of color variation have been performed within the species to date. Because other studies have demonstrated geographic pelage color gradients within small mammal species (Lai and others 2008), additional analyses will be required to determine if pelage coloration merely represents natural phenotypic variation within the species or if it reliably and convincingly distinguishes between valid taxonomic groups. Furthermore, additional fine-scaled genetic analyses of population structure also could be informative. If based on a sufficiently large number of tissue samples and collection locations, these analyses could lead to a better understanding of the biological cause and relevance of the observed north-south genetic discontinuity that was observed within the Red Tree Vole, and possibly also provide a basis for

suggesting the presence of other units of conservation concern within the species.

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