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A SUITABILITY MODEL FOR WHITE-FOOTED VOLES WITH INSIGHTS INTO HABITAT ASSOCIATIONS AT THE SOUTHERN BOUNDARY OF THEIR RANGE

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ABSTRACT—The White-footed Vole (*Arborimus albipes*) is one of the least-studied small mammals in North America. Most reported occurrence data come from incidental captures from larger trapping efforts and have demonstrated a strong affinity for Red Alder (*Alnus rubra*) trees. Recent research represented a range expansion in western Oregon, but little is known about the species at the southern end of its range in California. We developed a distribution model for the species to identify areas best targeted for additional White-footed Vole research. We used this model to survey by trapping in Humboldt and Del Norte Counties, California, and documented 3 new occurrences for the species. These 3 occurrences were incorporated into a final distribution model. This model suggests the possibility of White-footed Vole occurrence in southern Humboldt and northern Mendocino Counties, which would represent a southern expansion of their range. White-footed Voles were captured in areas with smaller alders than non-capture areas, supporting work from Oregon that suggests the species may not be tied to older stands as had been previously reported. Targeted trapping and physiological studies could clarify the environmental niche of this vole.

Key words: *Arborimus albipes*, Del Norte County, Humboldt County, Maxent, niche limits, species distribution model, White-footed Vole

The White-footed Vole (*Arborimus albipes*) is one of the more difficult-to-catch small mammals in North America (Maser and Johnson 1967; Manning and others 2003). The species is primarily folivorous (Voth and others 1983; Manning and others 2003) and at least semi-arboreal (Forsman and Swingle 2006), with most of the diet during spring and summer consisting of Red Alder (*Alnus rubra*) leaves (Voth and others 1983). Developing suitable bait has thus been difficult, and researchers have relied on pitfall traps to target the species. Although extensive trapping has been conducted in the previous 3 decades to describe small mammal communities in southwest Oregon with relative success capturing White-footed Voles (for example, Gomez and Anthony 1998; Martin and McComb 2002; Suzuki and Hayes 2003), trapping the species has been comparatively less common in northwestern California (for example, Ralph and others 1991; Raphael 1988). Recent efforts have shown that pitfall traps are the most effective method of detecting White-footed Voles (Manning and others 2003). The White-footed Vole is listed as a Species of Special Concern by the California Department of Fish and Wildlife (CDFW 2014), a Sensitive Species by the Oregon Department of Fish and Wildlife (Marshall and others 1996), and a Species of Concern by the Oregon office of the US Fish and Wildlife Service. Because little is known about the ecology of this species, identifying suitable areas for trapping is a primary research goal. A better understanding of range-wide and site-level suitability will facilitate future research efforts by enhancing our ability to trap at sites where individuals are more likely to be found.

The distribution of the White-footed Vole is bounded on the north by the Columbia River and to the west by the Pacific Ocean (Verts and Carraway 1995). The eastern and southern limits of the range are poorly documented, especially in northwestern California, where there are only a few records of the species. The southernmost occurrence is also the type specimen, from near Arcata, California, in 1899 (Merriam 1901). To our knowledge, the most recent reported White-footed Vole occurrences in California were reported from trapping efforts by the California Department of Fish and Wildlife in 1996 (California Department of Fish and Game, unpublished report), which resulted in 4 captures at 3 sites, all within 10 km of the coast in Humboldt County. Little is known about the physiology of the species or the abiotic factors that might limit distribution.

At a site level, early work suggested White-footed Vole affinity for riparian areas in northern California (Howell 1920, 1928). The most recent literature has focused on diet and 2nd- and 3rd-order (*sensu* Johnson 1980) habitat selection in the northern portions of their range. Specifically, Maser and Johnson (1967), Voth and others (1983), and Manning and others (2003) all presented evidence to support a strong association with stands of Red Alder. Manning and others (2003) suggested that any correlation with riparian features was more likely due to the species' preference for Red Alder, which typically grows along riparian corridors in northwestern California, or in extensive stands in both riparian and upland areas in coastal northwestern Oregon. Little is known about habitat selection in the southern portions of their range.

The modeling software Maxent has emerged as a commonly used tool for describing species distributions (Phillips and others 2006; Elith and Leathwick 2009). Although today it is frequently used for a range of applications in biogeography, invasive species management, and conservation planning, the software was initially produced for targeting surveys for rare or cryptic species (for example, Pearson and others 2007). Because of the correlative nature of species distribution models, it is difficult to determine the proximate cause of species limits (Valverde and Lobo 2008; Elith and Leathwick 2009), and therefore Maxent has been hotly contested when used to project outside of current conditions or to describe causal relationships (Araújo and Townsend Peterson 2012). Nevertheless, as a tool to identify priority areas for future surveys, Maxent and other species distribution modeling approaches have generally been quite successful even with small sample sizes (Hernandez and others 2006; Bean and others 2012), and have been shown to perform better than expert opinion (Pearce and others 2001).

Here, we used Maxent to estimate range-wide suitability for the White-footed Vole. We relied on a combination of museum specimen records and occurrences reported by CDFW, recent scientific literature, and additional trapping results from a field study that we conducted in summer 2014 in Humboldt and Del Norte Counties, California. We describe vegetation cover associated with areas where we sampled White-footed Voles and where we captured voles. The Maxent model offers a hypothesis about high-suitability areas that may allow for more targeted trapping to obtain additional information about the natural history of this species. Further, we suggest that habitat conditions at our trapping sites and at the actual capture locations in our study may provide insights into 2nd- and 3rd-order habitat selection by this poorly understood species.

Methods

Range-Wide Suitability

We obtained records of White-footed Vole occurrence from the Global Biodiversity Information Facility (GBIF), recent reports of occurrences in Oregon (Manning and others 2003), and reports by the California Department of Fish and Wildlife (CDFW, unpublished data). We then developed a preliminary range-wide suitability model using Maxent and a suite of abiotic predictor variables to identify areas in northern California for trapping efforts.

Based on 3 additional occurrences obtained from our trapping in 2014, we again used Maxent to create a new range-wide suitability model. We obtained abiotic predictor variables from the BIOCLIM dataset (Hijmans and others 2005). Because little is known about the abiotic limits to the species' range, we selected a suite of abiotic predictors that we believed best delineated different climatic niches within the study area and that were minimally correlated with one another. Specifically, we included BIO1 (annual mean temperature); BIO2 (mean diurnal

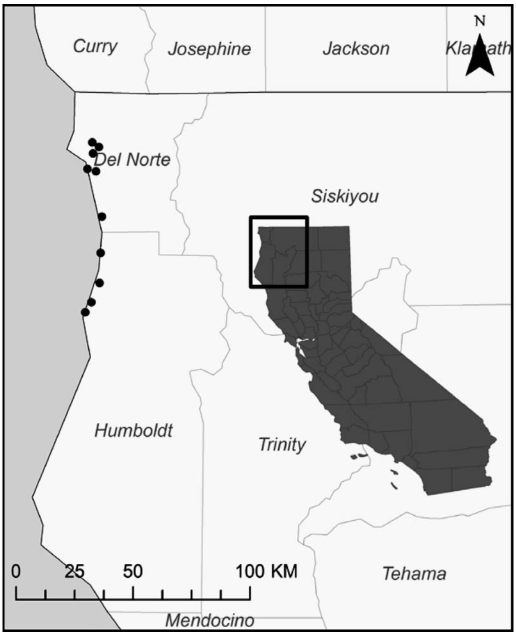

FIGURE 1. Locations of 10 grids where we conducted trapping studies of White-footed Voles in Humboldt and Del Norte Counties, California, 2014. All grids were in areas dominated by Red Alder.

temperature range); BIO6 (minimum temperature of coldest month); BIO7 (temperature annual range); BIO12 (annual precipitation); BIO13 (precipitation of wettest month); and BIO14 (precipitation of driest month). In addition, we included a measure of distance to nearest water body, constructed from the TIGER lines database (US Department of Commerce 2014). We defined the study area by buffering all known White-footed Vole occurrences by 75 km. We then ran a suite of Maxent models using all permutations of predictor variables and varying the "beta" parameter between 1, 2, and 3. We then used ENMTools (Warren and others 2010) to identify the best model using AICc. Finally, we ran 10 replicates of the best model using k-fold cross-validation to estimate an Area Under the Curve (AUC) score (Fielding and Bell 1997).

The abiotic predictor variables used to create the model were believed to be proxies for the "true" abiotic and biotic limitations to White-footed Vole distribution. Therefore, we do not present the response curves below but describe the general climatic conditions in which White-footed Voles should be found.

2nd- and 3rd-Order Habitat Selection at the Southern Range Boundary

Based on the preliminary suitability model produced by Maxent, we identified 7 sites to trap in Redwood National and State Parks in northern California (Fig. 1). We buffered all riparian areas within the parks by 100 m; we then restricted the sampling area to any location with a suitability score in the top quartile for the model. We then randomly selected 7 sites that met these criteria. We trapped at 3 additional sites where White-footed Voles had been captured by CDFW in 1996.

We placed one 8×8 trapping grid at each site. Trap stations were spaced 10 m apart and consisted of either 1 Sherman trap baited with oats and peanut butter or 1 dry pitfall trap constructed from two #10 coffee cans taped together. We alternated trap type by station within the grid. Each grid was set for 4 nights per site and checked 3 times per day, for a season total of 40 nights or 2560 trap nights.

White-footed Voles were distinguished using external characteristics including a blunt face, reddish-brown dorsal pelage, tail length >60 mm, and a lack of gray on the sides (Verts and Carraway 1995). We collected hair tufts for future genetic analysis and fecal pellet samples for dog-detection surveys. Finally, while waiting for additional fecal pellets, we conducted an impromptu diet study. Leaves from plant species at the study site were provided *ad libitum* and we recorded species consumed.

In order to describe site-level and trap-level vegetation associations, we measured a range of characteristics at each site. At the site-level, we measured vegetation at 5 plots stratified based on distinct cover types on the site and centered at the nearest trap. Surveys were conducted within 8-m and 13-m diameter circles. We estimated stand-level characteristics inside the larger circle and ground-level characteristics within the nested, smaller circle (Table 1; Mueller-Dombois and Ellenberg 1974). Canopy height was estimated using a range finder; a single observer stood at a suitable distance where they could observe the bottom and top of the canopy; the observer then measured the distance to the base of the tree, the bottom of the canopy, and the top of the canopy.

Habitat associations were analyzed using non-parametric univariate Mann-Whitney U tests.

TABLE 1. Vegetation and topographic variables measured at locations where we studied White-footed Voles in Redwood National and State Parks in 2014.

13-m plot	8-m plot
Tree Abundance	Leaf Litter[2] (%)
Tree DBH[1] (m)	Woody Litter[2] (%)
Tree Canopy Diameter[1] (m)	LWD[2] (%)
Tree Canopy lower limit[1] (m)	Stumps[2] (%)
Tree Canopy higher limit[1] (m)	Standing Water[2] (%)
LWD Diameter[1] (m)	Bare Ground[2] (%)
LWD Decay Class[1]	Moss/Bryophyte Cover[2] (%)
Snag Species[1]	Fern Cover[2] (%)
Snag DBH[1] (m)	Forb Cover[2] (%)
Snag Decay Class[1]	Graminoid Cover[2] (%)
Canopy Density (%)	Shrub Cover[2] (%)
Slope (°)	Sapling Cover[2] (%)
Distance to stream (m)	Plant Species
	Individual Species Cover[2] (%)

[1] for individual features; DBH = diameter at breast height (~1.5 m above ground); LWD = live woody debris
[2] ground cover measurement

Data were grouped based on 2nd-order and 3rd-order of habitat selection (Johnson 1980). At the 2nd-order (site level), we pooled all vegetation surveys into a single site-level estimate and compared sites where we captured White-footed Voles to sites where we did not capture White-footed Voles. At the 3rd-order (trap level), we compared forest cover characteristics at trap sites where we captured White-footed Voles to forest cover at the stratified locations surveyed at the same site. Results of habitat association analyses are presented to illustrate general patterns in habitat associations to add to the existing but scarce literature on White-footed Vole natural history. However, sample sizes were too small to conduct robust statistical analyses.

RESULTS

Range-Wide Suitability

Six models received more than 5% of the model weight based on AICc score (Table 2). No single predictor was included in all of the highest-weighted models. The best model included annual mean temperature (BIO1), minimum temperature of coldest month (BIO6), temperature annual range (BIO7), precipitation of wettest month (BIO13), and precipitation of driest month (BIO14) (Table 2, Fig. 2). Mean AUC score for the top model based on testing data and 10 k-fold cross-validation replicates was 0.861. Suitability values at known White-footed Vole sites ranged from 0.05 to 0.87. We applied a threshold to the suitability model to identify all areas with suitability values at least as high as the 95th and 90th percentile values in known sites (Fig. 2).

Highly suitable areas were predicted by: (1) a mean annual temperature of approximately 10°C; (2) high precipitation in the wettest month (the wettest sites in the study area were the most highly suitable, with suitability dropping off steeply below approximately 45 cm); (3) precipitation in the driest month of approximately 18 mm; (4) minimum temperature in the coldest month of 0°C; and (5) a low range in annual temperature (the sites with the smallest annual temperature range were the most highly suitable, with suitability dropping off above 15°C annual range). Perhaps unsurprisingly, these conditions describe the climate of coastal Oregon and northern California.

2nd- and 3rd-Order Habitat Selection at the Southern Range Boundary

We captured 3 White-footed Voles in the summer of 2014, all in stands of Red Alder in

TABLE 2. Top 6 Maxent suitability models used to estimate the potential distribution of White-footed Voles, arranged in order of increasing AICc values.

Predictors[1]	Maxent β	qLogLik	K	AICc	ΔAICc	Weight
1, 6, 7, 13, 14	1	–1789.19	21	3626.92	0	0.26
2, 7, 13, 14	1	–1792.33	19	3627.97	1.05	0.15
1, 6, 7, 12, 13, 14, distance to water	1	–1788.53	22	3628.30	1.38	0.13
2, 7, 13, 14, distance to water	1	–1791.63	20	3629.18	2.26	0.08
2, 6, 7, 12, 13, 14, distance to water	1	–1786.41	24	3629.51	2.59	0.07
6, 7, 12, 13, 14	1	–1789.19	22	3629.62	2.70	0.07

[1] Number codes indicate: (1) mean annual temperature; (2) mean temperature diurnal range; (6) minimum temperature of coldest month (6); (7) temperature annual range; (12) annual precipitation; (13) precipitation of wettest month; (14) precipitation of driest month. Predictors were obtained from the BIOCLIM dataset and distance to water estimated from TIGER lines.

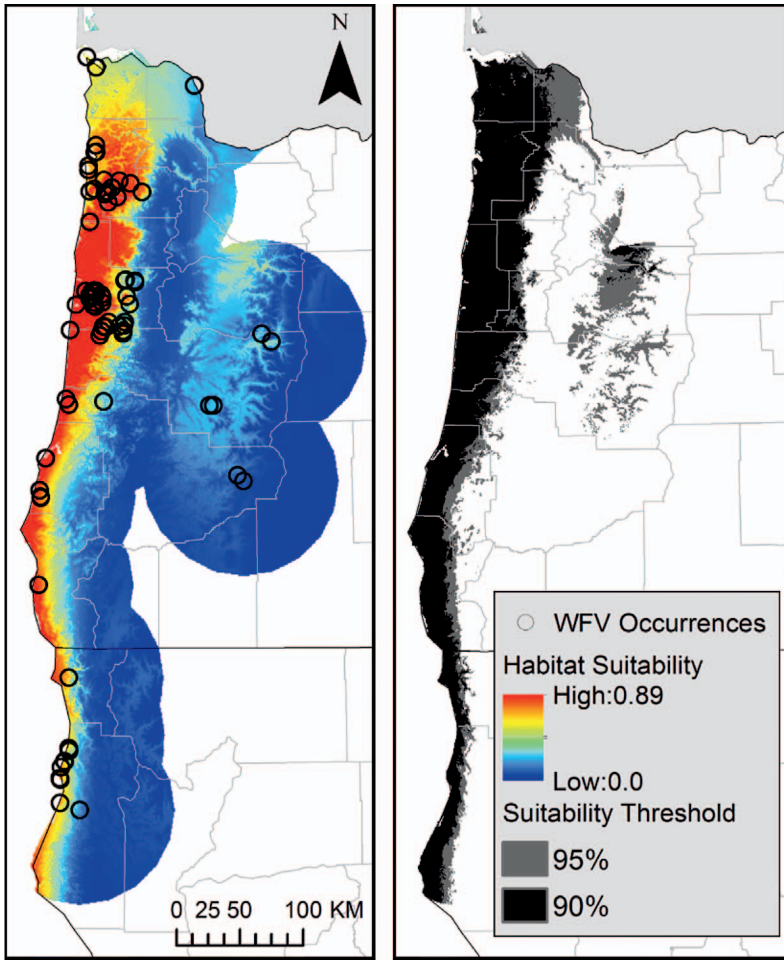

FIGURE 2. Suitability for White-footed Voles based on the top climate model in our analysis. Left image shows overall climate suitability; image on right shows all areas with suitability values greater than at 90% (black) and 95% (grey) of all available White-footed Vole occurrences.

riparian areas. Trap success was 0.117 per 100 trap nights (3 captures in 2560 trap nights). A male and female were captured at Harry A Merlo State Recreation Area, while the third, a male, was captured near Cedar Creek in Jedediah Smith State Park. The latter capture is believed to be the 1st recorded observation of a White-footed Vole in Del Norte County. Captured individuals consumed leaves of Red Alder (*Alnus rubra*), Beaked Hazel (*Corylus cornuta*), Salmonberry (*Rubus spectabilis*), Thimbleberry (*Rubus parviflorus*), and willow (*Salix* spp.); they investigated but did not consume Wild Ginger (*Asarum caudatum*), Stink Currant (*Ribes bracteosum*), or Sword Fern (*Polystichum munitum*). Sites where we captured White-footed Voles generally had smaller, less dense stands of Red Alder (Table 3). Within these sites, White-footed Voles were captured near smaller Red Alder with shallower canopies. However, due to the small sample of occupied sites, only Alder DBH (2nd-order) and Alder canopy depth (3rd-order) were significantly different.

DISCUSSION

We generated a range-wide suitability model for the elusive White-footed Vole and captured 3 new individuals from sites in Humboldt and Del Norte Counties, California. The occurrence in Del Norte is, to our knowledge, the 1st record

TABLE 3. Differences in vegetation at sites (2nd-order) and traps (3rd-order) where White-footed Voles were captured ("presence") and not captured ("background") in Redwood National and State Parks, California, 2014. Results are presented to illustrate differences and strength of effect, but p-values were not corrected for number of tests.

	2nd-order (site-level) selection			3rd-order (trap-level) selection		
	Median			Median		
Variable	Presence	Background	P	Presence	Background	P
tree density (trees/m^2)	0.094	0.092	0.89	0.261	0.339	0.19
Alder density (trees/m^2)	0.292	0.5	1.0	0.219	0.279	0.87
Alder canopy depth (m)	9.289	17.1	0.22	2.718	3.334	0.03
Alder DBH (cm)	25.4	36.9	0.06	52.1	63.4	0.44
Salmonberry cover (%)	1.321	1.259	0.89	0.398	0.299	0.38
shrub cover (%)	1.321	1.259	0.89	0.697	1.096	0.38
LWD (%)	0.11	0.259	0.4	0.02	0.1	0.36
slope (degrees)	4.8	9.4	0.27	5.0	5.0	0.98
distance to H_2O (m)	37.3	43.0	0.6	90.0	40.0	0.57
Maxent suitability	0.51	0.53	0.43	—	—	—

from that county. Previous trapping efforts in Oregon reported trap success for White-footed Voles ranging from 0.06 to 0.08 captures per 100 trap nights (for example, Gomez and Anthony 1998; Martin and McComb 2002; Suzuki and Hayes 2003). Our trap success of 0.117 was higher, although our efforts were deliberately targeted at the species. The model broadly followed known White-footed Vole occurrences, but (at least climatically) the entire Oregon coast appears to be suitable. Western Lane and Polk Counties, Oregon, may provide novel occurrence data for the species.

Perhaps of greater interest, Cape Mendocino in southern Humboldt County, Californa, appears climatically similar to areas where White-footed Voles have been captured previously in California. Any records from this area would represent a range extension for the species. In addition, recent captures from the central Cascade Range in Oregon suggest additional trapping in central Linn and Marion Counties could provide novel climatic regions that could add valuable data to our model. That is, sites in the central Cascade Range were generally colder and drier than sites on the coast, but support White-footed Vole populations. The model that we presented may simply be biased toward existing records and could be improved with records from the edge of the climatic niche. Spatial bias in known occurrences may be exacerbated by misidentifications in habitats not expected to support White-footed Vole populations (Manning and others 2003), and researchers at the periphery of White-footed Vole range should be aware of the potential for capturing this species.

With only 3 captures at 2 sites from our trapping, drawing strong inference about habitat characteristics that promote White-footed Vole occupancy was difficult. Our trapping efforts were designed to maximize capture success, and so our non-capture points generally appeared fairly similar to locations where we found White-footed Voles. However, we found some non-significant evidence that White-footed Voles occurred in smaller, less dense stands of alder. Manning and others (2003) suggested that White-footed Voles are found in early-successional and even recently logged stands. We therefore suggest that future work focus on young alder stands in the southern portions of the species' range.

The abiotic predictors we used in the range-wide model were not presented to indicate causation between the physiology of the White-footed Vole and direct climate limitations. It is just as likely that the climate conditions identified as important in the top models are correlated with biotic limits to distribution, for example presence of Red Alder or even anthropogenic effects like logging history. Nevertheless, Maxent has been shown to be quite useful at identifying novel survey sites for rare or cryptic species. While the pathway by which these climatic variables promote suitability is unknown, we believe the model offers useful locations to trap for this species. Similarly, while the 0°C minimum temperature is an appealing result to explain a range limitation, the recent captures in the Oregon sites had lower minimum temperatures ranging from –1 to –4°C.

It is unclear whether the "climatic" envelope that might restrict species at a range-wide scale has any effect on site-level habitat selection. Rather, habitat selection can occur in contradictory ways at multiple scales (Morrison and others 2006). White-footed Voles may be limited climatically to drier and warmer conditions on the coast, but it is unclear to what extent those climatic variables have a continuous effect on fitness (such as the colder the site, the lower the fitness; Hengeveld 1990; Brown and others 1996) or whether they serve as minima, above which fitness is unaffected (Liebig's Law). Additional studies on physiological tolerances would help to resolve this question. This may become increasingly important as the southern limit becomes hotter and drier. If this represents a true climatic limitation, White-footed Voles may be extirpated from California in the coming century. If, instead, suitability is more directly tied to biotic site-level conditions (such as logging history and presence of Red Alder), the threat to White-footed Voles from climate change may be smaller than expected, but habitat management will be critical for their persistence throughout their range.

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