



## Ecology, distribution, and predictive occurrence modeling of Palmers chipmunk (*Tamias palmeri*): a high-elevation small mammal endemic to the Spring Mountains in southern Nevada, USA

CHRISTOPHER LOWREY,\* KATHLEEN LONGSHORE, BRETT RIDDLE, AND STACY MANTOOTH

U.S. Geological Survey, Western Ecological Research Center, Las Vegas Field Station, 160 North Stephanie Street, Henderson, NV 89074, USA (CL, KL)

University of Nevada, Las Vegas, 4505 South Maryland Pkwy, Las Vegas, NV 89154, USA (BR)

Nevada State College, 1125 Nevada State Drive, Henderson, NV 89002, USA (SM)

\* Correspondent: [clowrey@usgs.gov](mailto:clowrey@usgs.gov)

Although montane sky islands surrounded by desert scrub and shrub steppe comprise a large part of the biological diversity of the Basin and Range Province of southwestern North America, comprehensive ecological and population demographic studies for high-elevation small mammals within these areas are rare. Here, we examine the ecology and population parameters of the Palmer's chipmunk (*Tamias palmeri*) in the Spring Mountains of southern Nevada, and present a predictive GIS-based distribution and probability of occurrence model at both home range and geographic spatial scales. Logistic regression analyses and Akaike Information Criterion model selection found variables of forest type, slope, and distance to water sources as predictive of chipmunk occurrence at the geographic scale. At the home range scale, increasing population density, decreasing overstory canopy cover, and decreasing understory canopy cover contributed to increased survival rates.

Key words: abiotic, Basin and Range, biotic, GIS, habitat associations, scale, Sciuridae, small mammals, survival

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Understanding the principal ecological attributes that determine habitat occupancy and limits to geographic distribution is an essential element of any wildlife conservation strategy. Several studies have recommended that conservation strategies for wildlife incorporate information on species distributions (Aspinall and Mathews 1994; Laliberte and Ripple 2004), quantification of habitat parameters that underlie survival of populations (Krohne 1997; Sureda and Morrison 1999; Jorgensen 2004), and development of models that can be used to predict the influence of anthropogenic effects such as climate change (Weigand et al. 1999; Inouye et al. 2000; Hannah et al. 2002) and habitat loss (Gibbs 2000) on the persistence of populations. However, comprehensive studies that incorporate these recommendations are absent from many ecologically sensitive areas. As a result, researchers and managers must often rely on limited information, and may inappropriately extrapolate ecological models beyond the study area (Peterson and Robbins 2003). It has long been recognized that these issues of ecological model performance may be addressed through multiscale approaches to wildlife-habitat interaction (Levin 1992). Recognizing that species respond to their habitats according to both home range-scale (forage, shelter) and geographic-scale (distribution,

expansion) requirements is a key to predict potential survival and distribution (Weins 1989). Studies are needed that connect home range-scale with geographic-scale models, predict how population parameters such as survival rates respond to habitat changes and anthropogenic activities, and directly address ecological theory (Lomolino 2001; Jorgensen 2004).

In the Basin and Range Province of southwestern North America, mountain ranges dominated by conifer forests are widely separated by desert and shrub steppe regions to form the so-called "sky island" landscapes, where a suite of mammal species have been postulated to have been isolated for millennia (Brown 1971). These populations have been considered to be susceptible to extinction in proportion to their inability to replenish populations by immigration, and to the size of the sky island inhabited. These same attributes could also increase extinction threats posed by global and regional environmental change (McDonald and Brown 1992; Rosenzweig and Clark 1994; Beever et al. 2005). These sky islands contribute greatly to overall regional biodiversity, yet many include endemic species whose ecologies are poorly studied (Lomolino 2001; Rickart 2001; McCain 2007; Rowe et al. 2011).

Palmer's chipmunk (Rodentia; Sciuridae; *Tamias palmeri*) is a high-elevation species endemic to the Spring Mountain range of southern Nevada (Best 1993). *T. palmeri* primarily occurs across 3 montane forest habitat types (*Pinus ponderosa*, *Abies concolor*, and *P. longaeva*) from about 2,300 m to the timberline (approximately 3,400 m), and is the most abundant diurnal mammal above 2,500 m (Deacon et al. 1964; Lowrey 2002). This species is the primary prey source for several predatory species such as the long-tailed weasel and red-tailed hawk (Lowrey 2002). Chipmunks also serve as important coniferous tree seed dispersers (Vander Wall 1995; Vander Wall and Joyner 1998). *T. palmeri* is a covered species under the Clark County Multi Species habitat Conservation Plan, considered as threatened by the state of Nevada, and as endangered by the IUCN (2004) and the Nevada Natural Heritage Program, designations that are primarily due to the isolation and restricted size of the Spring Mountain range. Anthropogenic risks include potential habitat exclusion due to recreation activity at spring and stream areas (Lowrey 2002), urban development, feral cats (Ambos and Tomlinson 1996), and increased risk of fire as recreational usage increases and climates warm (Bradley 2010)—for example, a fire in 2013 that burned over 11,300 forested hectares of the Spring Mountains. The range of *T. palmeri* overlaps with 3 other species of squirrel, the golden-mantled ground squirrel (*Callospermophilus lateralis*) occurs within much of the range of *T. palmeri* except at the higher elevations, albeit at a much lower density (McKeever 1964; Lowrey 2002). The rock squirrel (*Otospermophilus variegatus*) occurs infrequently, and is found mostly near rocky outcrops (Oaks et al. 1987). The Panamint chipmunk (*T. panamintinus*), occurs in drier and lower elevation pinyon-juniper habitat, but overlaps with *T. palmeri* below approximately 2,500 m (Best 1993, 1994; Lowrey and Longshore 2013). As climates warm, resulting in some montane forests potentially being replaced by warmer and more arid-adapted dwarf conifer forests (Bradley and Fleishman 2008), *T. palmeri* faces increasing competition from *T. panamintinus* and perhaps other ground squirrels. Given the isolated and relatively small area occupied by *T. palmeri*, these conditions may threaten the species with extinction. We believe *T. palmeri* to be an especially suitable species to use to examine landscape and local-scale population demographic and ecological parameters, with potential implications for similar species elsewhere in Basin and Range landscapes (McGill et al. 2006; Moritz et al. 2008).

Although animals respond to habitat along a continuum (Levin 1992), habitat use and population parameters can be measured within 2 broadly defined scales. The 1st-order scale has been defined as the selection of the physical or geographic range, and the 2nd-order scale defined as the home range of an individual or social group (Johnson 1980). Earlier ecological theory predicts abiotic and biotic conditions as major causal factors governing 1st-order distributions and 2nd-order habitat selection variables, respectively (Grinnell 1924; MacArthur 1958). However, recent studies have shown both abiotic and biotic variables, as well as their interactions play an important role in population ecology across different scales, such that

an understanding of attributes at each scale can lead to more accurate prediction of occupancy models (Cunningham et al. 2008; Landry-Cuerrier et al. 2008; Wang et al. 2011; Gonzales-Salazar et al. 2013). Although several authors have addressed small mammal habitat relationships (Jorgensen and Demarais 1999; Bowman et al. 2001; Jorgensen 2004; Coppeto et al. 2006; Oatway and Morris 2007), we found few comparable studies with the replication needed to create predictive habitat occupancy models in a Basin and Range, sky island environment across both geographic and home range scales (Rowe et al. 2015). In this paper, we first examine the contributions of abiotic and biotic factors to *T. palmeri* survival at the home range scale. We then use geographic range-wide occurrences from trapping and a priori model selection to develop a geographic-scale model of the probability of *T. palmeri* occupancy in different habitats.

## MATERIALS AND METHODS

**Study area.**—The Spring Mountains are located within the northern Mojave Desert approximately 40 km northwest of Las Vegas, Nevada. The range is approximately 110 km long by 45 km wide, and is characterized by steep slopes and limestone cliffs. There are over 10 peaks above 3,300 m, the highest being Mt. Charleston at 3,632 m. *T. palmeri* habitat in the Spring Mountains is completely isolated from habitat in other ranges by desert basins that are just above 700 m. Vegetation above 2,500 m consists of 3 conifer forest associations: Ponderosa (*P. ponderosa*), White fir (*A. concolor*), and Bristlecone pine (*P. longaeva*). Patches of limber pine (*P. flexilis*) infrequently occur in pure stands. Below 2,500 m, single-leaf Pinyon pine (*P. monophylla*), Utah Juniper (*Juniperus osteosperma*), and curl-leaf Mountain mahogany (*Cercocarpus ledifolius*) occur (Sada and Nachlinger 1996). Climate change research has indicated an expansion of pinyon-juniper woodlands in this region, potentially decreasing upper-elevation tree communities in the Basin and Range (Breshears et al. 2008; Bradley 2010). Annual precipitation is typically less than 13 cm in the lower areas and as high as 71 cm in the higher elevations with the east side of the range receiving the majority of rain and snow. The upper slopes are subject to extreme seasonality with snow cover 5–8 months of the year. Mean yearly average temperature is 10°C at 2,000 m (Sada and Nachlinger 1996).

**Distribution.**—All techniques used to capture and handle animals followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the University of Nevada Las Vegas Institutional Animal Care and Use Committee. We used animal locations from 41 trapping transects each year to estimate the actual distribution of *T. palmeri*. We trapped 12 transects within the Pinyon pine/Juniper habitat association at the lowest elevations, 12 across the Ponderosa-Pinyon pine transition zone, 11 within the Ponderosa pine/white fir association, and 6 at the highest elevations across the bristlecone/above timberline transition zone to systematically sample the range from June through August of 2008 and 2009. Transects were 2 km in length and placed not

less than 2 km or more than 5 km apart. Within each transect, one 25×9×8 cm folding aluminum trap (H. B. Sherman Trap Co., Tallahassee, Florida) was placed every 40 m along a single line for 4 days (50 traps per transect). We maintained a buffer of 300 m below the lowest elevation of locations successfully capturing *T. palmeri* to estimate the distributional extent within the Spring Mountains.

*Identification of Tamias palmeri.*—Genetic identification is a necessary component of our research, primarily due to the difficulty of physically specifying between the 2 species of chipmunks occurring within the Spring Mountain range. We removed a small piece of ear tissue (3–5 mm<sup>3</sup>) to use as material to identify each chipmunk to species. Harvested tissues were placed in a small glass vials filled with laboratory grade 95% ethanol for storage. Prior to DNA extraction, each tissue sample was washed 3 times using 10% phosphate-buffered saline to remove as much ethanol as possible. Following standard protocols (Mantooth et al. 2013), we extracted total genomic DNA from the tissues using the Qiagen DNeasy Tissue Extraction Kit (Qiagen Inc., Valencia, California). For genetic identification, we amplified and sequenced a portion of the mitochondrial cytochrome-*b* (*Cytb*) gene, successfully used in previous studies to examine species level differentiation within *Neotamias* (Piaggio and Spicer 2001). We amplified the entire gene using polymerase chain reaction (PCR), gene-specific primers L14725 and H15915 (Kocher et al. 1989), and a PCR temperature profiles: 30 cycles of denaturation at 94°C for 40s, annealing at 50°C for 1 min, and extension at 72°C for 2 min. Double-stranded PCR products were qualitatively examined using a 0.8% agarose gel and the amplified PCR fragments were purified using Exo-SAP IT (USB Corp., Cleveland, Ohio), following the manufacturer's protocol. The purified PCR fragments (including both the light and heavy DNA strands) were sequenced using the ABI PRISM BigDye v3.1 Cycle Sequencing chemistry (Applied Biosystems Inc., Waltham, Massachusetts), using the same primers listed previously. Unincorporated dye terminators were removed using Sephadex spin columns (Centri-Sep Inc., Adelpia, New Jersey), and sequence data were generated on a 3130 Genetic Analyzer (Applied Biosystems Inc., Waltham, Massachusetts). We aligned strands of each gene using SEQUENCHER 4.9 (Gene Codes Corp., Ann Arbor, Michigan), followed by manual proofreading. A nucleotide BLAST search of the GenBank database (with a 90% similarity index) using a minimum of 500 base pairs from the *Cytb* gene from each individual was performed. Based on these criteria, the search results and genetic identifications were unambiguous in identifying each sample as only 1 species with > 90% similarity. Given this unambiguity, a more detailed phylogenetic analysis was unnecessary. Identification of introgression, which has been documented in western chipmunks (Reid et al. 2011), could not be ruled out as it requires evidence from nuclear as well as mitochondrial analysis. All sequence data will be catalogued in GenBank.

*Relative population density and survivorship.*—The ecology of *T. palmeri* is dictated by the extreme conditions of the high-elevation, mountainous environment. This environment forces

the species to fulfill mating, rearing, and food storage requirements within an approximately 3-month time period (Lowrey 2002). These conditions demand both a highly mobile resident and quickly dispersing juvenile population. Given these ecological conditions, we used an open population model (Jolly 1965) to estimate relative density and survival rates (Ecological Methodology version 7.2, Exeter Software, Setauket, New York). Open population models are appropriate for populations that may change over a short period of time, and have been demonstrated as robust against heterogeneity in capture probabilities (Pollock and Alpizar-Jara 2005). Given the extremely short active period of this species, we estimated an 8-day trapping period (approximately 10% of the active season) to be an appropriate time period of survival. Relative density was estimated from the formula:  $M_j = m_j + R_j \cdot Z_j / r_j$ , where  $M_j$  is the estimated population size at time  $j$ ,  $m_j$  is the number of animals captured at time  $j$  that are marked,  $R_j$  is the total number of animals captured at time  $j$  that are released,  $Z_j$  is the number of marked individuals not captured at time  $j$  that are captured again later, and  $r_j$  is the number of members of  $R_j$  captured again later.  $M_j$  is then divided by the effective trapping area (see subsequent) to derive the density estimate. Daily survival rates from time period  $j$  to  $j + 1$  were estimated from the formula  $M_{j+1} / M_j R_j - m_j$  (Pollock and Alpizar-Jara 2005). We used a grid design, which was independent of transects that were used to determine distribution, to estimate relative density and survivorship. Eight independent grids were trapped simultaneously during each month of the active season of *T. palmeri* (June, July, and August—Lowrey 2002) during 2008 and 2009. Grids were > 400 m apart to ensure independence over the trapping period (based on Lowrey 2002). Grids had a configuration of 8 by 5 traps (25×9×8 cm) spaced 30 m apart to create an effective rectangular trapping area of 3.6 hectares. Grids were baited and trapped daily for 8 days and checked twice per day, at sunrise and just before sunset. Animals were marked with aluminum ear tags (5.0×1.5 mm; Monel 1005-1, National Band and Tag Co., Tallahassee, Florida), weighed, sex and reproductive condition determined, and released. The 8 grids were reestablished at new locations each month for a total of 24 independent population estimates per year and a total of 48 grids and 1,920 traps over 2 years.

*Vegetation and topographic data collection.*—Vegetation species composition, structure, and topographical variables were measured within 8-m radius plots centered on each trap (40 traps or plots per grid) within each grid for a total of 1,920 plots. We measured several habitat variables thought to contribute to *T. palmeri* occurrence, survival, and abundance (Lowrey 2002; Tables 1 and 2). Our criteria for selecting habitat variables were based on vegetative and topographical structure, vegetation species composition, and elements within the plot, which may provide resources to the animal. We used a system of point counts along two 15 m perpendicular transects centered on each trap. Percentage of tree, shrub, and forest litter cover were estimated by standing at 20 systematically placed points (1.5 m apart) on each transect and looking straight up (canopy) and down (shrub, litter) through a 20 cm long by 3 cm diameter

**Table 1.**—Habitat variables measured for geographic-scale analyses of *Tamias palmeri* ecology.

Habitat variables measured
White fir–bristlecone tree cover (categorized)
White fir–Ponderosa mesic (categorized)
Ponderosa xeric (categorized)
Pinyon pine–juniper (categorized)
Slope percent
Distance to water
Aspect <sup>a</sup>
Tree cover category × slope <sup>b</sup>
Tree cover category × distance to water

<sup>a</sup> Aspect transformed into 2 categorical variables of northern (compass bearing  $\geq 270$  and  $\leq 90$ ) or southern ( $\leq 269$  and  $\geq 91$ ).

<sup>b</sup> Indicates interaction term.

**Table 2.**—Habitat variables measured for home range-scale analyses of *Tamias palmeri* ecology.

Habitat variables measured
Tree <sup>a</sup> percent cover
Tree density
Shrub ( <i>Ribes</i> spp.) density
Slope percent
Downed log density
Large rock density (> 1 × 1 m diameter)
Distance to water (m)
Aspect <sup>b</sup>

<sup>a</sup> Species: *Pinus ponderosa*, *Pinus longaeva*, *Abies concolor*, *Pinus flexilis*.

<sup>b</sup> Aspect transformed into 2 categorical variables of northern (compass bearing  $\geq 270$  and  $\leq 90$ ) or southern ( $\leq 269$  and  $\geq 91$ ).

tube. Percentage cover was derived by counting the number of times the canopy (or shrubs) covered the line of sight (hits) and dividing that number by 20 (total; modified from Dueser and Shugart 1978). Density of trees, shrub, snag, and large rocks was measured by counting each within each plot. We defined downed logs as > 0.5 m in diameter and > 2 m in length. Tree heights were measured with a hypsometer. Overstory (trees > 10 m in height) and understory (trees < 10 m in height) were measured as separate categories. Large rocks were defined as those > 1 m in height and width. Water source locations, either wet ground or open water, were also documented. Percentage slope, aspect (2 categorical variables of northern [compass bearing  $\geq 270$  and  $\leq 90$ ] or southern [ $\leq 269$  and  $\geq 91$ ]), and distance to water sources were measured using 30 m resolution digital elevation models (ArcMap 10.1. Environmental Systems Resource Institute, Redlands, California).

**Hypothesis development and model selection.**—Decreasing slope angle, northern aspects, and decreasing distance to water sources were found by Lowrey (2002) to increase the probability of *T. palmeri* occurrence in a previous small-scale study. We tested these potential relationships by randomly placing trapping grids within and outside those areas predicted to have greater and lesser density and survival rates. The 48 grids (24/year) were placed in areas with slopes of both greater and less than 25%, within and outside 200 m distance from permanent water sources, and on both northern and southern aspects.

All possible combinations of slope, aspect, and distance to water were included in the design. In addition to these variable combinations, we expanded model selection to include 4 types of conifer forest: White fir/Bristlecone pine, White fir/Ponderosa mesic, Ponderosa xeric, and pinyon pine/juniper/nonconifer woodland associations. Forest type classifications were defined by the Southwest Regional Gap Analysis Project (ReGap), which uses a multispectral analysis of LandSat satellite data. We physically confirmed the ReGap classifications at all trapping sites.

Two model sets were selected a priori for geographic (11 models; Table 3) and home range-scale (11 models; Table 4) analyses within an Akaike Information Criterion (AIC) framework (Burnham and Anderson 2004). Abiotic, biotic, and combined variable models were selected to address that variables contributed to *T. palmeri* occurrence (at the geographic scale) and *T. palmeri* survival (at the home range scale).

**Geographic-scale habitat relationships.**—The geographic scale was defined conservatively as those areas within the Spring Mountain range above 1,800 m, encompassing *T. palmeri*'s estimated population range (Lowrey 2002). We used binary logistic regression analyses, with locations successfully trapping *T. palmeri* and random points as dependent variables, to estimate whether locations can be predicted based on habitat (independent) variables (Table 1; Menard 1995; Manly et al. 2002). We did not attempt to identify random sites as unused. This type of analysis has been shown to yield estimates of habitat selection that are robust to issues of contamination across used and available locations that can lead to biased coefficients (Boyce and McDonald 1999; Johnson et al. 2006). The  $-2$  log likelihood values derived from these analyses were entered into the AIC formula ( $AIC = -2 \log \text{likelihood} + 2k$ ) where  $k$  = the number of habitat variables in the model + 1—Burnham and Anderson 2004). We used ArcMap 10.1 to generate the random points within the study area and spatially enforced a minimum distance of 10 m between all points. We entered the highest AIC-rated logistic regression equation into the GIS raster calculator to generate resource selection function (RSF) values that were then represented on a map of the Spring Mountain as the *T. palmeri* geographic habitat model. Given the impossibility of identifying random sites as unused, these RSF values are not absolute values but proportional to the relative probability of animal occurrence across the available habitat (Boyce and McDonald 1999; Johnson et al. 2006).

**Home range-scale habitat relationships.**—The home range scale was previously established by Lowrey (2002) at a mean of 0.23 ha ( $SD = 0.08$ ). Our grid size of 3.6 ha was 15.6 times average home range, thus increasing sample size, reducing problems with autocorrelation (Legendre 2010), and increasing sample independence. We linearly regressed mean daily survival on model variables (Table 2). Survival estimates were measured over 8 days of trapping, a time period that may encompass over 10% of the species' entire active season. We emphasize that our survival estimates do not distinguish between dispersal and mortality, and therefore do not represent true but residency or apparent survival estimates. However,

**Table 3.**—Models and Akaike Information Criterion (AIC) statistics for geographic-scale analyses of *Tamias palmeri* probability of occurrence.

Geographic-scale models	–2 LL <sup>a</sup>	AIC	Δ	Weight
TCVR <sup>b</sup> + SLP <sup>c</sup> + DWTR <sup>d</sup> + (TCVR * SLP) + (TCVR * DWTR)	5,598.23	5,624.23	0.00	0.883
TCVR + SLP + DWTR	5,615.11	5,629.11	4.88	0.077
TCVR + SLP + ASP <sup>e</sup> + DWTR	5,614.43	5,630.43	6.20	0.040
SLP + DWTR + (SLP * DWTR)	5,707.32	5,717.32	93.09	0.000
SLP + DWTR	5,717.00	5,725.00	100.77	0.000
SLP + ASP + DWTR	5,716.21	5,726.21	101.98	0.000
TCVR + DWTR + (TCVR * DWTR)	5,879.42	5,897.42	273.19	0.000
TCVR + DWTR	5,906.93	5,918.93	294.70	0.000
TCVR + SLP + (TCVR * SLP)	6,559.11	6,577.11	952.89	0.000
TCVR + SLP	6,567.07	6,579.07	954.84	0.000
TCVR + SLP + ASP	6,566.65	6,580.65	956.42	0.000

<sup>a</sup> –2 log likelihood (LL) from binary logistic regression.

<sup>b</sup> TCVR = Tree cover type.

<sup>c</sup> SLP = Slope (percentage).

<sup>d</sup> DWTR = Distance to water.

<sup>e</sup> ASP = Aspect transformed into 2 categorical variables of northern (compass bearing ≥ 270 and ≤ 90) or southern (≤ 269 and ≥ 91).

**Table 4.**—Akaike Information Criterion (adjusted for small sample size; AIC<sub>c</sub>) variables and values for home range-scale analyses of *Tamias palmeri* survival.

Predictor variables	RSS <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	Δ	Model weight
Principal component (PC) of overstory canopy cover (OC) + Population density (PD)	0.407	–220.03	0.00	0.340
PC OC + PC understory density (UD) + PD	0.388	–219.83	0.20	0.307
PC OC + PD + Large rock density	0.400	–218.37	1.66	0.148
PC OC + PD + <i>Ribes spp.</i> shrub density	0.404	–217.89	2.14	0.116
PD + Slope (%) + PC OC + PC UD	0.390	–216.96	3.07	0.073
PD + Distance to water + Aspect + PC OC + PC UD	0.381	–212.44	7.59	0.007
Slope + Distance to water + PD	0.482	–209.42	10.61	0.001
Slope	0.534	–209.38	10.65	0.001
Distance to water	0.543	–208.58	11.45	0.001
Slope + Large rock density + Log density	0.497	–207.94	12.08	0.0008
Slope + Distance to water + Aspect <sup>c</sup>	0.522	–205.59	14.44	0.0002

<sup>a</sup> RSS = Residual sum of squares.

<sup>b</sup> AIC<sub>c</sub> adjusted for small sample size.

<sup>c</sup> Aspect transformed into 2 categorical variables of northern (compass bearing ≥ 270 and ≤ 90) or southern (≤ 269 and ≥ 91).

we believe the consistent methodology under which all animals were captured, the random and independent placement of the 48 trapping grids, and the a priori selection of habitat parameters result in a robust sample of apparent survival rates, which are relative to each other, and represent a range of values which are suitable for comparison across the changing habitats. Correlated variables were identified with principal component (PC) analyses. Two separate PC analyses were calculated: The 1st combined the overstory canopy cover of 3 tree species, and the 2nd combining the understory density of 3 tree species (Table 5). Each of these analyses resulted in a single PC, 1 for overstory, and 1 for understory. The limit on the number of axes to estimate was determined by eigenvalues. Although there was some correlation between overstory and understory variables (variance explained 44.1%), we did not find them correlated highly enough to justify a single PCA for both. Percent cover variables were arcsine square root transformed and density variables were square root transformed before PC analysis. PC scores were then used as independent variables. Based on the distance between grids (> 400 m) and the 8-day time period, we

treated each grid each year as independent measures of population density and survival ( $n = 48$ ). We entered the residual sum of squares values into the AIC<sub>c</sub> (adjusted for small sample size) formula to rank our model set (Burnham and Anderson 2004).

## RESULTS

*Distribution and genetic identification.*—Data from transects was used to determine distribution only. Forty-one 2-km transects were trapped for 5 days each year resulting in 26 transects capturing 293 individual chipmunks. Genetic identification was completed on 235 chipmunk samples. Of these, 174 were identified as *T. palmeri* and 59 identified as *T. panamintinus*. We trapped between 1,760 and 3,294 m in elevation, capturing *T. palmeri* from 2,085 m (pinyon–juniper forest) to 3,285 m (Bristlecone forest).

*Geographic-scale habitat relationships.*—We used 2,100 *T. palmeri* locations and 2,100 randomly distributed points to estimate habitat relationships at the geographic scale. Given the longer trapping duration that occurred at grid sites relative

**Table 5.**—Variables within each Principal Component Analysis (PCA) used in *Tamias palmeri* home range-scale habitat modeling.

Variables in percent cover PCA	Loadings	Eigen value	Percent variance <sup>a</sup>
Fir percent cover	0.846	2.068	68.9
Bristlecone percent cover	0.777		
Limber pine percent cover	0.866		
Variables in tree density PCA			
Fir density	0.811	2.027	67.5
Bristlecone density	0.806		
Limber pine density	0.849		

<sup>a</sup> Percent variance explained from the 1st principal component. Only 1 principal component was derived from each PCA.

**Table 6.**—AIC habitat variable weightings from geographic-scale analyses of *Tamias palmeri* habitat.

Geographic-scale variables	Weight
Treecover type	0.99
Slope (%)	0.99
Distance to water	0.99
Treecover × distance to water <sup>a</sup>	0.88
Treecover × slope	0.88
Aspect	0.04
Slope × distance to water	0

<sup>a</sup> Indicates interaction term.

to transects, we believed animals captured in grids were more likely to reflect occurrences of habitat selection than those captured at transect locations. Therefore, animal occurrences from grid trapping and not transects were used to estimate geographic-scale habitat use. AIC model selection found probability of *T. palmeri* occurrence was related to geographic-scale variables of slope, distance to water, and tree cover type (Tables 3 and 6). Specifically, *T. palmeri* probability occurrence was greater in areas of relatively lower slope, closer to water sources, and within the white fir and Ponderosa vegetation types. Logistic regression performance analyses of the highest rated model found an area under the receiver operating characteristic curve of 84.4% ( $SD = 0.005$ ). Probability analysis (1 – exponential of the logistic regression coefficient \* 100—Manly et al. 2002) indicated *T. palmeri* occurrence increased by a factor of 4.18 (418%; 95% CI 2.87–5.80) within the White fir/Bristlecone forest, 4.40 (3.01–6.01) when within the xeric Ponderosa forest, and 2.71 (1.83–4.02) when within the mesic White fir/Ponderosa forest (all 3 relative to the pinyon–juniper/nonconifer woodland association). We found occurrence reduced by a factor of 0.1 (0.096–0.104) for every 100 m increase in distance from permanent water sources, and reduced by a factor of 0.35 (0.32–0.38) for every 10% increase in percent slope. The highest rated model had 2 interaction terms: the effect of (decreasing) slope on probability of occurrence was 6% greater within the xeric than mesic forests, indicating that low slopes may be more important in dry areas; the effect of distance to water was increased by 2% in the mesic forests than in the xeric or white fir–limber–bristlecone, but the latter effect may not be biologically meaningful. Our model predicted *T. palmeri* available

habitat is restricted to approximately 220.7 sq. km within the Spring Mountains (Fig. 1).

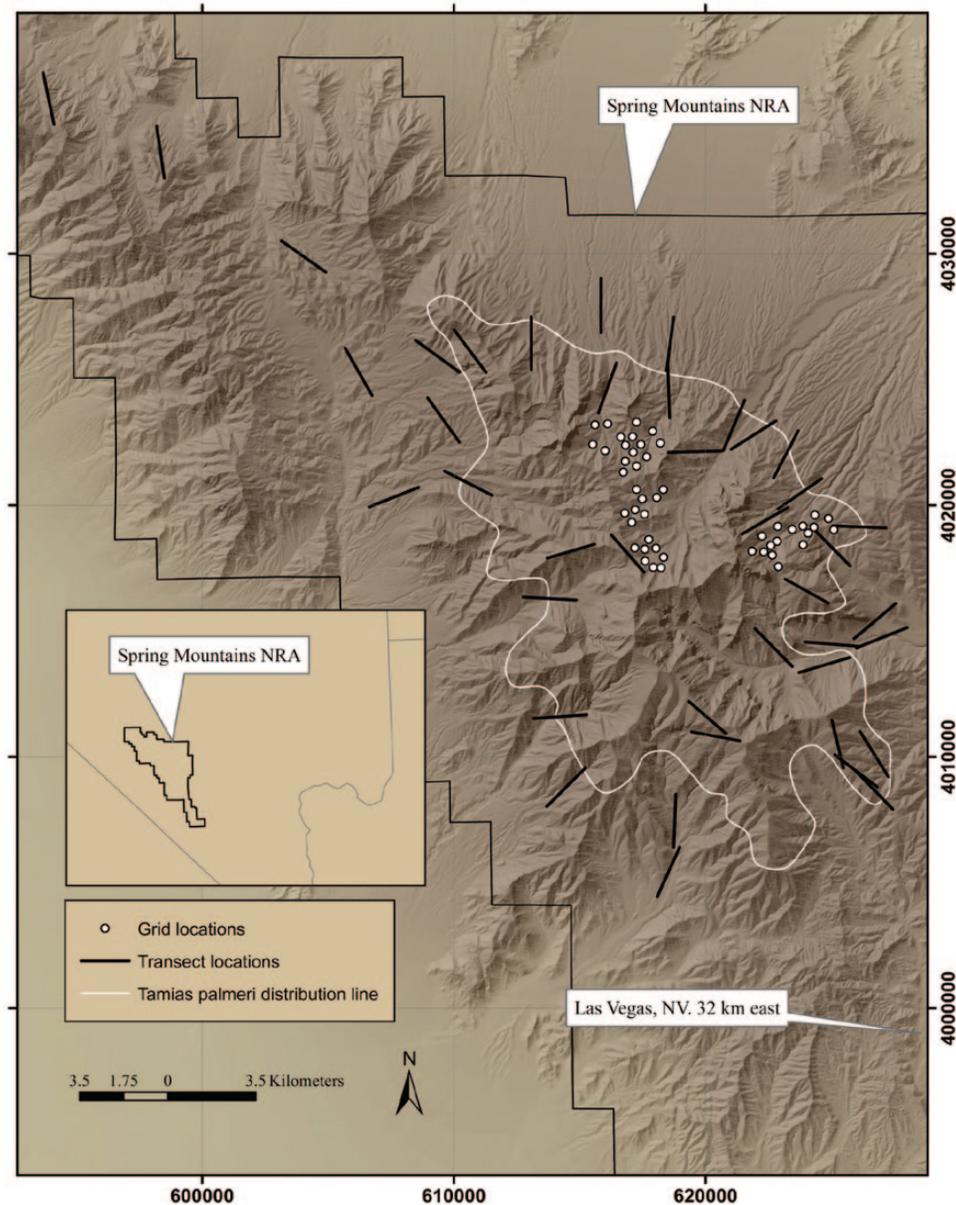
**Home range-scale habitat relationships.**—AIC model selection determined 3 closely related models ( $\Delta < 2$ ) best explained variability in *T. palmeri* apparent survival. Population density and the PC of overstory tree canopy cover comprised the highest ranked model (Tables 4 and 7). Specifically, survival increased with increasing population density ( $\beta = 0.042$ ,  $SD = 0.014$ ), decreasing overstory tree canopy cover ( $\beta = -0.049$ ,  $SD = 0.15$ ), and decreasing understory tree density ( $\beta = -0.018$ ,  $SD = 0.015$ ). We found no difference in overall survival rates between months ( $F_{2,45} = 1.26$ ,  $P = 0.29$ ) or between years ( $F_{1,46} = 1.27$ ,  $P = 0.27$ ), which would indicate an effect of temperature or other factors within the study period. Mean apparent survival rates across all 48 trapping grids were 0.848 ( $SD = 0.106$ , range 0.601–1.0). Estimates of population density had a mean of 4.05 animals per hectare ( $SD = 2.26$ , range 0.89–9.42).

**Geographic-scale modeling.**—The RSF model predicted increasing probability of occurrence on relatively gradual slopes, well within the white fir–upper Ponderosa pine community. Nearness to water sources was an important component, however, *T. palmeri* were more likely to occur within the xeric than mesic tree cover-type areas (Fig. 2). The specific model was relative probability of *T. palmeri* occurrence =  $(-0.034 * \text{percentage slope}) + (-0.001 * \text{distance to water sources [m]}) + (1.035 * \text{White fir–Bristlecone forest}) + (1.078 * \text{xeric Ponderosa forest}) + (0.626 * \text{mesic White fir–Ponderosa})$ .

## DISCUSSION

Our study predicted that at the geographic scale, the distribution of *T. palmeri* is constrained to occur on lower slopes, near water sources, and within conifer forests above 2,400 m. Although *T. palmeri* occurs within these broadly defined habitats, this species was more commonly found within the White fir/bristlecone communities and the more xeric Ponderosa forests, which occur, in general, above 2,600 and below 2,900 m (Fig. 2). More specifically within these parameters, our results suggested that survival at the home range scale increased in mixed-age forests (decreasing canopy cover and understory tree density) and with increasing population density. We infer 2 potential mechanisms for this habitat selection: 1) physiological constraints in terms of maintaining body temperature, and 2) behavioral constraints in terms of food handling efficiency and/or predation risk.

*Tamias palmeri* has a narrow thermoneutral zone of 32–34°C, and onset of hyperthermia above this zone may constrain the species to higher elevations (Heller 1971; Best 1994). High temperatures may force *T. palmeri* to seek shelter during daylight hours, decreasing time available to forage at lower relative to the upper/cooler elevations (Yunger et al. 2002). Conversely, heavy snows can remain on northern-facing, mesic forests well into the short active season (Lowrey 2002), thus diminishing both breeding and foraging opportunities. This may partly explain the greater occurrence of *T. palmeri* within the xeric areas versus the mesic areas of the range (Fig. 2).



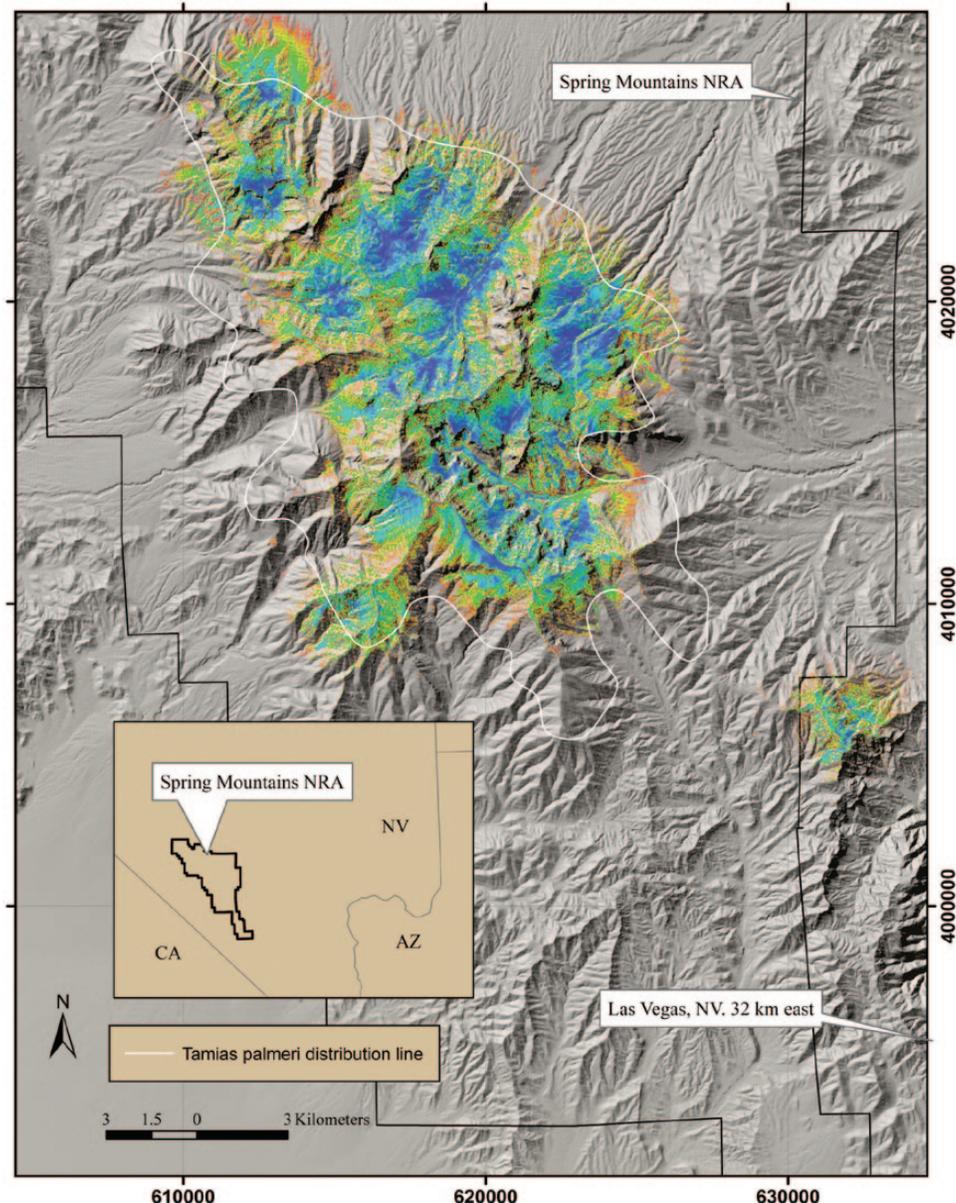
**Fig. 1.**—Distribution extent, trapping grid locations, and trapping transects of *Tamias palmeri* within the Spring Mountains, Nevada, 2010.

**Table 7.**—Home range-scale habitat variable weightings from AIC analyses.

Habitat variable	AIC <sub>c</sub> Weight
PC overstory cover	0.994
Population density	0.996
PC understory density	0.389
Large rock density	0.149
<i>Ribes spp.</i> density	0.117
Slope (%)	0.079
Distance to water	0.011
Aspect	0.008
Downed log density	0.001

Survival increased within the mixed-age forest, as overstory tree canopy cover decreased and, to a lesser extent, understory tree density decreased (Table 7). This pattern suggests

disadvantages in using relatively mature forests, which present challenges for small herbivores in terms of foraging efficiency and predation risks. Fir and ponderosa trees, which dominate much of this landscape, can reach 20–25 m in height. A mature forest requires chipmunks to scale these heights repeatedly to obtain food, resulting in relatively higher energy expenditures. Mature forests in this range have open understories and significant distances between trees, a pattern that may result in increased exposure to predation relative to dense forests as animals move across open ground (Lagos et al. 1995; Diaz et al. 2005; Creel and Christianson 2008). Alternatively, open ground (relative to heavy understory) may increase foraging efficiency by decreasing travel time. The data strongly suggest a survival advantage to use a mixed-age forest, risking greater exposure to predation to both increase foraging efficiency and limit energy expenditures. Home range habitat model selection indicated



**Fig. 2.**—*Tamias palmeri* relative probability of occurrence model. Cool colors (blue–green) are higher relative probability areas, warm colors (yellow–red) are lower probability. Spring Mountains, Nevada, 2010.

that as opposed to the biotic factors just described, abiotic factors did not contribute measurably (either positively or negatively) in our analyses of survival. This result, and the fact that at least some animals were captured within each trapping grid, may indicate the ability of the species to exist locally in conditions which on a geographic scale would appear detrimental to occurrence. For example, animals were found, albeit uncommonly, in grids with very steep terrain or areas of dense understory. However, whether these subpopulations represent those in a sink environment is unknown.

We found increasing survival strongly dependent upon increasing population density. *T. palmeri* have been observed foraging in groups, associated with sentry activity, where 1 chipmunk stops foraging and observes potential threats, while the rest of the group feeds (Lowrey, pers. obs.). Sentry

behavior and warning calls (chirp calls, trills) may contribute to greater survival under higher *T. palmeri* population densities by increasing detection of predators through increased vigilance (Carey and Moore 1986; Gannon and Stanley 1991). Greater population size may therefore diminish risk of exposure inherent in foraging across open ground, increasing survival. An alternative to this hypothesis is the assumption that greater population size is simply an indicator of higher quality habitat, which in itself would lead to greater survival rates.

Although *T. palmeri* was occasionally found in areas remote from permanent water (often occurring as wet ground or seeps), our findings indicate reduced probability of occurrence at the geographic scale as distance to water increases. It has been demonstrated that a lack of water sources may limit the reproductive success of *Tamias* species (Heller and Poulson 1970;

Hirshfeld 1975). Hirshfeld (1975) found that lactating females and juveniles consumed more water than other *T. palmeri*, indicating the importance of water for reproduction. The ability to dissipate heat through rolling and squatting behaviors in these wet areas may also be an important adaptation to an animal with a narrow thermoneutral zone (Heller and Poulson 1970). *T. palmeri* has been observed drinking, rolling in, and defending wet areas from conspecifics (Lowrey, pers. obs.), and the presence of water may allow increased foraging times for animals with access to it. The presence of water in the soil has also been shown to increase the ability of chipmunks to detect pine seed, thus increasing foraging efficiency (Vander Wall 1995, 1998).

Probability of occurrence increased with decreasing slopes or steepness of grade. We infer that lower slopes provide greater resources to *T. palmeri* in the form of increasing shrub availability and increasing soil depth. Greater shrub cover has been associated with lower slopes within the Spring Mountain range (Lowrey 2002). Although shrub cover was not statistically a highly ranked variable, *T. palmeri* have consistently been observed foraging, defending, and storing the berries of the shrub *Ribes cereum* in the fall months just before hibernation (Lowrey, pers. obs.). Increasing soil depth has been determined to increase overwinter survival for other burrowing forest chipmunk species such as *T. quadrivittatus*, *T. umbrinus*, and *T. minimus* (Bergstrom and Hoffman 1991). Kawamichi (1996) demonstrated in *T. sibiricus* that juveniles selected hibernation burrows only after adults had selected theirs, suggesting that burrow availability may be a limiting factor to overwinter survival. Soil depth is determined largely by slope, and areas with lower slope may therefore allow *T. palmeri* to more easily find or establish burrow sites.

*Contribution of abiotic and biotic factors and future research.*—Incorporating both abiotic and biotic factors improved our knowledge of how the environment affected *T. palmeri* probability of occurrence and distribution (Martin 2001; Guisan et al. 2006; Gonzales-Salazar et al. 2013). Specifically, tree cover type was a strong predictor and interacted with both slope and distance to water, evidence that small mammals change their use of biotic resources as abiotic resources change and vice versa in the Spring Mountain range (Kelt et al. 2004). Additionally, the use of abiotic–biotic interactions increased the predictive ability of occurrence models compared to previous work (Lowrey 2002) by measuring the rate of change in occurrence as slope and/or distance to water changed. At the home range scale, the greater strength of models that included interactions between biotic and abiotic factors suggests a potentially beneficial approach to predict how some species may alter their use of resources under changing conditions. For example, mammals restricted on islands, in patches, or otherwise isolated may be able to adapt to different habitat types (i.e., xeric tree cover) if other conditions (i.e., lower slopes, nearness to water) are maintained. Our research provides evidence these kinds of questions on adaptability, which are relevant to occurrence, survival, and extinction of species in isolated systems, are best addressed by measuring at multiple scales, and should inform conservation planning.

Our determination of the distribution and probability of occurrence across the entire range of *T. palmeri* permits increasingly specific predictions to be evaluated, such as whether areas predicted as high quality comprise source populations, and if dispersal from source populations sustains populations in less productive areas (Sharp et al. 2009). Our probability model is by no means perfect, and appears to deteriorate along the southern edge of the range where chipmunks were found beyond where the model predicted. We recommend directly measuring reproductive rates in areas predicted at different levels of habitat quality to better understand potential source–sink, patch, and distribution dynamics (Kanda et al. 2009; Furrer and Pasinelli 2015). Additionally, focusing this research on the leading edges of White fir/Ponderosa forest types could ascertain potential impacts of climate change across sky island habitats of the Basin and Range region.

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