



Niche conservatism versus niche differentiation in sympatric chipmunks in the northern Sierra Nevada

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Closely related species are predicted to have similar fundamental niches, and therefore to compete locally and possibly be constrained to occur allopatrically. Over time, niche differentiation should lead to divergent use of niche axes, such as food or habitat. Most studies of niche divergence or of niche conservatism have focused on multiple species at large spatial scales. We studied two species of closely related chipmunks at two spatial scales in the northern Sierra Nevada. The Long-eared Chipmunk (*Tamias quadrimaculatus*) and the Shadow Chipmunk (*T. senex*) are subcryptic species that exhibit extensive geographic overlap in the northern and central Sierra Nevada. Habitat use at the macrohabitat scale was similar, with both species reaching their highest mean abundance in Red Fir (*Abies magnifica*) forests, but exhibiting divergent secondary affinities. Additionally, macrohabitat associations of *T. senex* appear to differ from those reported 50 years ago within the same forest, suggesting flexibility in the face of structural habitat changes resulting from forest management actions, climate change, or other factors. At a finer spatial scale, habitat affinities of these chipmunks differed modestly, suggesting that local distribution emphasizes slightly different microhabitat characteristics. We conclude that these species exhibit niche conservatism overall, but whether microhabitat differences reflect competition or niche divergence requires further study. Because *T. quadrimaculatus* has the smallest geographic range of any Sierra Nevada sciurid, it may be at risk of local extirpation or substantial range restriction in the face of climate change, large-scale high-severity wildfires, and other stochastic threats; the present research sheds light on the ecology of these species, but has important relevance for regional resource managers as well.

Key words: California, chipmunks, habitat associations, niche conservatism, niche partitioning, Sierra Nevada, spatial scale, species coexistence, *Tamias quadrimaculatus*, *Tamias senex*

Niche partitioning by co-occurring, ecologically similar species remains a potent theme in community ecology, and nearly 75 years of research has been devoted to understanding the patterns and processes of species coexistence (Chase and Leibold 2003). Whereas some authors have questioned the utility of niche-based explanations as applied to entire communities (Bell 2000, 2001; Hubbell 2001), it remains a very useful framework for understanding the coexistence of species (Chase and Leibold 2003).

Differential use of habitat is an important form of niche segregation, as habitat is one of the most important dimensions of the niche of an organism (Schoener 1974). Manifestation of habitat partitioning among closely related species may be constrained by niche conservatism, the tendency for species to retain similar niches over evolutionary time (Peterson et al. 1999; Wiens and Graham 2005). Because closely related species generally retain similar niche parameters, they should compete strongly, and so should co-occur less frequently than

expected by chance (da Silva et al. 2020), which may explain why most studies of niche conservatism in closely related species have emphasized allopatric conditions (Losos et al. 2003). Most authors have applied very broad-scale data, frequently employing niche modeling to infer niche space, and hence overlap (Olalla-Tarraga et al. 2017; Sales et al. 2017; Garcia-Navas and Westerman 2018). The paucity of studies assessing niche characteristics among closely related species under sympatric conditions leaves ambiguous the question of whether convergent or divergent forces dominate in ecological or evolutionary assembly of communities (Losos et al. 2003).

The spatial and phylogenetic scale of study may greatly influence interpretations of community assemblage (Cavender-Bares et al. 2006; Swenson et al. 2006). Thus, while studies at large ecological (Peterson et al. 1999; Kozak and Wiens 2006) or phylogenetic scales (Slingsby and Verboom 2006) have found positive evidence for niche conservatism, work at finer taxonomic resolution has demonstrated niche divergence (Losos et al. 2003; Cavender-Bares et al. 2004, 2006; Slingsby and Verboom 2006; Swenson et al. 2006), suggesting that niche divergence may be more common or more tractable at finer spatial scales (Losos et al. 2003; Cavender-Bares et al. 2004, 2006; Swenson et al. 2006). For co-occurring and ecologically similar small mammal species, however, niche partitioning studies do not show a clear spatial trend. Whereas microhabitat partitioning has often been implicated in species coexistence (Price 1978; van Snik Gray and Stauffer 1999; Jorgensen 2004; Kelt 2011), many studies have reported that macrohabitat descriptors (e.g., 'forest type') provide better predictors of abundance and distribution than do microhabitat characteristics (Morris 1984, 1987; Jorgensen and Demarais 1999). Consequently, studies at single spatial scales risk misinterpreting potentially important associations (Sherry and Holmes 1985; Wiens et al. 1986; Bissonette et al. 1997; Kelt et al. 1999; Avila-Flores et al. 2002). To counter such biases a number of researchers have suggested a nested, multiscale approach (Morris 1984; Maurer 1985; Wiens et al. 1987; Kelt et al. 1994, 1999).

Chipmunks of western North America (*Tamias*, subgenus *Neotamias*) appear well suited to such efforts. This lineage comprises a fairly recent and rapid radiation (Reid et al. 2012; Sullivan et al. 2014), one consequence of which is that most species have similar fundamental niches and therefore do not coexist readily with congeners. This results in a number of examples of very limited overlap among parapatric species across ecological gradients (summarized by Sullivan et al. 2014:186). Often, one member of these species pairs is a narrowly distributed habitat specialist, while the other is more widely distributed and more of generalist (Sullivan et al. 2014).

In the northern Sierra Nevada (Western United States), the geographic range of the Shadow Chipmunk (*T. senex*) almost completely encompasses that of the closely related Long-eared Chipmunk (*T. quadrimaculatus*; Johnson 1943; Sutton 1995), hinting at conservative niches at this scale. Indeed, both species occur in mid- to high-elevation coniferous forests of the Sierra Nevada (Ingles 1965; Jameson and Peeters 2004; Fig. 1), where they exhibit mixed evidence of habitat partitioning. *Tamias*

quadrimaculatus, though generally uncommon, has been associated with logged areas and habitats with open or partly open canopies and brushy understories, such as chaparral, mixed-conifer, Douglas-fir, and Ponderosa Pine forest types (Tevis 1955; Sharples 1983; Clawson et al. 1994). In contrast, *T. senex* in northeastern California (outside the range of *T. quadrimaculatus*) has been reported to be most common in dense, moist forests with closed canopies and lacking a large proportion of understory vegetation (Tevis 1955; Sharples 1983; Gannon and Forbes 1995), although populations in coastal habitat have responded positively to logging practices that open the forest canopy and increase understory vegetation (Tevis 1956). Whereas Grinnell and Storer (1924) reported elevational segregation by these species in the central Sierra Nevada, they also noted that they were very similar in habits and habitat preferences; Sutton (1995:848) also noted "similar ecological requirements" but that these species "often are collected in the same locality." Given its larger geographic range and broader regional environmental tolerances of *T. senex*, we expected this species to be more of an ecological generalist than is *T. quadrimaculatus* (Brown 1984, 1995), and we expected it to occur in a broader array of habitat conditions in our study area. Moreover, we expected these species to segregate by habitat, with *T. quadrimaculatus* in more open forests and *T. senex* in forests with more closed canopies.

We asked three questions of ecological interest. First and most fundamentally, what are the habitat characteristics associated with *T. quadrimaculatus* and *T. senex*? As these species appear quite similar at the largest scale of geographic ranges (at least within the Sierra Nevada), we focus this question at the subordinate spatial scales of macrohabitat (e.g., forest type) and microhabitat (e.g., trap stations). Second, do these species exhibit niche divergence by partitioning habitat at either of these scales and, if so, how? Third, at which spatial scale(s) (if any) do these species diverge in habitat use? If divergent forces have prevailed over convergent drivers in these taxa, then they should exhibit increasingly distinct niche parameters (here defined by microhabitat use) at finer spatial scales. In addition to providing insight to the nature of local and regional coexistence in ecologically similar species, these results are essential to resource managers in effectively preserving the unique and rich biodiversity of the Sierra Nevada, including endemic and range-restricted species such as *T. quadrimaculatus*.

MATERIALS AND METHODS

Study area.—We conducted field studies on small mammals in the Plumas National Forest (PNF), located in the northern Sierra Nevada of California. The PNF ranges from about 280 to 2,550 m in elevation, straddles the crest of the Sierra Nevada, and supports relatively mesic habitats on the western slopes as well as more xeric forests on the eastern slopes. We define forest types by the dominant live tree species representing $\geq 70\%$ of total tree composition; these include White Fir (*Abies concolor*), Red Fir (*A. magnifica*), mixed-fir (co-dominant mix of White Fir and Douglas-fir, *Pseudotsuga menziesii*), pine-cedar

(co-dominant mix of Ponderosa and Jeffrey Pine [*Pinus ponderosa* and *P. jeffreyi*] and Incense Cedar [*Calocedrus decurrens*]), and mixed-conifer (co-dominant mix of fir and pine). Overall, the PNF is dominated by *A. concolor* and *P. menziesii* so these forest types received proportionally greater sampling effort in our study (see below). Study sites ranged from 1,180 to 2,250 m elevation. Mean annual precipitation from 1997 through 2003 was 975.5 mm, and mean temperatures ranged from 2.8°C (range of means: −9.3 to 13.2°) in January to 20.6°C (range of means: 3.3 to 38.5°) in July (NOAA—National Climatic Data Center 1997–2003).

Focal species.—The Shadow Chipmunk (*T. senex*) occurs in the Cascade and Sierra Nevada ranges from northern Oregon south to the region of Yosemite National Park, and from the Klamath Mountains in northern California east to the Warner Mountains (Gannon and Forbes 1995). *Tamias senex* was long treated as a subspecies of *T. townsendii*, but the latter taxon is now recognized as four distinct species (Gannon and Forbes 1995). The sister taxon to the rest of the *townsendii* species group is the Long-eared Chipmunk (*T. quadrimaculatus*; Reid et al. 2012; Herrera et al. 2022). Restricted to the Sierra Nevada, the geographic range of *T. quadrimaculatus* is almost completely overlapped by that of *T. senex* (ca. 80% overlap; Hall 1981; Best et al. 1994; Gannon and Forbes 1995; Sutton 1995). The latter species has been reported at elevations from 960–2,250 m and the former above 1,500 m (Clawson et al. 1994; Gannon and Forbes 1995). However, these species overlap in all external characters (although bacula are distinct; White 1953; Sutton and Nadler 1974), such that differentiation is very challenging in the field (Ingles 1965; Sutton 1995; Jameson and Peeters 2004). Aggravating this, these species are known to hybridize (Frare et al. 2017); to address this we confirmed all identifications using DNA analysis (see below). It is worth noting that our study area (Fig. 1) lies near the northern edge of the range of *T. quadrimaculatus*.

Spatial scales studied.—Given that the extensive spatial overlap in ranges of these species in the Sierra Nevada hints at conservatism in niche space, we surveyed chipmunks and measured habitat characteristics at two subordinate spatial scales, based on trapping data from a multiyear research program on small mammal dynamics in the PNF. The larger spatial scale (macrohabitat) refers to 18 live-trapping grids (described below) grouped according to forest type ($n = 3\text{--}5$ grids per forest type). The finer (microhabitat) scale was extracted from trapping data and 18 habitat metrics recorded at individual trap stations ($n = 120$ trap stations per trapping grid).

Small mammal sampling.—In the summer and fall of 2003 and 2004, we censused small mammals at 18 long-term sampling grids in five primary forest types of the PNF; reflecting the relative distribution of forest types in the region, we placed five grids in mixed-fir forest, four in White Fir forest, and three each in mixed-conifer, pine-cedar, and Red Fir. Seventeen grids consisted of a 6×6 array with 72 Tomahawk live traps (one ground trap and one arboreal trap; Model 201, $40.6 \times 12.7 \times 12.7$ cm, Tomahawk Live Trap, Tomahawk, Wisconsin) with 30-m trap spacing (3.24 ha including a buffer of $\frac{1}{2}$ intertrap distance). Within this grid we established a 10×10 array of

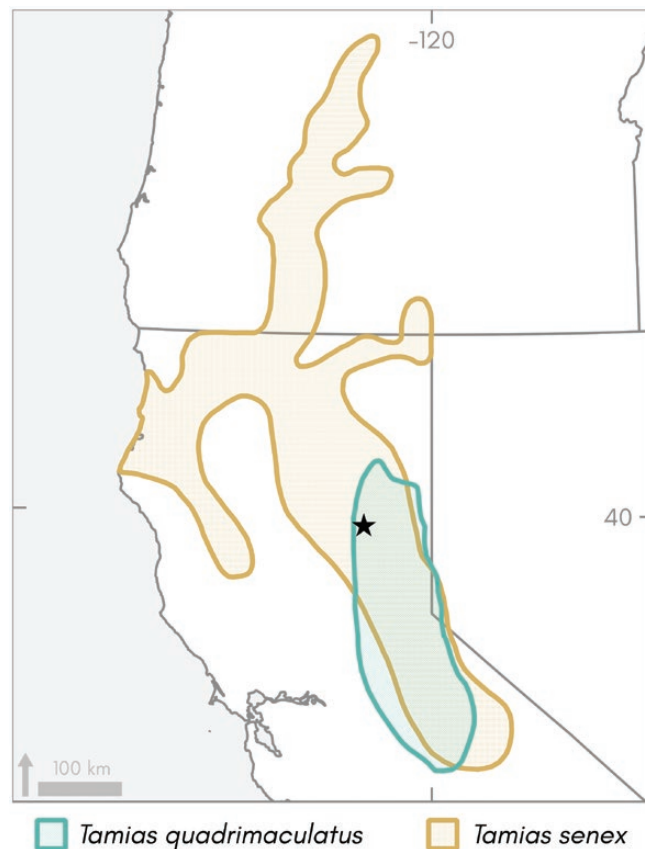


Fig. 1.—Geographic ranges of *Tamias quadrimaculatus* and *T. senex*. Our research was based near the town of Quincy, which is indicated by a star. Map modified from Sutton (1995); cartography by Michele M. Tobias, UC Davis DataLab.

Sherman live traps (100 traps; Model XLK, $7.6 \times 9.5 \times 30.5$ cm, H. B. Sherman Traps, Inc., Tallahassee, Florida) with 10-m trap spacing (1.00 ha assuming a buffer of $\frac{1}{2}$ intertrap distance). Our final grid was constrained by road configuration, but consisted of a 4×9 array of Tomahawk trap stations with 30-m spacing (3.24 ha), within which we placed a standard 10×10 array of Sherman traps. Thus, all grids had 120 trap stations and supported 172 traps. We removed all arboreal Tomahawk traps in August 2004 because of consistently poor capture rates. Minimum distance among trapping grids was 1 km with the exception of two Red Fir grids that were approximately 700 m apart. We did not document any small mammal movement between trapping grids.

Field crews sampled trapping grids monthly for four consecutive nights from July through October 2003, and from May through October 2004. Traps were set and baited every evening just before dusk and checked just after dawn. Sherman traps were then closed until dusk, whereas Tomahawk traps were rebaited and checked again at midday, at which point they were closed until dusk. Traps were baited with rolled oats and black oil sunflower seeds coated with peanut butter. Coverboards and synthetic bedding were provided as needed for protection from heat and cold. Inclement weather precluded sampling on all Red Fir grids in May 2004, and unanticipated problems

precluded sampling on 12 grids in July 2004. To equalize sampling efforts, we present data from July, August, September, and October 2003, and from June, August, September, and October 2004. All field methods were approved by the University of California Institutional Animal Care and Use Committee and conform with guidelines published by the American Society of Mammalogists (ASM ACUC 1998; Sikes et al. 2016).

All animals were provisionally identified in the field using pelage characteristics (Ingles 1965; Jameson and Peeters 2004), but because *T. quadrimaculatus* and *T. senex* are not reliably distinguished in the field using external morphological characters (Sutton 1995; Frare et al. 2017), we confirmed identification with DNA analysis. We collected tissue samples from the ears (hole punches) of all *Tamias* individuals after weighing, sexing, determining reproductive status, and ear tagging (National Band and Tag, Salt Lake City, Utah). Whole genomic DNA was extracted from >600 ear clips using Qiagen DNeasy kits (Qiagen, Valencia, California) following manufacturer's instructions. Approximately 800 bp of the 5' end of mitochondrial gene cytochrome b (*Cytb*) were amplified by polymerase chain reaction (PCR); reagent volumes, thermal profiles, and *Tamias*-specific primers were used following Demboski and Sullivan (2003). Amplicons were purified using Qiagen Qiaquick PCR purification kits and cycle sequencing reactions performed using a BigDye kit (Applied Biosystems, Inc.). Sequencing reactions were purified using 5% G-50 Sephadex in Centri-sep spin columns (Princeton Separations, Adelphia, New Jersey) and analyzed on an ABI 3130 automated sequencer (Applied Biosystems, Inc.). Sequences were aligned (using Sequencher 4.0) with all published *Tamias* mitochondrial *Cytb* gene sequences (Good and Sullivan 2001; Piaggio and Spicer 2001; Demboski and Sullivan 2003) as well as numerous unpublished sequences collected by J. L. Patton as part of ongoing research; unpublished sequences were collected from individuals for which bacular morphology had been used to verify field identifications (Patton J. L., University of California Berkeley, Berkeley, California, personal communication). We identified 16 unique haplotypes for *T. quadrimaculatus* and 33 unique haplotypes for *T. senex*. Sequences for these species differ from 6–7% uncorrected sequence divergence, while the maximum divergence within a species was 0.9%, so sequences can be unambiguously attributed to one species or the other. A neighbor-joining tree was constructed on maximum likelihood distances. Distances were estimated under the HKY+ Γ model, which was selected using DT-ModSel (Betancourt and Saavedra 2002; Minin et al. 2003; Abdo et al. 2005). This approximate phylogeny estimate is sufficient for assigning mitochondrial DNA (mtDNA) haplotypes to species.

Given that these species may hybridize (Frare et al. 2017), and mtDNA may introgress across species boundaries in other species of *Tamias* (Good and Sullivan 2001; Good et al. 2003; Sullivan et al. 2014), we chose a subset of 28 individuals, some of whose field IDs based on pelage characteristics conflicted with mtDNA, and we sequenced intron 7 and part of exon 8 (700 bp) of the nuclear gene beta-fibrinogen (*β -fib*) using the same protocols as above, but with primers used by Matocq et al. (2007). For heterozygous individuals, gametic phase was

determined using PHASE (Stephens and Donnelly 2003). All haplotypes were assigned unambiguously ($P > 0.95$). Two unique *β -fib* haplotypes were identified for *T. quadrimaculatus* and two for *T. senex*. The *β -fib* and *Cytb* trees were completely congruent with respect to assignment of individuals to species (the purpose of the analysis), indicating that mtDNA introgression between these species in our study area is unlikely and confirming the species identifications derived using *Cytb*. Note that this analysis was not intended as an assessment of introgression between these taxa, but as an evaluation of whether or not the discrepancy between mtDNA and field assignment was attributable to mtDNA introgression in these specific individuals, versus incorrect field identification. Sequences were uploaded to GenBank under accession numbers: *Cytb*, OQ748876 - OQ749356; *β -fib*, OQ749357 - OQ749382.

Vegetation sampling.—As noted above, we defined five macrohabitats (forest types)—White Fir, Red Fir, mixed-fir, mixed-conifer, and pine-cedar—based on dominant tree species. We quantified the composition of adult tree species (diameter at breast height ≥ 10 cm) at each trapping grid in July and August 2003 using point-centered quarter sampling (Mueller-Dombois and Ellenberg 1974) at 18 stratified Tomahawk trap stations. We used mean values across trapping grids to represent parameters at the macrohabitat (forest type) scale. Four of these forest types occurred at similar elevations; Red Fir forests were consistently at higher elevations than other forest types (Fig. 2A).

At the microhabitat scale we recorded 18 habitat metrics within a 1-m radius circular plot (3.14 m²) centered at every trap station. All microhabitat characteristics were recorded by S. A. Coppeto during July–August 2003. We visually estimated percent cover (in 5% increments, plus a 'trace' category for items $<< 5\%$ cover) of 12 ground cover variables: rocks, bare ground, forbs + grasses, litter, branches (dia. >10 cm), both small (dia. 10–50 cm) and large logs (dia. >50 cm), live shrubs, dead shrubs, vegetation mats (*Ceanothus prostratus*), saplings, and nonwoody perennials (shrub- and forb-like vegetation lacking woody stems). We tallied the number of species of both live shrubs and saplings at each trap station. We measured tree canopy openness at every trap station by taking a single, color digital photograph with a hemispherical lens mounted 1.4 m above ground. We calculated percent canopy openness (the proportion of horizon to horizon view that was open sky) using Gap Light Analyzer v. 2 (Frazer et al. 2000). Aspect was measured with a compass by estimating the direction that water would flow from the center of a trap station; these were converted to North–South (e.g., -90° to $+90^\circ$) and West–East (-90° to $+90^\circ$) components (hence, positive values were associated with southern and eastern exposure, respectively). Slope was measured with a clinometer as the general decline of the substrate within each circular plot. Substrate (ground) hardness represents a mean of four measurements (one per quadrant) within each circular plot and was measured using a soil penetrometer (Pocket penetrometer, Geotest Instrument Corp., Evanston, Illinois) after removing the surface duff layer composed of litter, downed wood, and rocks. In July 2004, we resampled microhabitat vegetation (excluding canopy) at 30 stations (25%) in six randomly

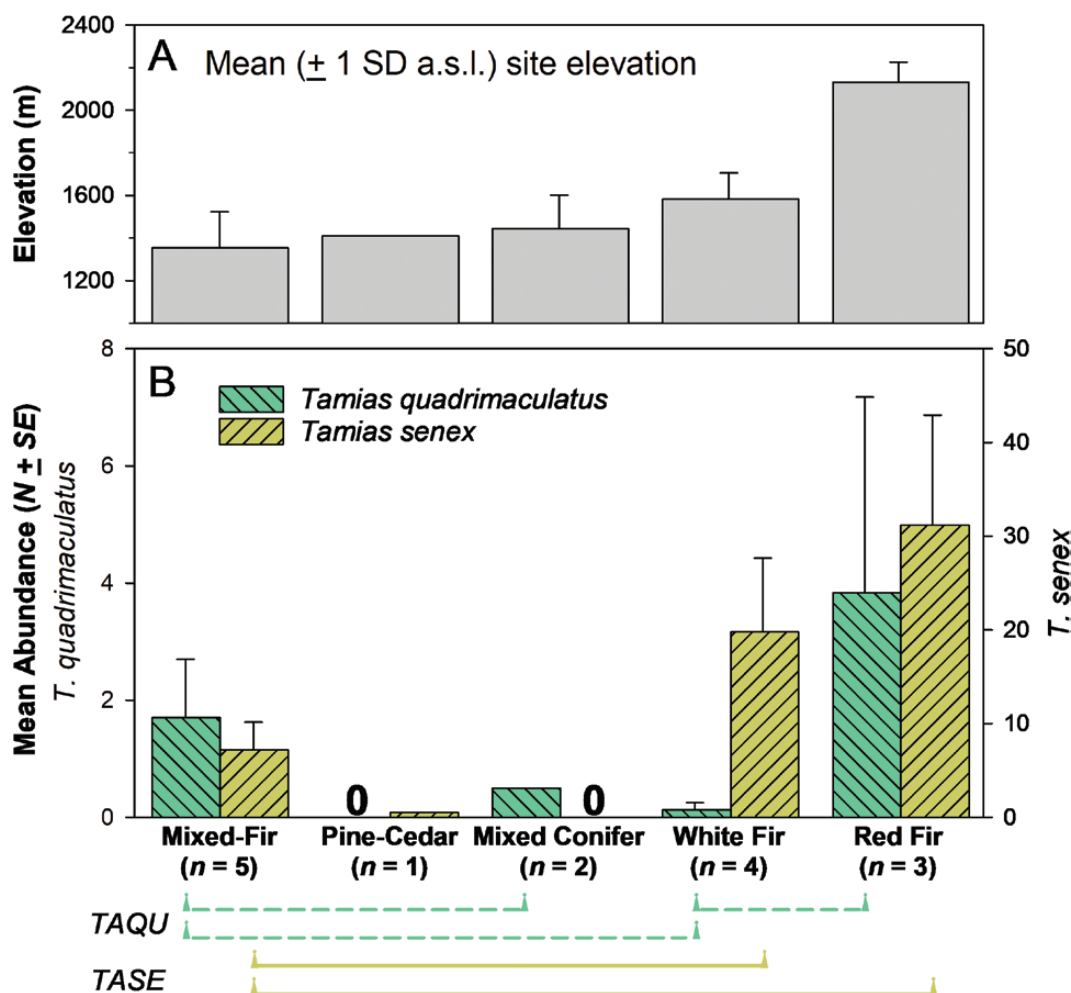


Fig. 2.—(A) Mean (\pm SD) elevation (a.s.l. = above sea level) of forest types sampled in the Plumas National Forest, California, and (B) mean (\pm SE) abundance of long-eared (*Tamias quadrimaculatus*) and shadow (*T. senex*) chipmunks in each forest type. Horizontal lines and arrows indicate forest pairs for which SE do not overlap.

chosen grids representing all forest types. Paired *t*-tests documented no change in these metrics between years, indicating that these parameters were relatively invariant, at least within the time span under consideration. Therefore, we applied the measurements recorded in 2003 for analysis of small mammal habitat associations in both 2003 and 2004.

Analyses.—At the macrohabitat scale we quantified abundance of both chipmunk species as the mean number of unique individuals captured within forest types. Limited captures precluded use of more robust estimates of population size (e.g., maximum likelihood estimators in Program MARK). At both spatial scales, we include data from only the 15 trapping grids that yielded at least one *Tamias* individual, and repeat captures of individuals at grids and trap stations were not included in macro- and microhabitat analyses, respectively. Because our data included large numbers of zeros (e.g., trap stations where chipmunks were not captured), we applied nonparametric univariate and multivariate analyses to examine differences in species abundance between years and among forest types. A two-tailed Wilcoxon signed-rank test documented no significant differences in abundance of these species between sample

years ($n = 15$ grids; *T. quadrimaculatus*: $Z = -0.62$, $0.54 > P > 0.27$; *T. senex*: $Z = -0.67$, $0.5 > P > 0.25$), so we applied a Kruskal–Wallis test to evaluate differences in mean abundance of each species among forest types. All analyses were conducted using SAS v 9.4 (SAS Institute Inc. 2012).

At the microhabitat scale, we quantified preferences for all measured parameters by calculating differential use of sites with select microhabitat characteristics, relative to the availability of these characteristics across all trap sites. We determined the statistical significance of these values by bootstrapping the original data to develop a distribution of expected values as well as 95% confidence intervals (CIs). We conducted two bootstrap efforts for each species, resampling n sites 10,000 times in each case, where n is the number of sampling stations where the focal species was captured (for *T. quadrimaculatus*, $n = 73$; for *T. senex*, $n = 372$). In the first pair of bootstraps, we resampled n sites (with replacement) from the entire distribution of sites, producing a mean and 95% CI for the availability of each microhabitat feature. In the second set of bootstraps, we resampled n sites (with replacement) from the subset of sites where each species was captured, thereby producing mean

and 95% CI for comparing the two species. We inferred habitat selection if the 95% CI of bootstrapped estimates for use did not overlap the 95% CI of bootstrapped estimates for availability. We inferred that microhabitat use by the two species differed when 95% CI of bootstrapped values for use by one species did not overlap that of the other species. Bootstrap analyses were conducted in SAS 9.4 (SAS Institute Inc. 2012; Wicklin 2018). Because autocorrelation among habitat variables has the potential to inflate the number of apparently 'significant' associations, we evaluated correlations among all microhabitat variables. Only 3 of 153 pairs of variables exhibited correlation coefficients > 0.5 (Live shrub cover vs. Canopy openness, $r = 0.58$; Tree cover vs. No. sapling species, $r = 0.64$; Live shrub cover vs. No. shrub species, $r = 0.70$), suggesting that the risk of artificially inflating associations was low.

We then applied stepwise logistic regression (SLR) to presence/absence data pooled across sample years to describe the microhabitat characteristics associated with the likelihood of capturing *T. quadrimaculatus* and *T. senex*. The dependent variable in each model was presence/absence of a species. Independent variables representing 18 microhabitat metrics were entered into a model and retained if $P \leq 0.05$. We evaluated the fit of the models with Hosmer–Lemeshow tests, and we calculated the odds ratio and 95% CI for all significant variables retained in the final models. The odds ratio represents the change in the probability of capturing either species given a unit change in each independent variable, when all other independent variables in the model are held constant. The final models produced by stepwise selection were confirmed by conducting identical analyses with forward selection (in SAS, forward selection constrains development of more complex models to include all effects selected in less complex models; in stepwise selection, effects in simpler models may or may not be retained in more complex models). Logistic regression was conducted using Proc Logistic in SAS v 9.4 (SAS Institute Inc. 2012). A common “rule of thumb” with logistic regression is that the number of observations (events) required for a reliable result should be about 10 or more for each parameter estimated (e.g., Peduzzi et al. 1996). Whereas we captured more than enough *T. senex* to meet traditional events per variable (EPV) guidelines, this was not the case for *T. quadrimaculatus* (see Results). However, this so-called EPV guideline has been disputed recently, with van Smeden et al. (2016:1) concluding that “evidence supporting EPV rules for binary logistic regression is weak,” and van Smeden et al. (2018:2455) noting that “EPV does not have a strong relation with metrics of predictive performance, and is not an appropriate criterion for (binary) prediction model development studies.” In both papers they highlight the need for research on sample size criteria. Given these caveats, we apply SLR to our data as an exploratory approach, but we interpret these results cautiously.

We opted not to pursue a model selection framework (Burnham and Anderson 2002) because we did not feel comfortable developing competing a priori models to describe habitat use by these species. The risks associated with model development in the absence of sufficient ecological insight are

well-known, including the elevation of ecologically uninformative parameters (Arnold 2010). We hope that the present study will provide the foundation for further efforts that may employ defensible a priori models at multiple sites.

Finally, we reduced the dimensionality of our microhabitat data using principal components analysis (PCA, using a correlation matrix), and overlaid both chipmunk species in ordination space to evaluate similarity in habitat use by these species in ordination space. PCA is the most basic form of ordination and is an indirect, or unconstrained, form of ordination, involving reduction in dimensionality of a single data matrix (in this case a matrix of microhabitat traits) without consideration of any corresponding matrices (e.g., of chipmunk species). PCA assumes approximately linear relationships among variables, and may suffer when species response curves are unimodal. Our data included a large number of zeros (e.g., trapping sites where neither chipmunk species was captured), such that both species were effectively linearly arranged along environmental gradients. Although PCA is robust to modest deviations from normality, we screened our data for outliers with the “Outlier Analysis” tool in PC-Ord v. 7.09 (McCune and Mefford 2018); we calculated the Euclidean distances among all 1,800 sample sites, and then excluded 104 stations lying $> 2 SD$ from the mean. We compared the output from PCA with separate redundancy analysis, which is a direct (constrained) ordination suitable to data with underlying linear relationships (Legendre and Legendre 2012). These two approaches often provide complementary results; in our case, results were qualitatively very similar, so we present only the former analyses. A third approach, canonical correspondence analysis, is frequently applied to analyses of this type, but assumes a unimodal distribution of data, which was not the case here. All ordinations were conducted in PC-Ord v. 7.09 (McCune and Mefford 2018).

These three analyses—microhabitat selectivities, SLR, and PCA—make different assumptions and apply data differently; additionally, only the former of these evaluates differential use of habitat characteristics (e.g., preference or selection). Additionally, selectivities are analyzed separately for each microhabitat variable, whereas regression and PCA integrate all variables simultaneously. And whereas stepwise regression strives to discern the single 'best' variable to explain the distribution of chipmunk species (then the two best, three best, and so on), PCA simply ordines all habitat metrics, striving to reduce dimensionality, and small mammals are then superimposed on this 'ordination landscape.' Hence, each analysis is likely to produce different but complementary results, providing deeper insight to the environmental parameters that are associated with the distribution of these small mammals.

RESULTS

In 2003 we captured 247 unique chipmunks in 49,536 trap-nights of effort (28,800 Sherman and 20,736 Tomahawk). Of these, 20 individuals were identified using mtDNA as *T. quadrimaculatus* and 157 as *T. senex*. In 2004 we captured 330 chipmunks in 42,660 trap-nights of effort (28,800 Sherman, 13,860

Tomahawk); 17 individuals were identified using mtDNA as *T. quadrimaculatus* and 201 as *T. senex*. Forty-seven individuals (five *T. quadrimaculatus*, 42 *T. senex*) were captured in both years. An additional 182 animals (70 in 2003, 112 in 2004) were not identified genetically, due either to a lack of tissue sample, loss of a sample, or inconclusive results from genetic analyses. Analyses reported here pertain solely to genetically identified individuals.

Macrohabitat scale.—These two chipmunk species exhibit similar and overlapping patterns of habitat use at the macrohabitat scale (Fig. 2B). Both species achieved their highest mean abundance in Red Fir forest, the highest elevation forests, although they diverged otherwise, with *T. quadrimaculatus* exhibiting lower abundances in mixed-fir and mixed-conifer forests, and *T. senex* doing so in White Fir and then mixed-fir types; notably, both species were associated with fir-dominated ecosystems as opposed to those dominated by pine or cedar. Mean abundance (N) of *T. quadrimaculatus* did not vary significantly among forest types, although this may reflect limited power due to lower capture rates for this species. In contrast, *T. senex* varied significantly among forest types (Fig. 2B; $\chi^2 = 9.51$, d.f. = 4, $P < 0.05$), with similar abundances in the two preferred forest types (Red Fir and White Fir) but markedly lower

abundances in mixed-fir and pine-cedar (Fig. 2B). We captured no *T. quadrimaculatus* in pine-cedar forests, and no *T. senex* in mixed-conifer forests.

Microhabitat scale.—At the microhabitat scale, *T. quadrimaculatus* and *T. senex* both selected nonrandom subsets of multiple habitat characteristics, and differed notably from each other in their habitat associations (Fig. 3). Relative to available habitat (symbols vs. bars in Fig. 3), *T. quadrimaculatus* was captured at nonrandom microsities in terms of all but one metric recorded; they used dead shrubs in proportion to their availability on the landscape. Similarly, *T. senex* was captured at nonrandom microsities with respect to all parameters except aspect and cover by dead shrubs, large logs, and mat vegetation. Hence, relative to available microsities, both species were captured at sites with greater ground cover by rock, bare ground, forbs and grasses, litter, small logs, and both live shrubs and trees. They selected sites with firmer substrate, more shrub and tree species, more open forest canopy, and steeper slopes. Whereas *T. senex* did not appear to favor any particular aspect, *T. quadrimaculatus* was captured at sites with more western and northern exposure.

Relative to each other (symbols and error bars in Fig. 3), *T. quadrimaculatus* occurred at sites with more rock cover, less

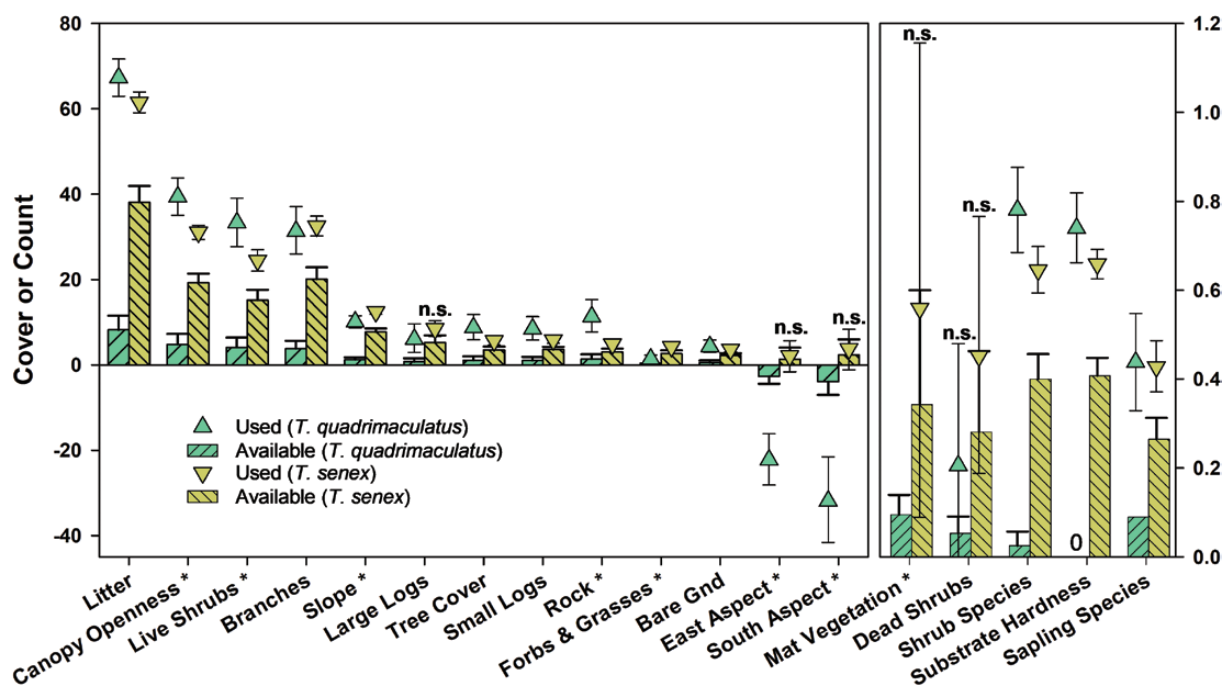


Fig. 3.—Use vs. availability of microhabitat metrics recorded at 1,800 trapping stations in the Plumas National Forest. Vertical bars (habitat availability) represent the mean and 95% confidence interval (5th and 95th percentiles) based on 10,000 bootstrap samples drawn with replacement from all stations in the five trapping grids that yielded both *Tamias quadrimaculatus* (light) and *T. senex* (dark). Light bars are based on 73 stations per bootstrap (reflecting the number of *T. quadrimaculatus* captured), while dark bars are based on 372 stations (reflecting the number of *T. senex* captured). Light and dark symbols (habitat use) and associated error bars provide the mean value of each habitat metric recorded at sites where these species were captured; in this case, error bars are based on 10,000 bootstrap samples (with replacement) from only those stations where each species was captured. Hence, each species may be considered to use habitat metrics nonrandomly if error bars associated with vertical bar charts and associated symbols do not overlap (we highlight the six instances of nonsignificance with 'n.s.' placed above the symbols in the figure). The two species may be considered to use habitat metrics differently if the error bars associated with paired symbols do not overlap (indicated with an asterisk following the x-axis tick label). To facilitate interpretation, note that the caps on habitat availability (vertical bars) error bars are wider than those for habitat use (symbols).

cover by forbs and grasses, more live shrubs, more open canopy, less mat vegetation, and more western and northern exposure, relative to sites where *T. senex* was captured. All other metrics were similarly favored by these species.

SLR reaffirmed many observations from differential habitat use (Table 1). Variables retained in the final model for *T. quadrimaculatus* indicated that this species was positively associated with sites characterized by open canopies, cover by rocks, and multiple sapling species, and negatively associated with east- or south-facing aspect; in contrast to selectivity analyses, regression suggested a negative association between the presence of this species and slope, although the coefficient was small (Table 1). *Tamias senex* also favored open canopies, but diverged from *T. quadrimaculatus* by preferring traps on south-facing slopes and with multiple shrub species, and aversion to traps covered by litter and 'ground-hugging' vegetation mats. The models correctly classified (i.e., high concordance) *T. quadrimaculatus* and *T. senex* presence at 77.3% and 74.4% of traps, respectively.

When microhabitat metrics were reduced through ordination, 8 of 18 resulting axes had eigenvalues >1.0, but only seven of these were significantly larger than expected (based on 999 randomizations of the data). A scree plot highlighted the clear dominance of the first axis, and a notable 'break' after the third axis; given inherent challenges in integrating across too many axes, we emphasize the first three axes here (Table 2; Fig. 4). Although this ordination was based solely on microhabitat measurements, both chipmunk species associated most strongly with the first PC axis and, in general, they share similar orientation in ordination space, with relatively acute angles separating their respective vectors in all biplots (Fig. 4). Both species generally favored sites with high canopy openness, cover by live shrubs and rocks, and numerous shrub species, and few branches (PC1). These chipmunks diverged modestly on the second and third PC axes. On the former, *T. senex* favored sites with east and south aspect, whereas *T. quadrimaculatus* tended to favor sites with more shrub cover, mat vegetation, and perhaps steeper slopes. Finally, PC3 suggested that both species favored sites with higher cover by a diverse shrub community, but this was more strongly expressed by *T. quadrimaculatus* than by *T. senex* (Fig. 4; Table 2).

Table 1.—Stepwise logistic regression models of *Tamias quadrimaculatus* and *T. senex* microhabitat (trap scale) associations in Plumas National Forest, California (2003 and 2004 pooled); variables are ordered by parameter estimate.

Model	Variables	Estimate	SE	Wald χ^2	P	Odds ratio	Goodness of fit
<i>Tamias quadrimaculatus</i>							
	Canopy openness	0.030	0.006	22.12	<0.0001	1.030 (1.018–1.043)	$\chi^2 = 3.60$ d.f. = 8
	Cover by rocks	0.024	0.009	7.03	0.0080	1.025 (1.006–1.043)	
	Sapling species richness	0.018	0.007	6.00	0.0143	1.018 (1.004–1.033)	P = 0.89
	East aspect	–0.008	0.003	6.85	0.0089	0.992 (0.986–0.998)	
	South aspect	–0.013	0.003	25.41	<0.0001	0.987 (0.982–0.992)	
	Slope	–0.045	0.020	4.91	0.0268	0.956 (0.918–0.995)	
<i>Tamias senex</i>							
	Shrub species richness	0.623	0.086	52.94	<0.0001	1.865 (1.577–2.206)	$\chi^2 = 10.43$ d.f. = 8
	Canopy openness	0.019	0.004	26.59	<0.0001	1.019 (1.012–1.026)	
	South aspect	0.007	0.001	38.21	<0.0001	1.007 (1.004–1.009)	P = 0.24
	Cover by litter	–0.009	0.002	14.47	0.0001	0.991 (0.987–0.996)	
	Cover by mats	–0.029	0.010	9.18	0.0025	0.971 (0.953–0.990)	
	Substrate hardness	–0.460	0.121	14.30	0.0002	0.633 (0.499–0.802)	

DISCUSSION

Tamias quadrimaculatus and *T. senex* are closely related and they share similar ecological requirements (Grinnell and Storer 1924; Johnson 1943; Sutton 1995). They may be very challenging to distinguishable in the field (Sutton 1995), and they are known to hybridize (Frare et al. 2017). These difficulties pose challenges to management and conservation plans but also raise questions concerning niche structure. Our objectives were to assess the habitat niche of these species in the northern Sierra Nevada to better understand whether these species have diverged or if they retain broadly similar (e.g., conservative) niche characteristics.

We had predicted that these species would segregate by habitat, with *T. quadrimaculatus* occurring in more open forests than *T. senex*, and while this proved to be the case, our results highlight more nuanced dynamics. At both spatial scales studied, overall distribution as reflected in our live-trapping efforts suggest broadly similar patterns of use (e.g., niche conservatism), generally with similar 'primary' patterns of use complemented by modest divergence in 'secondary' attributes. Hence, both species were most abundant in Red Fir forest, but whereas *T. quadrimaculatus* exhibited secondary abundances in mixed-fir and then mixed-conifer forests, *T. senex* did so in White Fir followed by mixed-fir types. At finer scales of assessment, both species occurred in a nonrandom subset of available microhabitats, but they generally occurred at sites with similar levels of most traits recorded—cover by bare ground, litter, branches, logs, and so forth. These species do appear to differ in that *T. quadrimaculatus* occurred at sites with more cover by rock and live shrubs, more open canopies (as we had predicted), less cover by forbs and grasses and by mat vegetation, and sites oriented more to the west and north; *T. senex* tended to favor lower levels of most of these characters (other than mat vegetation), and sites oriented more to the east and south (Fig. 3). Similarly, logistic regression generally highlighted different variables for each species; both species were positively influenced by open canopies (albeit more strongly for *T. quadrimaculatus*), but they diverged in preference for south aspect, and shared no other variables in the final models (Table 1). Finally, PCA emphasized overall similarities more than differences in

Table 2.—Detailed output for first three principal components axes (see Fig. 4). The upper portion presents the eigenvectors for each axis, the percentage of the variance explained (individually and cumulatively), the results of a randomization algorithm that estimates the probability that a given axis is larger than expected by chance (based on 999 randomizations); the middle portion presents the eigenvectors for each axis (light and dark shading highlights metrics loading <-0.3 and >0.3 , respectively); the bottom portion presents the position of both chipmunk species on each axis (calculated as the weighted average across all sites in PC space).

Parameter	Principal component axis		
	1	2	3
Eigenvector	2.778	1.901	1.466
% Variance explained	15.436	10.563	8.142
Cumulative variance explained	15.436	25.999	34.140
Pr(obs > exp)	0.001	0.001	0.001
Bare ground (BA)	-0.178	0.025	-0.227
Branches (BR)	0.324	0.310	0.208
Canopy openness (CO)	-0.489	-0.009	0.099
Dead shrubs (DS)	-0.045	-0.044	-0.068
East aspect (EW)	0.005	0.107	-0.501
Forbs and grasses (FG)	-0.059	0.004	-0.246
Litter (LI)	0.120	-0.222	0.233
Large logs (LL)	0.033	0.004	-0.034
Live shrubs (LS)	-0.460	-0.008	0.305
Mat vegetation (MA)	-0.029	-0.147	-0.318
South aspect (NS)	-0.166	0.126	-0.141
Rock (RO)	-0.352	-0.045	-0.021
Substrate hardness (SH)	-0.138	-0.206	-0.273
Small logs (SL)	0.062	0.113	-0.022
Slope (SO)	-0.060	-0.290	-0.393
Shrub species (SS)	-0.433	0.005	0.210
Tree cover (TR)	0.114	-0.561	0.151
Tree (sapling) species (TS)	0.111	-0.589	0.113
<i>Tamias quadrimaculatus</i>	-1.043	-0.406	0.821
<i>Tamias senex</i>	-1.140	0.292	0.364

microhabitat use, as both species exhibited similar orientation in ordination space (Fig. 4).

The three sets of analyses presented here apply data differently, and they make different assumptions to address related but distinct questions. Hence, it should not be surprising that parameters emerging as 'important' in one analysis failed to do so in others. These analyses may be thought of as falling on a continuum of broad to narrow 'focus'; ordination and regression both integrate all microhabitat parameters simultaneously, but whereas the former ignores the distribution of chipmunk species (this is subsequently superimposed in ordination space), the latter seeks to extract those habitat parameters that best explain the distribution of each chipmunk; as such, many variables may be 'modestly' influential yet left out of final regression models. Importantly, ordination and regression may show differences in habitat use between species, but these do not compare such use to habitat availability, and so cannot be used to infer selection by these species. In contrast, selectivity analyses integrate the use and availability of all habitat parameters; additionally, this does so for each habitat metric individually. As such, we would expect a greater number of 'significant' associations using selectivities than with ordination, and this in turn would be expected to emphasize more variables than regression.

For example, ordination suggested that both chipmunk species tended to occur at sites with few branches, less litter, and low tree cover or tree (sapling) species richness; selectivities suggested that they both occurred at sites that favored each of these characteristics. The former analysis simply overlays the observed distribution of each chipmunk over an ordination landscape based simultaneously on all habitat metrics, whereas the latter evaluates use versus availability of each parameter individually, to the exclusion of all other parameters. Comparing all three analyses, selectivities and ordination both suggested a positive association of *T. quadrimaculatus* with steeper slopes, whereas regression yielded a negative coefficient for this parameter. For *T. senex*, ordination and regression both suggested a negative association of this species with litter, whereas selectivities showed that they occurred at sites with higher litter cover than expected. Hence, results vary across these analyses, but such variance reflects at least in part the way in which data are integrated. Overall, however, these analyses provide complementary and generally similar insights to microhabitat use by these species in the northern Sierra Nevada.

Habitat segregation by these species appears to be scale-dependent, hierarchical in nature, and subtle. Although temporal comparisons from field efforts using very different approaches need to be tempered, our observations seem to differ from those of earlier researchers. In the central Sierra Nevada, Grinnell and Storer (1924:188) reported that the "range [of *T. quadrimaculatus*] is almost complementary to that of the Mariposa [*T. merriami*] and Allen [*T. senex*] chipmunks, the other two large sized species in the region, for the former does not anywhere go above 5000 feet, and the latter is seldom found far below the 7000 foot contour." In the northern Sierra Nevada and the region of our study, Tevis (1955:71) highlighted that *T. senex* "[i]nhabits forests that are relatively dense, also brushy areas that are relatively moist," whereas *T. quadrimaculatus* is "[t]he common species of brushfields and of open or partly open mixed coniferous forests." Hence, *T. senex* tended toward moister habitats than did *T. quadrimaculatus*. Although our sampling yielded support for such differences at the microhabitat scale, the differences were subtle and limited (Fig. 3), and we documented only modest segregation at the macrohabitat (forest type) scale. And it seems notable that *T. quadrimaculatus* was captured more on northern and western sloping sites than was *T. senex*, which did not exhibit preference for any aspect.

Although logistic regression suggested that these chipmunks emphasize different environmental characteristics, both selectivities and PCA suggested more modest segregation in niche characteristics, at least as measured here, and would appear to support the niche conservatism model. If this is the case, however, one would expect greater spatial segregation, and at least some areas where the more restricted-range, presumably specialist species (*T. quadrimaculatus*) could avoid competition with the more wide-ranging, presumably more generalist *T. senex*. Although no such areas of allopatry were found in the PNF, this is near the northern extent of the geographic range of *T. quadrimaculatus*, and it may be more ecologically

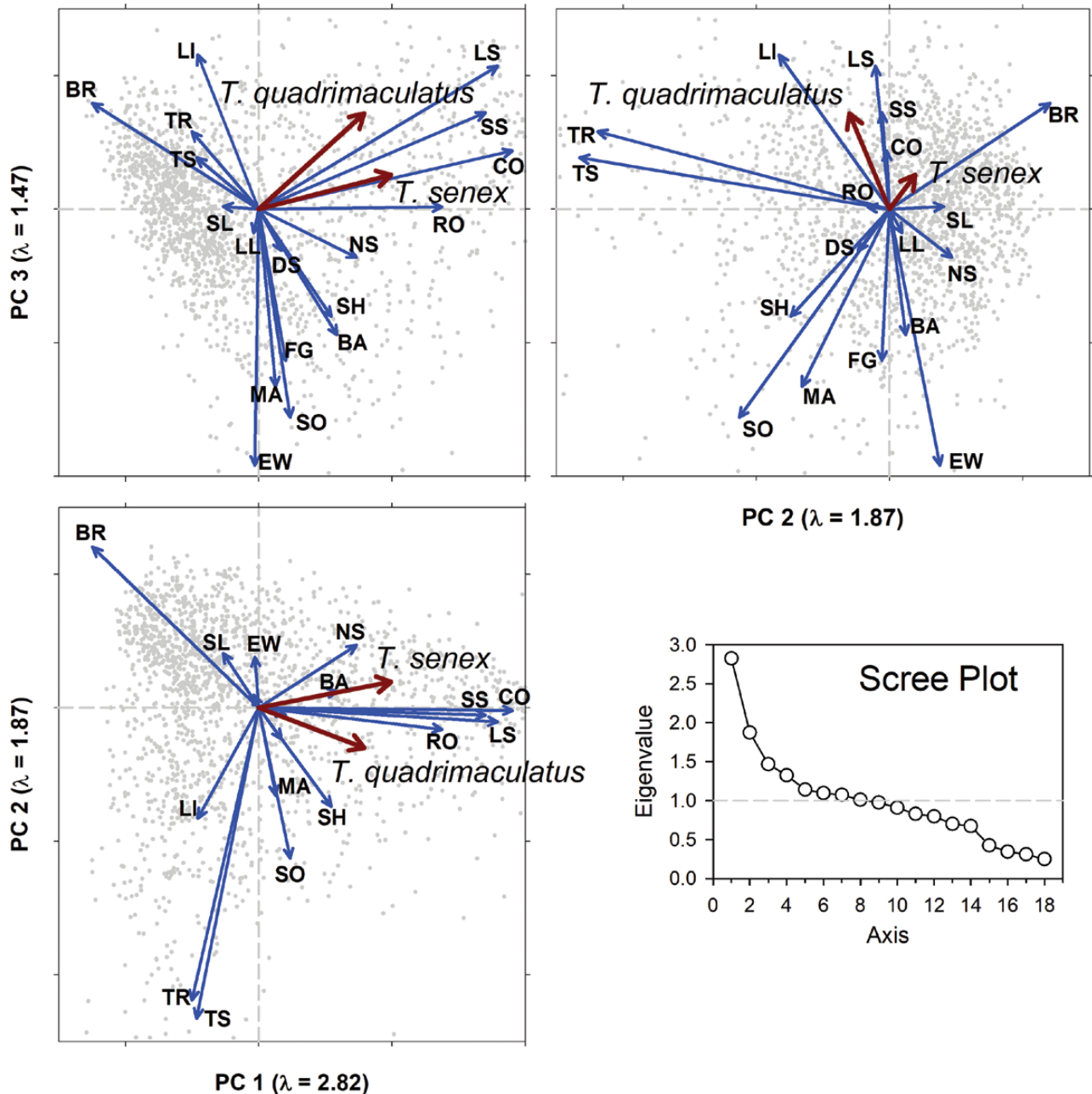


Fig. 4.—Biplots showing the first three axes of a principal components analysis (PCA) of microhabitat characteristics recorded at 1,800 trapping sites (light gray circles) in the Plumas National Forest, California (2003–2004). Superimposed are vectors for most microhabitat metrics (thin lines, open heads) and for both *Tamias quadrimaculatus* and *T. senex* (thick lines, filled heads). Microhabitat variables follow: BR = branches; CO = canopy openness; DS = dead shrubs; EW = east aspect; FG = forbs and grasses; LL = large logs; LI = litter; LS = live shrubs; MA = mat vegetation; RO = rock; SS = shrub species; SO = slope; SL = small logs; NS = south aspect; SH = substrate hardness; TR = tree cover; TS = tree (sapling) species. The bottom right panel is a scree plot, showing the relative magnitudes of all eigenvectors.

constrained here than at sites to the south, where full allopatry may be more common (Sharples 1983). If this is the case, then we also would expect population growth rates to be lower in our study area for this species than for *T. senex*, with lower survival, greater mortality, and possibly differential recruitment; only further investigation can resolve this uncertainty.

Another factor that may be constraining the ecological distribution of these species (and of others) is changing forest

structure and dynamics over the past half century (Dolanc et al. 2014a, 2014b; McIntyre et al. 2015). A combination of fire suppression and forest management throughout the Sierra Nevada over the past century have favored shade tolerant White Fir at the expense of less shade tolerant species such as Ponderosa Pine (Kilgore and Taylor 1979; Ansley and Battles 1998; Barbour et al. 2002), and shifted the landscape from one comprised of heterogeneous stands to one dominated by more

closed canopies, thereby decreasing understory plant diversity (Halpern and Spies 1995). Given this, an alternative explanation for the shared habitat niches of these chipmunks would emphasize the deterioration of habitat favorable for at least one of these species (e.g., dominance by dense stands of White Fir, loss of shrub layer, accumulation of fine woody debris, etc.), leading them both to become relatively more abundant in (relatively) less impacted Red Fir forests.

One observation in support of such a convergence in habitat use is that in addition to chipmunks, four other small mammal taxa (*Callospermophilus lateralis*, *Glaucomys oregonensis*, *Microtus* spp., and *Peromyscus maniculatus*), reached their greatest mean abundance in this high-elevation forest type (Coppeto et al. 2006). Our Red Fir trapping grids had an open stand structure (166 stems/ha) and open canopies (mean canopy openness 47%), and presented a high density of shrub and sapling types, and high cover by rocks, exposed soils, and live shrubs. They also were characterized by a high density of manzanita (*Arctostaphylos* spp.) and other shrubs, which are important in the diets of these species (Tevis 1952, 1953; Linsdale and Tevis 1956; Laacke and Tappeiner 1996). In contrast, mixed-fir and White Fir forests in our study were characterized by higher tree density (440 and 645 stems/ha, respectively), closed canopies (mean canopy openness 12% and 11%, respectively), deep duff layers (up to 15 cm), and heavy fuel and litter loads. The widespread occurrence of relatively homogeneous White Fir forests remains capable of supporting populations of the ubiquitous *T. senex*, but the heterogeneous nature of high-elevation Red Fir forests (and, to a lesser extent, mixed-fir) may allow the small scale (e.g., plot level) coexistence of ecologically similar species (Jorgensen 2004).

This report raises numerous areas for investigation. In addition to the demographic research mentioned above that could shed light on putative 'range edge' impacts on *T. quadrimaculatus*, here we highlight three themes that we believe are particularly important. First, assessing microhabitat use from live-trapping studies may be biased by the placement of trapping stations; animals may be attracted to stations occurring in microhabitat that they might otherwise not use as heavily. As with most grid-based studies, this issue is to a large extent minimized by the fact that only the first station is subject to such bias; all subsequent stations were fixed by the metrics of our study design. However, the potential for bias remains, and calls for further study using animals equipped with transmitters, so that they can be monitored passively as they pursue their daily activities (White and Garrott 1990; Kenward 2001; Ribble et al. 2002; Lira and Fernandez 2009). Additionally, further work is needed in additional forest types, ideally with additional replication within forest type. Second, complementing our habitat assessment with dietary studies using stable isotopes (Post 2002; Newsome et al. 2007) or DNA metabarcoding from feces (Kartzinel et al. 2015; Iwanowicz et al. 2016; Aylward et al. MS-b) would shed important light on what each species is consuming where they co-occur, as well as in areas of allopatry. Such work is increasingly cost-effective, and recent developments of noninvasive sampling methods (Aylward et al. MS-a) make this increasingly attractive. Finally, further work is

needed in forests more central to the historic range of *T. quadrimaculatus* to clarify whether results presented here reflect niche conservatism by these two chipmunks, as opposed to ecological constraints on *T. quadrimaculatus* reflecting range-edge dynamics (Sexton et al. 2009; Hardie and Hutchings 2010). In the face of both climate change and increasing threat of high-severity wildfire (Burke et al. 2021; United Nations Environment Programme 2022), a clearer understanding of the habitat associations and needs of these species is essential for resource managers. Lacking such insight, questions of niche conservatism versus niche differentiation may become moot points.

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LITERATURE CITED

- Abdo Z., Minin V.N., Joyce P., Sullivan J. 2005. Accounting for uncertainty in the tree topology has little effect on the decision-theoretic approach to model selection in phylogeny estimation. *Molecular Biology and Evolution* 22:691–703.
- Ansley J.-A.S., Battles J.J. 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. *Journal of the Torrey Botanical Society* 125:297–308.
- Arnold T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management* 74:1175–1178.
- ASM ACUC. 1998. [Animal Care and Use Committee] Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- Avila-Flores R., Flores-Martinez J.J., Ortega J. 2002. *Nyctinomops laticaudatus*. *Mammalian Species* 697:1–6.
- Aylward C.M., Grahn R.A., Barthman-Thompson L., Kelt D.A., Sacks B.N., Statham M.J. MS-a. 2022. A novel non-invasive genetic survey technique for an endangered rodent. *Journal of Mammalogy* 103:1441–1447. <https://doi.org/10.1093/jmammal/gyac070>.
- Aylward C.M., Statham M.J., Barthman-Thompson L., Kelt D.A., Sacks B.N. MS-b. 2022. Dietary characterization of the endangered salt marsh harvest mouse and sympatric rodents using DNA metabarcoding. *Ecology and Evolution* 12:e9121. <https://doi.org/10.1002/ece3.9121>.
- Barbour M., Kelley E., Maloney P., Rizzo D., Royce E., Fites-Kaufmann J. 2002. Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. *Journal of Vegetation Science* 13:461–472.
- Bell G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- Bell G. 2001. Neutral macroecology. *Science* 293:2413–2418.

- Best T.L., Clawson R.G., Clawson J.A. 1994. *Tamias speciosus*. Mammalian Species 478:1–9.
- Betancourt J.L., Saavedra B. 2002. Rodent middens, a new method for Quaternary research in arid zones of South America. *Revista Chilena de Historia Natural* 75:527–546.
- Bissonette J.A., Harrison D.J., Hargis C.D., Chapin T.G. 1997. The influence of spatial scale and scale-sensitive properties on habitat selection by American marten. In: Bissonette J.A., editor. *Wildlife and landscape ecology: effects of pattern and scale*. Springer, New York City, New York, USA; p. 368–385.
- Brown J.H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124:255–279.
- Brown J.H. 1995. *Macroecology*. University of Chicago Press, Chicago, Illinois, USA.
- Burke M., Driscoll A., Heft-Neal S., Xue J., Burney J., Wara M. 2021. The changing risk and burden of wildfire in the United States. *Proceedings of the National Academy of Sciences of the United States of America* 118:e2011048118.
- Burnham K.P., Anderson D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. Springer, New York City, New York, USA.
- Cavender-Bares J., Ackerly D.D., Baum D.A., Bazzaz F.A. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163:823–843.
- Cavender-Bares J., Keen A., Miles B. 2006. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:S109–S122.
- Chase J.M., Leibold M.A. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Clawson R.G., Clawson J.A., Best T.L. 1994. *Tamias quadrimaculatus*. Mammalian Species 469:1–6.
- Coppeto S.A., Kelt D.A., Van Vuren D.H., Wilson J.A., Bigelow S. 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. *Journal of Mammalogy* 87:402–413.
- da Silva D., Aires A.E., Zurano J.P., Angel Olalla-Tarraga M., Martinez P.A. 2020. Changing only slowly: the role of phylogenetic niche conservatism in Caviidae (Rodentia) speciation. *Journal of Mammalian Evolution* 27:713–721.
- Demboski J.R., Sullivan J. 2003. Extensive mtDNA variation within the yellow-pine chipmunk, *Tamias amoenus* (Rodentia: Sciuridae), and phylogeographic inferences for northwest North America. *Molecular Phylogenetics and Evolution* 26:389–408.
- Dolanc C.R., Safford H.D., Dobrowski S.Z., Thorne J.H. 2014a. Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA, US. *Applied Vegetation Science* 17:442–455.
- Dolanc C.R., Safford H.D., Thorne J.H., Dobrowski S.Z. 2014b. Changing forest structure across the landscape of the Sierra Nevada, CA, USA, since the 1930s. *Ecosphere* 5(8):101. <http://dx.doi.org/10.1890/ES14-00103.1>.
- Frare C.F., Matocq M.D., Feldman C.R., White A.M., Manley P.N., Jernstad K.D., Hekkala E.R. 2017. Landscape disturbance and sporadic hybridization complicate field identification of chipmunks. *Journal of Wildlife Management* 81:248–258.
- Frazer G.W., Canham C.D., Lertzman K.P. 2000. Gap Light Analyzer (GLA), version 2.0. *Bulletin of the Ecological Society of America* 81:191–197.
- Gannon W.L., Forbes R.B. 1995. *Tamias senex*. Mammalian Species 502:1–6.
- Garcia-Navas V., Westerman M. 2018. Niche conservatism and phylogenetic clustering in a tribe of arid-adapted marsupial mice, the Sminthopsini. *Journal of Evolutionary Biology* 31:1204–1215.
- Good J.M., Demboski J.R., Nagorsen D.W., Sullivan J. 2003. Phylogeography and introgressive hybridization: chipmunks (genus *Tamias*) in the northern Rocky Mountains. *Evolution* 57:1900–1916.
- Good J.M., Sullivan J. 2001. Phylogeography of the red-tailed chipmunk (*Tamias ruficaudus*), a northern Rocky Mountain endemic. *Molecular Ecology* 10:2683–2695.
- Grinnell J., Storer T.I. 1924. *Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada*. University of California Press, Berkeley, California, USA.
- Hall E.R. 1981. *The mammals of North America*. 2nd ed. John Wiley & Sons, Inc., New York City, New York, USA.
- Halpern C.B., Spies T.A. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5:913–934.
- Hardie D.C., Hutchings J.A. 2010. Evolutionary ecology at the extremes of species' ranges. *Environmental Reviews* 18:1–20.
- Herrera N.D., Bell K.C., Callahan C.M., Nordquist E., Sarver B.A.J., Sullivan J., Demboski J.R., Good J.M. 2022. Genomic resolution of cryptic species diversity in chipmunks. *Evolution* 76:2004–2019.
- Hubbell S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Ingles L.G. 1965. *Mammals of the Pacific States: California, Oregon, and Washington*. Stanford University Press, Stanford, California, USA.
- Iwanowicz D.D., Vandergast A.G., Cornman R.S., Adams C.R., Kohn J.R., Fisher R.N., Brehme C.S. 2016. Metabarcoding of fecal samples to determine herbivore diets: a case study of the endangered Pacific pocket mouse. *PLoS One* 11:e0165366.
- Jameson E.W., Peeters H.J. 2004. *Mammals of California*, revised edition. University of California Press, Berkeley, California, USA.
- Johnson D.H. 1943. Systematic review of the chipmunks (genus *Eutamias*) of California. University of California Publications in Zoology 48:63–146.
- Jorgensen E.E. 2004. Small mammal use of microhabitat reviewed. *Journal of Mammalogy* 85:531–539.
- Jorgensen E.E., Demarais S. 1999. Spatial scale dependence of rodent habitat use. *Journal of Mammalogy* 80:421–429.
- Kartzinel T.R., Chen P.A., Coverdale T.C., Erickson D.L., Kress W.J., Kuzmina M.L., Rubenstein D.I., Wang W., Pringle R.M. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 112:8019–8024.
- Kelt D.A. 2011. Comparative ecology of desert small mammals: a selective review of the past 30 years. *Journal of Mammalogy* 92:1158–1178.
- Kelt D.A., Meserve P.L., Lang B.K. 1994. Quantitative habitat associations of small mammals in a temperature rainforest in southern Chile: empirical patterns and the importance of ecological scale. *Journal of Mammalogy* 75:890–904.
- Kelt D.A., Meserve P.L., Patterson B.D., Lang B.K. 1999. Scale dependence and scale independence in habitat associations of small mammals in southern temperate rainforest. *Oikos* 85:320–334.
- Kenward R. 2001. *A manual for wildlife radio tagging*. Academic Press, San Diego, California, USA.
- Kilgore B.M., Taylor D. 1979. Fire history of a sequoia mixed-conifer forest. *Ecology* 60:129–142.
- Kozak K.H., Wiens J. 2006. Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* 60:2604–2621.

- Laacke R.J., Tappeiner J.C. 1996. An overview of fire in the Sierra Nevada. In: Erman D.C., editor. Sierra Nevada Ecosystem Project, final report to Congress. Volume III: assessment, commissioned reports, and background information. University of California, Centers for Water and Wildland Resources, Davis, California, USA; p. 1–10.
- Legendre P., Legendre L. 2012. Numerical ecology. 3rd ed. Elsevier.
- Linsdale J.M., Tevis L. Jr. 1956. A five-year change in an assemblage of wood rat houses. *Journal of Mammalogy* 37:371–374.
- Lira P.K., Fernandez F.A.D. 2009. A comparison of trapping- and radiotelemetry-based estimates of home range of the Neotropical opossum *Philander frenatus*. *Mammalian Biology* 74:1–8.
- Losos J.B., Leal M., Glor R.E., de Queiroz K., Hertz P.E., Rodríguez Schettino L., Chamizo Lara A., Jackman T.R., Larson A. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* 424:542–545.
- Matoq M.D., Shurtliff Q.R., Feldman C.R. 2007. Phylogenetics of the woodrat genus *Neotoma* (Rodentia: Muridae): implications for the evolution of phenotypic variation in male external genitalia. *Molecular Phylogenetics and Evolution* 42:637–652.
- Maurer B.A. 1985. Avian community dynamics in desert grasslands: observational scale and hierarchical structure. *Ecological Monographs* 55:295–312.
- McCune B., Mefford M.J. 2018. PC-ORD. Multivariate analysis of ecological data. Version 7.09. MjM Software, Gleneden Beach, Oregon, USA.
- McIntyre P.J., Thorne J.H., Dolanc C.R., Flint A.L., Flint L.E., Kelly M., Ackerly D.D. 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences of the United States of America* 112:1458–1463.
- Minin V., Abdo Z., Joyce P., Sullivan J. 2003. Performance-based selection of likelihood models for phylogeny estimation. *Systematic Biology* 52:674–683.
- Morris D.W. 1984. Patterns and scale of habitat use in two temperate-zone, small mammal faunas. *Canadian Journal of Zoology* 62:1540–1547.
- Morris D.W. 1987. Ecological scale and habitat use. *Ecology* 68:362–369.
- Mueller-Dombois D., Ellenberg H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, Inc., New York City, New York, USA.
- Newsome S.D., Martínez del Río C., Bearhop S., Phillips D.L. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5:429–436.
- NOAA—National Climatic Data Center. 1997–2003. Annual climatological summary. Quincy Weather Station.
- Olalla-Tarraga M.A., Gonzalez-Suarez M., Bernardo-Madrid R., Revilla E., Villalobos F. 2017. Contrasting evidence of phylogenetic trophic niche conservatism in mammals worldwide. *Journal of Biogeography* 44:99–110.
- Peduzzi P., Concato J., Kemper E., Holford T.R., Feinstein A.R. 1996. A simulation study of the number of events per variable in logistic regression analysis. *Journal of Clinical Epidemiology* 49:1373–1379.
- Peterson A.T., Soberón J., Sánchez-Cordero V. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Piaggio A.J., Spicer G.S. 2001. Molecular phylogeny of the chipmunks inferred from mitochondrial cytochrome b and cytochrome oxidase II gene sequences. *Molecular Phylogenetics and Evolution* 20:335–350.
- Post D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718.
- Price M.V. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921.
- Reid N., Demboski J.R., Sullivan J. 2012. Phylogeny estimation of the radiation of western North American chipmunks (*Tamias*) in the face of introgression using reproductive protein genes. *Systematic Biology* 61:44–62.
- Ribble D.O., Wurtz A.E., McConnell E.K., Buegge J.J., Welch K.C. 2002. A comparison of home ranges of two species of *Peromyscus* using trapping and radiotelemetry data. *Journal of Mammalogy* 83:260–266.
- Sales L.P., Ribeiro B.R., Hayward M.W., Paglia A., Passamani M., Loyola R. 2017. Niche conservatism and the invasive potential of the wild boar. *Journal of Animal Ecology* 86:1214–1223.
- SAS Institute Inc. 2012. SAS for Windows. Release SAS 9.4. SAS Institute Inc., Cary, North Carolina, USA.
- Schoener T.W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Sexton J.P., McIntyre P.J., Angert A.L., Rice K.J. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- Sharples F.E. 1983. Habitat use by sympatric species of *Eutamias*. *Journal of Mammalogy* 64:572–579.
- Sherry T.W., Holmes R.T. 1985. Dispersion patterns and habitat responses of birds in northern hardwood forests. In: Cody M.L., editor. *Habitat selection in birds*. Academic Press, San Diego, California, USA; p. 283–310.
- Sikes R.S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Slingsby J.A., Verboom G.A. 2006. Phylogenetic relatedness limits co-occurrence at fine spatial scales: evidence from the schoenoid sedges (Cyperaceae: Schoeneae) of the Cape Floristic Region, South Africa. *American Naturalist* 168:14–27.
- Stephens M., Donnelly P. 2003. A comparison of Bayesian methods for haplotype reconstruction from population genotype data. *American Journal of Human Genetics* 73:1162–1169.
- Sullivan J., Demboski J.R., Bell K.C., Hird S., Sarver B., Reid N., Good J.M. 2014. Divergence with gene flow within the recent chipmunk radiation (*Tamias*). *Heredity* 113:185–194.
- Sutton D.A. 1995. Problems of taxonomy and distribution in four species of chipmunks. *Journal of Mammalogy* 76:843–850.
- Sutton D.A., Nadler C.F. 1974. Systematic revision of three Townsend chipmunks (*Eutamias townsendii*). *Southwestern Naturalist* 19:199–211.
- Swenson N.G., Enquist B.J., Pither J., Thompson J., Zimmerman J.K. 2006. The problem and promise of scale dependency in community phylogenetics. *Ecology* 87:2418–2424.
- Tevis L. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. *Journal of Mammalogy* 33:198–205.
- Tevis L. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. *Journal of Mammalogy* 34:316–324.
- Tevis L. 1955. Observations on chipmunks and mantled squirrels in northeastern California. *American Midland Naturalist* 53:71–78.
- Tevis L. 1956. Responses of small mammal populations to logging of Douglas fir. *Journal of Mammalogy* 37:189–196.
- United Nations Environment Programme. 2022. Spreading like wildfire—the rising threat of extraordinary landscape fires. A UNEP rapid response assessment, Nairobi, Kenya; p. 124.
- van Smeden M., de Groot J.A.H., Moons K.G.M., Collins G.S., Altman D.G., Eijkemans M.J.C., Reitsma J.B. 2016. No rationale

- for 1 variable per 10 events criterion for binary logistic regression analysis. *BMC Medical Research Methodology* 16:163.
- van Smeden M., Moons K.G.M., de Groot J.A.H., Collins G.S., Altman D.G., Eijkemans M.J.C., Reitsma J.B. 2018. Sample size for binary logistic prediction models: beyond events per variable criteria. *Statistical Methods in Medical Research* 28:2455–2474.
- van Snik Gray E., Stauffer J.R. 1999. Comparative microhabitat use of ecologically similar benthic fishes. *Environmental Biology of Fishes* 56:443–453.
- White G.C., Garrott R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.
- White J.A. 1953. The baculum in the chipmunks of western North America. University of Kansas publications, Museum of Natural History 5:611–631.
- Wicklin R. 2018. The bootstrap method in SAS: a t-test example. SAS blogs. <https://blogs.sas.com/content/iml/2018/06/20/bootstrap-method-example-sas.html>. Accessed 17 January 2022.
- Wiens J.A., Addicott J.F., Case T.J., Diamond J. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. In: Diamond J., Case T.J., editors. *Community ecology*. Harper & Row, New York City, New York, USA; p. 145–153.
- Wiens J.A., Rotenberry J.T., Van Horne B. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos* 48:132–147.
- Wiens J.J., Graham C.H. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36:519–539.

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