HABITAT INTERACTION BETWEEN TWO SPECIES OF CHIPMUNK IN THE BASIN AND RANGE PROVINCE OF NEVADA

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ABSTRACT.—Interspecies interactions can affect how species are distributed, put constraints on habitat expansion, and reduce the fundamental niche of the affected species. Using logistic regression, we analyzed and compared 174 *Tamias palmeri* and 94 *Tamias panamintinus* within an isolated mountain range of the Basin and Range Province of southern Nevada. *Tamias panamintinus* was more likely to use pinyon/ponderosa/fir mixed forests than pinyon alone, compared to random sites. In the presence of *T. palmeri*, however, interaction analyses indicated *T. panamintinus* was less likely to occupy the mixed forests and more likely near large rocks on southern aspects. This species-by-habitat interaction data suggest that *T. palmeri* excludes *T. panamintinus* from areas of potentially suitable habitat. Climate change may adversely affect species of restricted distribution. Habitat isolation and species interactions in this region may thus increase survival risks as climate temperatures rise.

RESUMEN.—Las interacciones entre las especies pueden afectar la manera en que se distribuyen, imponer restricciones a la expansión del hábitat y reducir el nicho fundamental de las especies afectadas. Por medio de regresión logística, analizamos y comparamos 174 *Tamias palmeri* y 94 *Tamias panamintinus* dentro de una cadena aislada de montañas de la región Basin and Range del sur de Nevada. Se encontró a *T. panamintinus* con más frecuencia en los bosques mixtos de pinos piñoneros, ponderosa y abetos que en los bosques conformados únicamente de pinos piñoneros, al comparar con lugares al azar. Sin embargo, los análisis de interacción indicaron que, en presencia de *T. palmeri*, hubo menos probabilidad de que *T. panamintinus* se encontrara en los bosques mixtos y más probabilidad de que se encontrara cerca de las rocas grandes en la parte sur. Esta interacción entre especies y hábitat sugiere que *Tamias palmeri* excluye a *T. panamintinus* de áreas donde el hábitat podría ser apropiado. El cambio climático puede afectar de manera desfavorable a especies con distribución restringida. Por lo tanto, el aislamiento del hábitat y la interacción entre las especies en esta región pueden incrementar los riesgos de supervivencia al aumentar las temperaturas ambientales.

When 2 or more similar species exhibit habitat overlap, important ecological questions arise about the way these species successfully occupy the same place concurrently (Brown 1971), the role of habitat structure and composition in the maintenance of species separation (Sharples 1983), and the potential interactions between these species (Schoener 1974, Trombulak 1985). Overlap zones are sometimes found at habitat edges where vegetation structure and composition are transitioning (Sheppard 1970). In mountainous regions, where an elevation gradient additionally affects temperature and precipitation, these overlap zones may be especially affected by climate change (Inouye et al. 1999). Determining specific environmental correlates of separation is an important step in understanding potential reasons for the maintenance of species separation (Sharples 1983) and is essential for predicting the potential effects of climate change (Ditto and Frey 2007). Determination of these

correlates requires measuring habitat use of sympatric species both independently and simultaneously. A change in habitat use of one or more species due to the presence of the other can be a strong indicator of species interaction (Chappell 1978). The genus *Tamias* has 22 species in North America, 21 of which occur in the West. The genus generally occurs in forested regions from valley floors to above timberline. Several *Tamias* species overlap in their distribution, and the attributed causes for why they remain separated are varied (Brown 1971, Chappell 1978, Sharples 1983, Perault et al. 1997). Sympatric *Tamias* express a range of tolerance from mutual exclusion (Chappell 1978) to broad overlap (Sharples 1983). Brown (1971) found that separation between *T. dorsalis* and *T. umbrinus* in the central Great Basin was explained by competitive exclusion. *Tamias amoenus* similarly excludes *T. minimus* in Alberta (Sheppard 1970). *Tamias speciosus* and *T. amoenus* in the

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northern Sierra Nevada Mountains (Sharples 1983), and *T. minimus* and *T. umbrinus* in the Uinta Mountains of northeastern Utah (Perault et al. 1997), maintain sympatric overlap by using different vegetation types.

Much research on *Tamias* species separation has naturally occurred within the northwestern United States, likely because this is where many *Tamias* species occur. However, an excellent opportunity exists for expanding our understanding of species separation within the southern Basin and Range Province of North America. This landscape provides advantages to researchers addressing species interactions and the potential effects of climate change on species borders. It is an area of high mountain islands separated by low deserts that have isolated many species for thousands of years (Rickart 2001); the steep elevation gradient provides clear demarcation of habitat types; and the endemic species contribute significantly to the biodiversity of the surrounding region (Allen et al. 1991, Lomolino 2001, Rickart 2001, McCain 2007). Global and regional environmental change threatens species of restricted distributions (McDonald and Brown 1992, Rosenzweig and Clark 1994), and these small, isolated populations are more susceptible to extinction due to their inability to replenish populations by immigration. The effects of environmental change on isolated populations is of particular importance in arid regions of southwestern North America, where a transition to more arid climatic conditions has been documented, resulting in less precipitation (Seager et al. 2007) and shifts in the timing of precipitation (Weltzin et al. 2003).

Tamias palmeri and *Tamias panamintinus* are isolated species with overlapping distributions on the Spring Mountains of southern Nevada. *Tamias palmeri* occurs from approximately 2200 m to above 3000 m in elevation (Best 1993), while *T. panamintinus* occurs below 2500 m to approximately 1230 m (Best et al. 1994). *Tamias palmeri* occurrence is associated with the lower slopes of fir (*Abies concolor*) forest and proximity to water, and in this species, population size and survival increases with increasing density of shrub species (*Ribes cereum*) (Lowrey and Longshore in review). *Tamias panamintinus* has been associated with singleleaf pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*) forests (Best et al. 1994). *Tamias panamintinus* has been found at

elevations up to 3000 m (Best et al. 1994); however, it is not found at these elevations in the Spring Mountains (Deacon et al. 1964).

In this study, we compare and contrast the habitat associations of *T. palmeri* and *T. panamintinus* and estimate the actual distribution of these 2 species from genetically verified location data. We then model the potential distribution based on habitat use and compare the actual to the potential distributions. Finally, we analyze the environmental variables within the overlap zone to determine species interaction in terms of habitat use.

METHODS

Study Area

The Spring Mountains are located in the Basin and Range Province of the eastern Mojave Desert, approximately 40 km northwest of Las Vegas, Nevada. The range, consisting largely of sedimentary limestone (Longwell 1951), contains over 10 peaks above 3300 m, the highest at 3632 m. Vegetation above 2500 m consists of conifer/mixed conifer forest associations: ponderosa (*Pinus ponderosa*), white fir (*Abies concolor*), and bristlecone pine (*Pinus longaeva*). Areas below 2500 m and above the desert region are dominated by single-leaf pinyon pine and curl-leaf mountain mahogany (Sada and Nachlinger 1996). *Tamias* habitat is isolated from similar habitat in neighboring mountain ranges by the surrounding desert floor that is just above 700 m. Annual precipitation is typically <13 cm in the lower areas and as high as 71 cm at higher elevations. The upper slopes are further subject to extreme seasonality, with snow cover 5–7 months of the year. Mean yearly average temperature is 10 °C at 2000 m (Sada and Nachlinger 1996).

Animal Location Data, Identification, and Actual Distribution

We used animal locations from thirty-four 2-km trapping transects to estimate the actual distribution of *T. panamintinus*. We trapped 12 transects within the pinyon pine/juniper habitat association at the lowest elevations, 12 across the ponderosa–pinyon pine transition zone, and 10 within the ponderosa pine association to systematically sample the range from June through August of 2008 and 2009. Transects were 2 km long and placed not less

TABLE 1. Habitat variables measured for a Panamint and Palmer's chipmunk interaction study in the Spring Mountains, Nevada, 2008–2009.

Habitat variable	Mean	SD	Range
% cover pinyon-juniper	25.7	28.2	0–95
% cover mahogany	12.6	9.2	0–95
% cover ponderosa	8.3	12.4	0–95
% cover fir	3.5	13.0	0–85
% cover sagebrush	17.4	23.0	0–100
% cover <i>Ribes</i> shrub	2.7	6.4	0–45
% cover forest litter	37.4	32.3	0–80
Pinyon-juniper density/plot	1.8	2.8	0–13
Mahogany density/plot	2.1	3.7	0–20
Ponderosa pine density/plot	1.4	3.0	0–33
Fir density/plot	3.4	5.9	0–39
Sagebrush density/plot	6.4	9.3	0–58
<i>Ribes</i> shrub density/plot	1.3	2.8	0–17
Distance to water (m)	2158.2	1797.7	80–8026
Occurrence of water source	0.02	0.1	0–1
Density of downed log/plot	0.5	1.2	0–15
Density of large rocks ^a /plot	0.5	1.2	0–10
% slope	35.5	16.4	0–122
Hillshade ^b	141.9	104.7	0–254

^aLarge rocks = 1 m × 1 m.^bMeasure of sun radiation intensity as a function of surface angle. Azimuth from 12pm 7/2009.

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, FL) was set every 40 m along a single line for 4 days (50 traps per transect). Different chipmunk species are generally difficult to distinguish, and *T. palmeri* and *T. panamintinus* are especially similar in appearance (Best 1993). Therefore, we used genetic (mitochondrial amplification) analyses on tissue samples to identify species (B. Riddle and S. Mantooth, University of Nevada, Las Vegas, genetics lab). We maintained a buffer of 300 m above the highest elevational extent of locations successfully capturing *T. panamintinus* to estimate the distribution area across the Spring Mountains. To establish the actual distribution of *T. palmeri*, we used the results from Lowrey and Longshore (in review), who used similar methods.

Vegetation and Topographic Data Collection

Vegetation species composition, structure, and topographical variables were measured within 8 m radius plots centered on each trap that successfully captured a chipmunk (Table 1). Habitat variables were also measured at 350 plots randomly placed throughout the study area. Percentage of tree, shrub, and forest litter cover were estimated by standing at 20 systematically placed points within each plot and looking straight up (canopy) and down

(shrub, litter) through a 20 cm long by 3 cm diameter 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). Densities of trees, shrubs, snags, downed logs (>0.5 m in diameter and >2 m in length), and large rocks (≥1 m × 1 m) were measured by census within each plot. Tree heights were measured with a hypsometer. Water source locations, either wet ground or open water, were also documented. Percentage slope, aspect (2 categorical variables of north [=1] or south [=0] facing), and distance to water were measured in a GIS application (ArcMap 9.3, Environmental Systems Resource Institute, Redlands, CA). Hillshade, a geometric measure of how much radiation the surface is exposed to as a function of surface angle (range 0–255, 255 = maximum radiation), was measured in a GIS application. As a measure of general forest type, we used the *P. monophylla*, *A. concolor*, and *P. ponderosa* mixed forest vegetation classifications of the Southwest Regional Gap Analyses Project (ReGap; 2007) as categorical variables (either species present = 1, not present = 0).

Habitat Availability and Interaction

We used logistic regression analyses with 94 successful *T. panamintinus* and 150 random

Fig. 1. Actual distribution extents of *Tamias palmeri* and *T. panamintinus* estimated from genetically verified location data. Spring Mountains, Nevada, 2009.

points to create the *T. panamintinus* resource selection function (RSF) model of habitat availability (Menard 1995, Manly et al. 2002, Johnson et al. 2006; SPSS statistical software, Somers, NY). These RSF values are

proportional to the relative probability of animal occurrence across the available habitat (Boyce and McDonald 1999, Johnson et al. 2006). We then used the RSF model as developed by Lowrey and Longshore (in review;

TABLE 2. Habitat variables contributing to *Tamias panamintinus* occurrence in the Spring Mountains, Nevada.

Habitat variable	β	SE	Wald	df	P
Hillshade ^a	0.0262	0.004	42.37	1	<0.000
Pinyon pine forest ^b	1.968	0.563	4.517	1	0.033
Pinyon/ponderosa mixed forest ^b	2.856	0.884	10.44	1	0.001

^aMeasure of sun radiation intensity as a function of surface angle. Azimuth from 12pm 7/2009.

^bCategorical variable: 1 = pinyon, 2 = pinyon/ponderosa. Values relative to the pinyon forest type (reference category).

RSF = $[-0.0365 * \text{percent slope}] + [-0.0018 * \text{distance to water sources}] + [0.1562 * \text{aspect}] + [0.7164 * \text{bristlecone/fir mixed forest}] + [-1.326 * \text{ponderosa/pinyon pine mixed forest}]$ to determine *T. palmeri* habitat availability. Aspect and forest variables were categorical. Model chi-square tests and Wald statistics were used to assess overall model fit and the strength of individual variable contributions. Model strength and accuracy was evaluated using the area under the curve (AUC) of a receiver operating characteristic (ROC) analyses. We used the Hawth's Tools[©] extension within ArcMap to generate the random points across the study area and spatially enforced a minimum distance of 10 m between points. We confirmed our logistic regression results by using a general linear model (GLM) to determine habitat use differences between the 2 species within the overlap zone.

To analyze interaction between the 2 species, we first constrained our used and available data to the areas above the lower distribution line of *T. palmeri* (within the actual overlap zone). We used a single logistic regression model to compare habitat use for both species. Where the response variable was use versus available, species was a covariate factor in the model, and all interaction terms between species and covariates were present (Manly et al. 2002). Random points were generated independently for each species.

RESULTS

Transects captured 293 individual chipmunks, of which 268 were genetically identified (174 *T. palmeri* and 94 *T. panamintinus*). All *T. panamintinus* were captured below 2660 m, including 8 above 2400 m ($\bar{x} = 2328$, $SD = 188.8$), and all *T. palmeri* were found above 2085 m ($\bar{x} = 2593$, $SD = 318$). Chipmunks were captured on 28 of the 34 transects, which allowed us to estimate the actual distribution of *T. panamintinus* and compare it directly to Lowrey and Longshores' (in review) *T. palmeri*

distribution (Fig. 1). We found that *T. panamintinus* occurrence, compared against all available habitat, was predicted by pinyon pine, by increasing hillshade values (increasing exposure to radiation), and by the occurrence of ponderosa/pinyon pine mixed forest of the Spring Mountains (overall model: $\chi^2 = 163.42$, $R^2 = 0.66$; Table 2). Area under the curve (AUC) of 0.910 from ROC analysis indicated a strong ability of the model to discriminate *T. panamintinus* points from random points. *Tamias palmeri* occurrence was predicted by slope, aspect, distance to water, fir trees, and increasing shrub (*Ribes* spp.) cover (Lowrey and Longshore in review). Our RSF models indicated habitat suitability for *T. panamintinus* extended significantly above the distribution estimated by location data (Fig. 2). Our GLM analyses of habitat use between these 2 species confirmed the greater use of fir trees by *T. palmeri* (Deacon et al. 1964, Best 1993) and the greater use of pinyon pine and large rocks by *T. panamintinus* (Best et al. 1994; overall model: $F_{4, 187} = 73.33$, $P \leq 0.001$; Table 3). Using data occurring only within the overlap zone (144 *T. palmeri* and 64 *T. panamintinus*), interaction terms indicated that, relative to *T. palmeri*, *T. panamintinus* was more likely to be near large rocks and southerly facing aspects and less likely to be near fir trees within the pinyon/ponderosa mixed forest (Table 4).

DISCUSSION

Although we found significant potential for habitat overlap (Fig. 2), location data indicated that *Tamias palmeri* and *T. panamintinus* remain generally well separated within the Spring Mountains. Compared to random points not constrained to the overlap zone, *T. panamintinus* demonstrated a preference for pinyon/ponderosa mixed forest habitats at the upper elevation range of the pinyon forests (Best et al. 1994). However, when we constrained the analyses to the species overlap

Fig. 2. Actual distribution extent of both species of chipmunk and habitat models indicating potential distributions for *Tamias panamintinus* and *T. palmeri* and their overlap zone within the Spring Mountains, Nevada, 2009.

zone within presence of *T. palmeri* in the interaction analyses, no such preference was found, and *T. panamintinus* was more likely found outside these mixed ponderosa areas in exclusively pinyon pine habitat associations. This suggests

potential exclusion of *T. panamintinus* from areas with ponderosa and fir trees, a likely food source for both chipmunk species (Best et al. 1994).

Tamias panamintinus occurs in areas of relatively high solar exposure and, as a result, is

TABLE 3. General linear model results showing significantly different habitat use variables within the overlap zone of *Tamias palmeri* and *Tamias panamintinus*. Spring Mountains, Nevada, 2009.

Habitat variable	F	P	Mean difference	SE
% fir tree cover	13.51	<0.001	9.3 ^a	2.5
Pinyon-juniper density	9.05	0.003	1.3 ^b	0.4
% sagebrush shrub cover	17.94	<0.001	15.1 ^b	3.4
Large rock ($\geq 1 \text{ m} \times 1 \text{ m}$) density	13.64	<0.001	0.7 ^b	0.2

^a*T. palmeri* > *T. panamintinus*.^b*T. panamintinus* > *T. palmeri*.TABLE 4. Significant interactions between *Tamias palmeri* (reference category) and *Tamias panamintinus* within the Spring Mountains of southern Nevada, 2009.

Habitat variable interactions	β	SE	Wald	df	P
Species ^a $\times$ fir tree density	-0.0975	0.0740	4.90	1	0.027
Species ^a $\times$ large rock density ^b	0.5095	0.2005	6.46	1	0.011
Species ^a $\times$ aspect ^c	2.152	0.4828	19.86	1	<0.0001

^aReference category = *T. palmeri*.^bLarge rocks $\geq 1 \text{ m} \times 1 \text{ m}$.^cCategorical: 0 = southerly facing slopes, 1 = northerly facing slopes (reference category).

able to exploit the pinyon forest on the lower elevation and southerly exposed areas. In contrast, *T. palmeri* is known to have a narrow thermoneutral zone (Best 1993) and is likely physiologically unable to exploit areas of higher temperatures. *Tamias panamintinus* has been found in areas above 3100 m (Best et al. 1994), suggesting a potentially broad overlap of the fundamental niche of these species. However, intensive trapping shows *T. panamintinus* is not found above 2600 m in the Spring Mountains (Deacon et al. 1964, Lowrey and Longshore in review), and this elevational limit represents an unexplained constraint on the species distribution. Based on changes in habitat use of *T. panamintinus* in the presence of *T. palmeri*, the known physiological constraints of *T. palmeri*, and the lack of occurrence of *T. panamintinus* at higher elevations, we speculate that *T. panamintinus* is excluded from areas within the thermoneutral zone of *T. palmeri* by habitat preference. This may represent a distributional limit for *T. panamintinus*, established through habitat selection as a mechanism by which the species avoids energetically costly encounters with the larger *T. palmeri* (States 1976, Sharples 1983). If *T. panamintinus* was primarily excluded by behavioral interaction, we would expect *T. panamintinus* to be found at higher elevations (Chappell 1978). However, whether behavior represents an additional mechanism of separation remains to be systematically investigated.

The isolation of conifer forests on the Spring Mountains makes the nonflying species there particularly susceptible to changes in climate (Rickart 2001, Ditto and Frey 2007). If *T. panamintinus*, already isolated at the lower elevations by desert and constrained at the higher elevations by habitat preference and interspecies interaction, is further subjected to increasing temperatures and dryer conditions of climate change, the probability of extinction for this species may increase (Ditto and Frey 2007).

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