

Spatiotemporal, Microhabitat, and Climatic Variance in Disjunct Populations of Co-occurring Pinyon-Juniper Woodland Dwelling Chipmunks and Brushmice

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There is wide-spread agreement that effective management and conservation of assemblages of co-occurring species necessitates baseline studies of spatiotemporal and climatological dynamics underlying community relationships. Such studies are particularly relevant to residual populations of relic species scattered throughout mountainous regions of the North American Southwest. Yet few investigations have examined effects of environmental covariates on disjunct populations of syntopic species in semi-arid woodland or montane forest landscapes. Here we present unpublished “archival” data (1996–1998) from endemic populations of the Colorado chipmunk (*Neotamias quadrivittatus*) and brushmouse (*Peromyscus boylii*), which coexist within mature multi-age stands of pinyon-juniper woodland. We evaluated variance in the spatiotemporal regimes of these two species in response to: 1) seasonal area climate, 2) microhabitat use; 3) reproductive output; and 4) estimates of population density. Results of our analysis showed that theoretical density plots and spatial structure of live-trap quadrat data were non-normally distributed for both species. Microhabitat use in each taxon was primarily associated with limestone escarpment-cliff edges and rock outcrops, particularly in chipmunks. Density estimates closely mimicked variance in seasonal climate but with some differences between species. Redundancy analysis showed that drivers of spatiotemporal patterns in these small mammals was predominantly due to seasonal variance in temperature, solar radiation, and humidity during summer, spring, and early fall. Because conservation of mature stands of pinyon-juniper woodlands and relic montane forest represent critical challenges for contemporary and future management of endemic species in these refugial ecosystems, our archival ecological data may facilitate understanding of the dynamics of ecosystem function, uncover legacy effect, and provide a reference for crafting contemporary management and future conservation goals, particularly in the era of rapid climate.

Keywords: American Southwest, Co-occurring, Live-trapped, Relic Species, Small Mammals, Syntopic Species

BACKGROUND

There is wide-spread agreement that effective management and conservation of multiple co-occurring species necessitates baseline studies of the

spatiotemporal and climatological dynamics underlying community relationships (Weldy et al. 2019; Scott et al. 2022). Such studies are particularly relevant to residual populations and endemic species scattered throughout mountainous regions of the North American Southwest.

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These relic populations from the post-Pleistocene epic may also be considered “early warning systems” when assessing initial stages of degradation in remnant patches of montane woodlands and forest ecosystems, which form a sizable part of the total habitat in the North American Southwest. These disjunct environments also are important as natural ecosystems and centers of irreplaceable biological diversity (Sullivan 1994 1996).

Variance in climate caused by fluctuations in seasons often drive the dynamics and adaptive responses of many ecological communities (Forrest and Miller-Rushing 2010; Williams et al. 2017). This process may ultimately determine the extent of diversity as a function of the presence and abundance of syntopic species (Shimadzu et al. 2013). Knowledge of the seasonal dynamics in syntopic assemblages of taxa is increasingly important in the era of rapid climate change (Pauli et al. 2013; Williams et al. 2014), particularly in more arid relic populations dominated by fluctuations between periods of resource abundance and deficit (Varpe 2017). Moreover, in suboptimal landscapes species may require use of a broader range of environmental conditions in their search for resources. This behavior may hamper the effectiveness of conservation-oriented management wherever landscape-scale factors are ignored.

Pinyon-juniper woodlands are widely distributed throughout the North American Southwest, equal to ~1/3 of the total area in the region (Zlotin and Parmenter 2008). Within this biome several species of small mammals co-occur in disjunct mesic pinyon-juniper vegetation and remnant montane conifer forests, mapped within Petran Montane Conifer forest surrounded by Great Basin Conifer woodland (Brown and Lowe 1980; Miller et al 2019). These taxonomic assemblages represent relict populations isolated by fragmentation of formerly continuous, montane vegetation following the Wisconsin glaciation (15,000–10,000 years ago; Patterson 1982; Sullivan 1985; Sullivan and Petersen 1988; Sullivan 1994 1996). Due to complex historical processes, and a diverse topographic and edaphic landscape (Jacobs et al. 2008; Waichler et al. 2001), these residual woodland and forest plant communities exist as a complex mosaic of older and younger stands, surrounded downslope by a transition into semiarid and arid conditions dominated by combinations of grasses, shrubs, or open non-vegetated landscapes, characterized sequentially as Semidesert Grassland and Chihuahuan Desert scrub (Brown and Lowe 1980).

Previous analyses of individual taxa or assemblages of species, inhabiting these semi-arid forest and woodland ecosystems, focused primarily on factors related to: 1) ecological succession, patterns of rain fall, fire regimes, and human disturbance (Stapp 2010; Thibault et al. 2010; Kelt 2011; Wiens

et al. 2012; Shenbrot 2014; Greenville 2016); and 2) models of species richness, site occupancy, and habitat suitability (Severson 1966; Hunt 1992; Willis and Miller 1999; Rompola and Anderson 2004; Rodhouse et al. 2010; Perkins-Taylor and Frey 2020; O’Connell and Frey 2024). Yet there are no studies linking spatiotemporal relationships to seasonal area climate, combined with habitat use, and variance in population parameters among heterospecific taxa co-occupying mountainous woodland regions of the North American Southwest. Given that relic woodland and mesic-montane communities encompass steep environmental gradients, in relatively small geographic areas, they provide natural laboratories for studies of biodiversity and endemism that merit cautious management and conservation. These fragile ecosystems are also appropriate for anticipating and conducting predictive modeling of future climate change and conservation, especially in landscapes undergoing contemporary anthropogenic degradation (Fisher and Ladle 2022; Sullivan and Wilson 2001).

Because ecosystems are inherently dynamic (White and Pickett 1985; Mori 2011), evaluation of natural variability over appropriate scales of time and space is crucial. Consequently, for comparative purposes, and in anticipation of potential future degradation of pinyon-juniper woodland landscapes, historical assessments are often useful as “benchmarks” by land managers to evaluate the natural range of variability linked to ecosystem health in contemporary landscapes (Cissel et al. 1994; Landres et al. 1999; Hessburg et al. 1999a; Keane 2012; Dickinson 2014; Keane and Loehmann 2019). Thus, we present unpublished “archival” data (1996–1998) obtained during investigations of the systematics, conservation, and ecology of the Oscura Mountains chipmunk (*Neotamias q. oscuraensis*) and the brushmouse (*Peromyscus boylii*) in the Oscura Mountains, New Mexico, USA (Sullivan and Wilson 2001). Our specific objectives were to evaluate variance in the spatiotemporal regimes of these two species in response to: 1) seasonal area climate, 2) microhabitat use; 3) reproductive output; and 4) estimates of population density based on capture-recapture methods.

MATERIALS AND METHODS

Study area

Our study was conducted in the Oscura Mountains, a ridge of mountains that are part of a fault block associated with the Rio Grande Rift, Lincoln and Socorro counties, south-central New Mexico, USA

(Fig. 1A). This range of mountains extends southward ~48 km and range in width from ~9.7 km to ~16 km. To the west, the Oscura Mountains drop sharply from the crest of Oscura Peak to the Jornada del Muerto Basin below (~1,500 m), to the southwest this range is separated by the lower-lying Little Burro Mountains

and to the south by the expansive San Andres Mountain range. To the east, the Oscura range slopes gently to the Tularosa Valley below (~1,500 m). This semi-arid mountain range is found within the U.S. Army White Sands Missile Range (WSMR) research, development, test, evaluation, and training facilities, which encompass

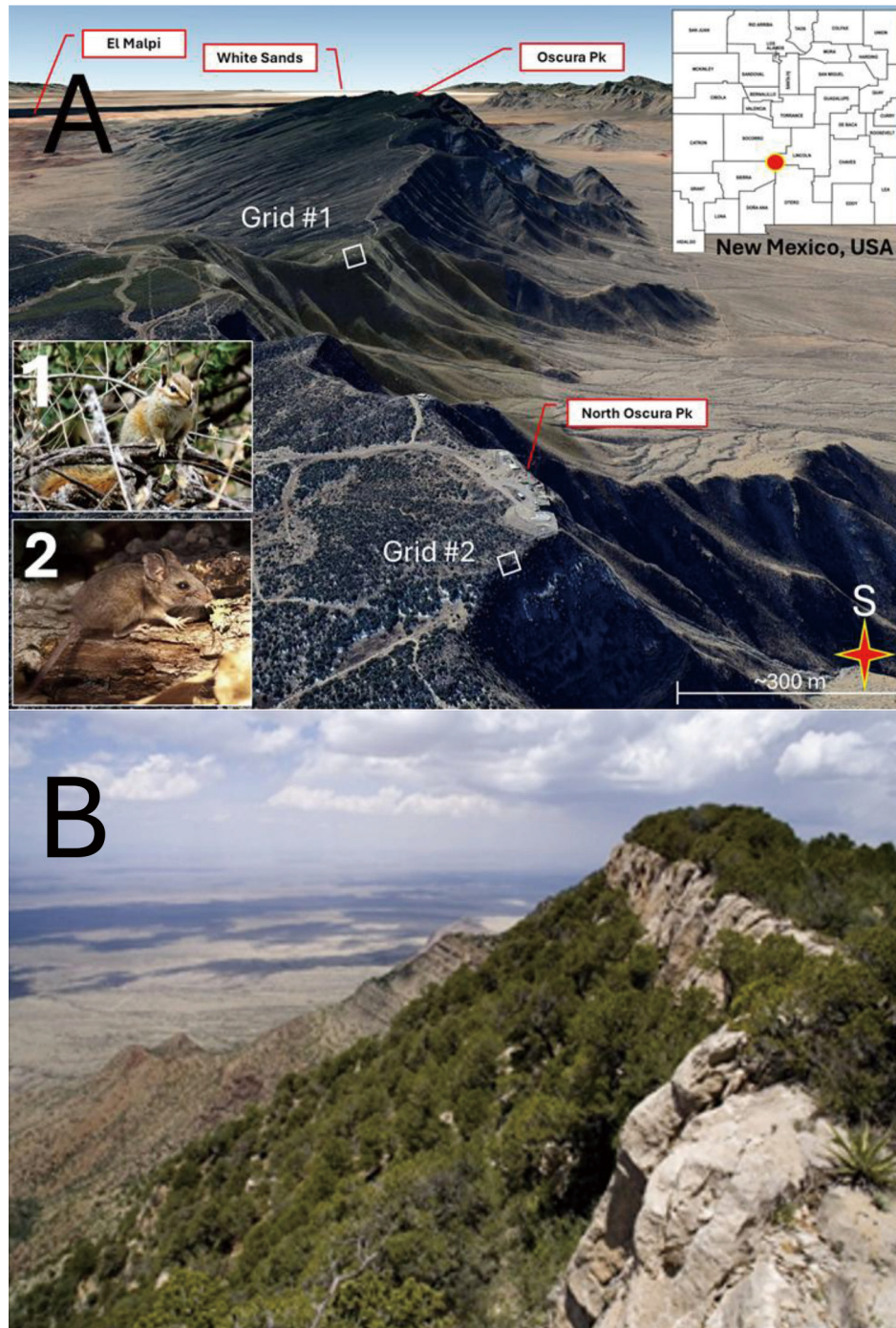


Fig. 1. A) Oscura mountains and surrounding semi-arid steppe and arid desert landscape (map from Google Earth); insert: 1 = Oscura Mountains chipmunk (*Neotamias quadrivittatus oscuraensis*; photo: D Burkett) and 2 = brushmouse (*Peromyscus boylii*; photo: MC Kalcounis-Rueppell). B) Typical mature pinyon-juniper-oak woodland habitat along NW-facing limestone escarpment-cliff edge; photo by P. Alexander.

~8,288 km². The Trinity site is ~11 km northwest of Oscura Peak and is the location of the first test of an atomic bomb in 1945. North Oscura Peak (NOP, 33.7875 N, -106.487 W; elevation ~2,437 m) is the location of the U.S. Air Force Research Laboratory and meteorological station.

The Oscura Mountains rise above semi-arid steppe and arid desert. Higher elevations of the mountains result in cooler temperatures and higher precipitation. Most precipitation is received during the monsoon season (July–October), with an average seasonal precipitation of ~15 cm, while the remaining months averaged ~12 cm total (O'Connell and Frey 2024). Surrounding areas receive ~25 cm annually in precipitation, while higher elevations receive from ~41 to ~51 cm on average, which is sufficient to support a community of mature pinyon-juniper-oak woodland surrounding northwest-facing limestone escarpment-cliff edges (Fig. 1B). Surface water is rare except for ephemeral streams on the east side of the range and a few springs. Average maximum temperatures at NOP range from ~27.3°C in June to ~5.2°C in January. Average minimum temperatures range from ~13.5°C in July to ~-3.2°C in January. Vegetation types within and surrounding the study area included 2-major groups: 1) moderately closed canopies of two-needle pinyon (*Pinus edulis*), one-seed juniper (*J. monosperma*), and wavyleaf oak (*Quercus undulata*) woodlands; and scattered shrub live oak [*Q. turbinella*]; Gambel oak (*Q. gambelii*), and 2) foothill-montane temperate grasslands (blue grama grass [*Bouteloua gracilis*], New Mexico needlegrass [*Achnatherum perplexum*], western wheatgrass [*Pascopyrum smithii*]; Muldavin et al. 2000a and 2000b).

Focal species

We addressed our objectives by use of disjunct pinyon-juniper woodland populations of the Oscura Mountains Chipmunk (hypothesized habitat specialist; O'Connell and Frey 2024) and brushmouse (hypothesized habitat generalist; Kalcounis-Rueppell and Spoon 2009). Although these two species have quite different evolved life history traits, they were selected not because they equate to a particular lifestyle, but because they were by far the most abundant species of small mammal within the biome surrounding our study area. The Oscura Mountains Chipmunk, a subspecies of the Colorado chipmunk, is a unique endemic. It is diurnal and associates predominantly with mesic pinyon-juniper woodland. It is the sister-subspecies to the Organ Mountain chipmunk (*N. q. australis*) found ~170 km south along the semi-arid San Andres Mountain corridor (Patterson 1980; Sullivan

1996). Conversely, the ubiquitous brushmouse is a cricetid rodent found within mountainous regions of the southwestern United States and northern Mexico. It typically occurs above ~1,500 m, is generally crepuscular or nocturnal, and normally prefers pinyon-juniper zones, brushy scrub oak woodland, and canyon-creek bottoms.

Grid sampling

Our study was conducted over an 18-month period. We conducted capture-recapture live-trapping by use of two grids (Grid 1 and Grid 2) of 100 Sherman live-traps each (23.5 × 7.5 × 9 cm; H. B. Sherman Traps, Tallahassee, FL, USA). Each trap was spaced 10 m apart (100 quadrants, 1 ha) and we assumed that each trap sampled an area of ~10 m on each side of the trap placement. Both grids were positioned on NOP in two separate locations (~2.1 km apart) within mature and multi-aged stands of pinyon-juniper woodland. We draped the first 10 live-traps in each grid over the limestone escarpment-cliff edge, which extended vertically downward to the basin floor below. The second tier of traps was placed along the edge of the escarpment, while the remaining 80 traps in each grid extended back away from the escarpment into interior woodland habitat.

We live-trapped animals from November 1996 through May 1998, but not during December of 1996 because of snow. Trapping episodes began during the second week of each month. Traps were set during an interval of 3 days (2-nights)/month, which resulted in 5,400 trap days/grid and 3,600 trap nights/grid. Live-traps were baited with oatmeal and peanut butter and checked at sunrise (~7:00), noon (12:00), and sunset (~17:00) weather and WSMR range closings permitting (weapons testing, explosive detonations, training maneuvers). Because our traps were not checked at night our analysis only represents diurnal activity patterns for both species. To reduce trapping-related mortalities, caused by rain and cool temperatures, we supplied each trap with a dry, cotton nestlet (nesting material). All individuals were identified to species, age (adults vs juveniles based on size and pelage color), sex, and reproductive condition (lactating vs testes scrotal). Time of capture and location of each trap in each quadrat by grid was recorded. Each individual was toe-clipped for identification and released at the capture site (Rudran 1996).

Spatial structure and demographics

We evaluated the dispersion pattern for spatial points within each grid by use of the quadrat test (χ^2 ;

Package “spatstat”, ver. 1.64-1). We gauged spatial randomness for a given point pattern based on quadrat counts assuming a null hypothesis of complete spatial randomness (Cressie and Read 1984; Baddeley et al. 2015). Area (volume) of each home range was estimated by use of the Exclusive Boundary Strip (EBS) method (ha) and Adjusted Range Length (ARL [m]) measured maximum length of each home range (Jennrich and Turner 1969; Brown and Orians 1970). We used the Package “Recapture” (ver. 1.4-4) for analysis of live-trapped capture-recapture data by use of the Jolly-Seber model (Caughley 1977; Wilson et al. 2011). This function used Poisson regressions to estimate various demographic parameters using a loglinear model for open populations (function “openp”) capture-recapture experiments. We used an open-population architecture for both species to estimate: 1) seasonal variance in population size, 2) model fit (deviance [Dev_m]), 3) capture probabilities, 4) survival probabilities, and 5) total number of units (n = individuals) that potentially ever inhabited the survey areas (grids) for each species.

Microhabitat variables

We used 10 microhabitat variables potentially important in influencing the distribution of chipmunks and brushmice at each trap-station for both grids: 1) percent slope (slight < 25° moderate > 25° and < 50°, steep > 50° and < 75°, extreme > 75°; 2) percent exposure in degrees (N, NE, NW, S, SE, SW, W, E); 3) distance to nearest tree (m) from trap-site (tree = any plant > 3 m tall with a trunk > 10 cm in diameter); 4) distance to nearest shrub (m) from trap-site (shrub = any plant < 3 m tall with a diameter < 10 cm in diameter); 5) distance to escarpment-cliff edge (m); 6) percent substrate upon which animal was captured (ground, rock, slash or brush pile, shrub, tree, log); 7) percent rock abundance within a 3-m radius of observation/trap-site (none, sparse, moderate, dense); 8) percent rock type within 3-m radius of observation/trap site (gravel, boulder, rock slab, cliff edge); 9) percent overstory cover (amount of light cast on a 3-m tape laid at right angles to observation/trap site (0–5, 6–25, 26–50, 51–75, 76–95, 96–100%); and 10) percent ground cover within a 3-m radius of observation/trap-site (none, forbs, grass, shrub, tree). We used Principal Components Analysis (PCA) modeled on scaled (standardized) variables to find the extent of association among microhabitat attributes, and to assess the relative ability of each parameter to explain variation between grids for each species. Range-wide microhabitat and suitability models, which followed our initial analyses in the late 90s, are provided elsewhere (Perkins-Taylor and Frey 2018 2020; O’Connell and Frey 2024).

Climatic variables and redundancy analysis

Our assessment of climate included 8-average monthly covariate predictors: 1) temperature, 2) solar radiation (Ly), 3) dew point (C), 4) humidity (%), 5) pressure (mb), 6) peak wind speed (kts), 7) wind direction (degrees), and 8) precipitation (mm) (Table S1; Fig. S1). These variables were used to evaluate variance in monthly mean climatic (seasonal weather) parameters for comparison with trends in the monthly live-trapped chipmunks and brushmice. Each climatic covariate has historically been recorded hourly at the NOP meteorological station for many years. Thus, we assumed that these covariate metrics were representative of weather conditions at both grids during the duration of our study given their proximity to NOP (straight line distance ~0.23 km to Grid 1, ~2.4 km to Grid 2). Because precipitation occurred so infrequently during our study, we used average monthly values obtained at Carrizozo, NM (~43 km from NOP; between 1981–2010) in our analysis of this variable. This allowed us to minimally evaluate the trend in seasonal precipitation in relation to monthly abundance of chipmunks and brushmice.

We used Redundancy Analysis (RDA) to test hypotheses about drivers of monthly seasonal patterns in the response matrix (totals “abundance” of individuals by month across grids) versus variance in our matrix of average monthly climatic attributes (Package “vegan” ver. 2.6-8). This function is a direct extension of multiple regression, to model the effect of a linear combinations of the predictor variables (standardized explanatory matrix-X of monthly climatic metrics) on the response matrix-Y (monthly species presence) to model the effect (maximum variation) of the explanatory matrix-X on the response matrix-Y. This process performs an ordination of the matrix-Y to obtain ordination axes that are linear combinations of the climatic matrix-X, which results in summary statistics, significance testing, and RDA plots to visualize the relationships between the two sets of variables. We used the function “vif.cca” (Program “vegan” ver. 2.6-8) to check for variance inflation factors in our hypothesized climate drivers.

Statistical analyses

We performed all analyses using programs that run on the R Statistical Software platform (R Core Team 2024, ver. 4.3.3) and set statistical significance at $\alpha < 0.05$. We used the Shapiro–Wilk’s statistic (W , Program “stats”, ver. 3.6.2) to test for normality in the distribution of animals within quadrants of each grid. We used the Package “fitdistrplus” (ver. 1.1-11) to

visually assess best fit to these data by use of Akaike's goodness of fit criterion (AIC; Akaike 1973). We used the Kruskal-Wallis (*KW*) non-parametric analysis of variance (ANOVA) rank sum test (Package "stats" ver. 3.62) to evaluate the null hypothesis of no significant difference between best fit distributions and timing of diurnal activity between species and between grids. We used the Spearman's rank correlation coefficient (r_s ; 2-tailed test; Package "easystats" ver. 0.7.1) to calculate the strength and direction of the relationship between numbers of individuals in each monthly age and sex category, and between species variables. We used the nonparametric Wilcoxon signed-rank test (*V*; Package "stats") with continuity correction to compare samples between grids based on paired microhabitat variables. We used semi-parametric Generalized Additive Models (GAM; Package "mgcv") in all regressions of density on frequency of quadrat use and climatic variables. We used a Poisson error-structure (family = "Poisson" [link = "log"]) to establish the relationship between response variables and smoothed functions of predictor variables. Statistics reported from each model included GAM *F*-statistic, *p*-value, 95% confidence bands for spline lines, adjusted regression coefficient (R^2) for the model, and proportion of null deviance explained (DevExp).

RESULTS

Theoretical density plots and density landscape

Pooled across both grids our live trapping produced 218 chipmunks (29.3%), 479 brushmice (64.3%), 10 deer mouse (*P. maniculatus*, 1.3%), 6 white-throated woodrats (*Neotoma albigula*, 0.8%), 16 rock squirrels (*Spermophilus variegatus*, 2.1%), and 16 Texas antelope ground squirrels (*Ammospermophilus interpres*, 2.1%). Data used in theoretical density plots and GAM regressions of quadrats where chipmunks and brushmice were captured are found in table S2 and summarized in figure S2. Shapiro-Wilk tests for normality showed that the specific quadrants where individuals of each species were live-trapped were not normally distributed within each grid. GAM modeling showed that the trend in concentration of animals toward the escarpment-cliff edge for chipmunks was significant for both grids (Fig. S2A, S2C). Yet while there was a significant decreasing trend in use of specific quadrants for brushmice on Grid 1, this was not the case for Grid 2 (Fig. S2F, S2H). For all species and grids, R^2 was not strong and the amount of variation explained was low.

Our 3-dimensional density plots of live-trapped chipmunks showed a highly aggregated spatial

distribution among quadrants (Fig. 2A, 2B); which departed significantly from a random distribution ($\chi^2 = 59.0$, *d.f.* = 24, $p < 0.001$ and $\chi^2 = 107.3$, *d.f.* = 24, $p < 0.001$, respectively).

Chipmunks were predominantly seen along NW-facing escarpment-cliff edges, shaded by thick stands of pinyon-juniper-oak woodland. For Grid 1, 71.4% ($n = 69$) of chipmunks live-trapped were within 10 m of the escarpment-cliff ledge and for Grid 2 it was 44.8% ($n = 149$). In contrast, brushmice were live-trapped in quadrants that were distributed to a greater extent throughout the interior woodland habitat compared to chipmunks (Fig. 2C, 2D). Although the spatial distribution of brushmice also deviated significantly from a random distribution on both grids ($\chi^2 = 213.9$, *d.f.* = 24, $p < 0.001$ and $\chi^2 = 111.4$, *d.f.* = 24, $p < 0.001$, respectively), the tendency to associate with rocky limestone-cliff face was considerably more subdued compared to chipmunks.

Seasonal and diurnal variation in activity patterns

Our seasonal data showed that adult chipmunks were most commonly live-trapped during the months of March, April, May, June, and July (Fig. 3A; Table S3A), which included both reproductive and non-reproductive seasons. December was the only month in which chipmunks were not seen or live-trapped on either grid, or because we could not get to the site due to snow in 1996. During winter, chipmunks were occasionally active when snow was on the ground, but these individuals were only seen or trapped during the mid-afternoon on sunny non-windy days. Adult brushmice, however, tended to be most commonly live-trapped during June, July, and surprisingly in November; however, they were also active during all other months (Fig. 3B; Table S3B).

Diurnal activity in live-trapped chipmunks occurred predominantly during the noon time (47.4%, $n = 218$), but they were about equally active in early morning (27.0 %) and late afternoon (25.6%, Fig. 3C). Peak activity in live-trapped brushmice was somewhat earlier in the morning (42.0%, $n = 479$) and at noon (46.8%), with a small pulse of activity in the late afternoon (11.3%, Fig. 3D). Overall, there was a significant difference in the timing of activity between species when both sexes and grids were combined ($KW = 24.3$, *d.f.* = 1, $p < 0.001$). Similarly, there was a significant difference between grids in the timing of diurnal activity for chipmunks, with individuals more active in the morning and around noon ($KW = 6.1$, *d.f.* = 1, $p = 0.014$). Yet we found no significant difference between grids for brushmice ($KW = 1.8$, *d.f.* = 1, $p = 0.185$).

Reproductive activity

Seasonal distributions of age, sex, and reproductive condition for chipmunks and brushmice live-trapped on Grid 1 and Grid 2 combined are illustrated in figure 3A and 3B (Table S3A and S3B). Chipmunks appeared more active on grids during spring while brush mice were more active in late summer; however, brushmice were more active throughout the year than chipmunks. Peak activity for all live-trapped sex and age classes of chipmunks showed the same general pattern of monthly seasonal activity. For chipmunks, 52.5% of live-trapped individuals were males, 44.0% females, and 3.2% subadults of both sexes (Table S3A). For brushmice 43.4% were males, 41.8% were females, and 14.8% were subadults of both sexes. The percentage of male chipmunks with scrotal testes was 68.7% (79/115) and for lactating females 51.0% (49/96). In brushmice the percentage of males with scrotal testes was 30.8% (64/208) and for lactating females 24.5% (49/200; Table S3B).

Reproductively active male chipmunks (scrotal testes) appeared in February through November (Fig. 3A); and peak reproduction occurred in May,

which equated to 75.9% (22/29) of the total number of adult males live-trapped during this time interval (Table S3A). Reproductively active (lactating) female chipmunks appeared in March through September, which suggested that conception occurred during the winter period of least activity (Fig. 3A). During peak reproduction also occurred in May, where lactating females equaled 80.0% (20/25) of the total adult females live-trapped during that month (Table S3A). There was no indication of a “bi-modal” pattern of seasonal reproduction, although one lactating female was handled in September. Our data showed a common pattern in peak seasonal reproduction occurring in May for both adult male and adult female chipmunks (27.8% [22/79] vs 40.8% [20/49]), respectively; Table S3A).

In male brushmice, reproductively active individuals (scrotal testes) appeared in March through October (Fig. 3B). Peak reproductive condition occurred in July and August, which equated to 91.7% (22/24) and 100% (17/17) of the total number of adult males trapped during this period, respectively (Table S3B). We live-trapped reproductively active female brushmice beginning in May through November (Fig. 3B). Peak lactation in August, September, and October equated to

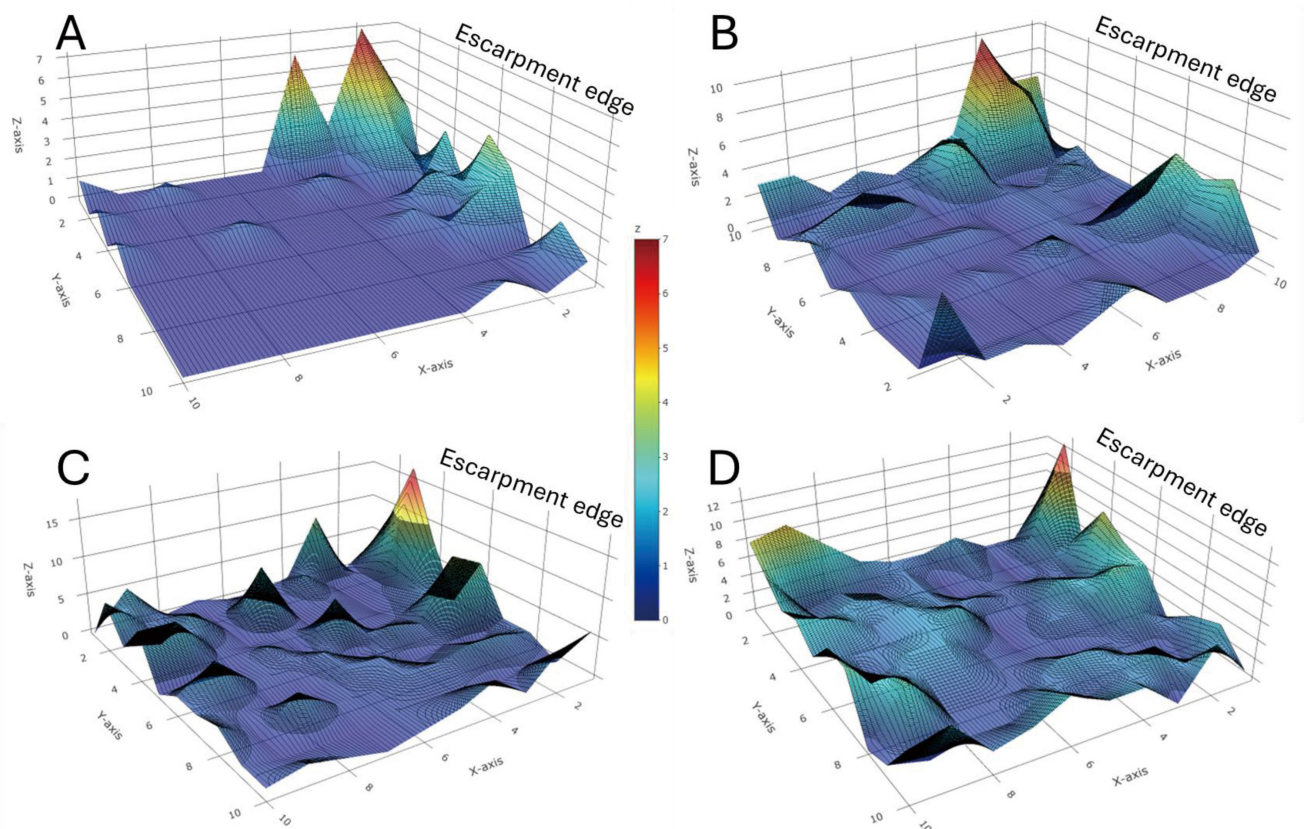


Fig. 2. Three-dimensional density plots showing the spatial landscape (distribution) of animals live-trapped within quadrants for *Neotamias* (A = Grid 1, B = Grid 2) and *Peromyscus* (C = Grid 1, D = Grid 2).

70.6% (12/17), 100% (11/11), and 50.0% (10/20) of the total number of females live-trapped during this period, respectively (Table S3B). Unlike chipmunks, lactation in female brushmice lagged behind development of scrotal testes in males, such that the peak pattern of reproductive activity between sexes was out of sync by one month. Overall, the correlation between total numbers of individuals in each monthly age (adult, subadult) and sex category, between chipmunks and brushmice, was significant but the strength of the relationship was not particularly strong ($r_s = 0.280$, $p = 0.028$, $n = 60$).

Mark-recapture and population density estimates

Our mark-recapture analyses showed that the estimated monthly population sizes were largely consistent with seasonal trends in both chipmunks (Fig. 4A, 4B) and brushmice (Fig. 4C, 4D). In all capture-recapture analyses model fit (Dev_m) was smaller for

chipmunks than for brushmice. Estimates of capture probabilities were not particularly high for chipmunks (Grid 1 = 0.30 [SE = 0.14], Grid 2 = 0.58 [SE = 0.17], or brushmice Grid 1 = 0.39 [SE = 0.16], Grid 2 = 0.57 [SE = 0.16]). However, estimates of survivability for chipmunks (Grid 1 = 0.78 [SE = 0.17], Grid 2 = 0.83 [SE = 0.14]) and brushmice were comparatively strong (Grid 1 = 0.72 [SE = 0.16], Grid 2 = 0.71 [SE = 0.25]). Model estimates of the total number of chipmunks estimated to “ever” inhabited each grid was 24.9 for Grid 1 and 34.8 for Grid 2, and for brushmice it was 55.9 for Grid 1 and 60.5 for Grid 2.

Despite small sample sizes, female chipmunks had significantly larger ARL compared to males for pooled grids ($KW = 6.2$, $d.f. = 1$, $p = 0.010$; Table S4). Average ARL for adult female chipmunks was 103.3 m (80–110 m) and for adult males it was 73.5 m (35–110 m). Average EBS for adult female chipmunks was 0.33 ha (0.16–0.51 ha) and for adult males it was 0.21 ha (0.09–0.58 ha). Although female chipmunks had

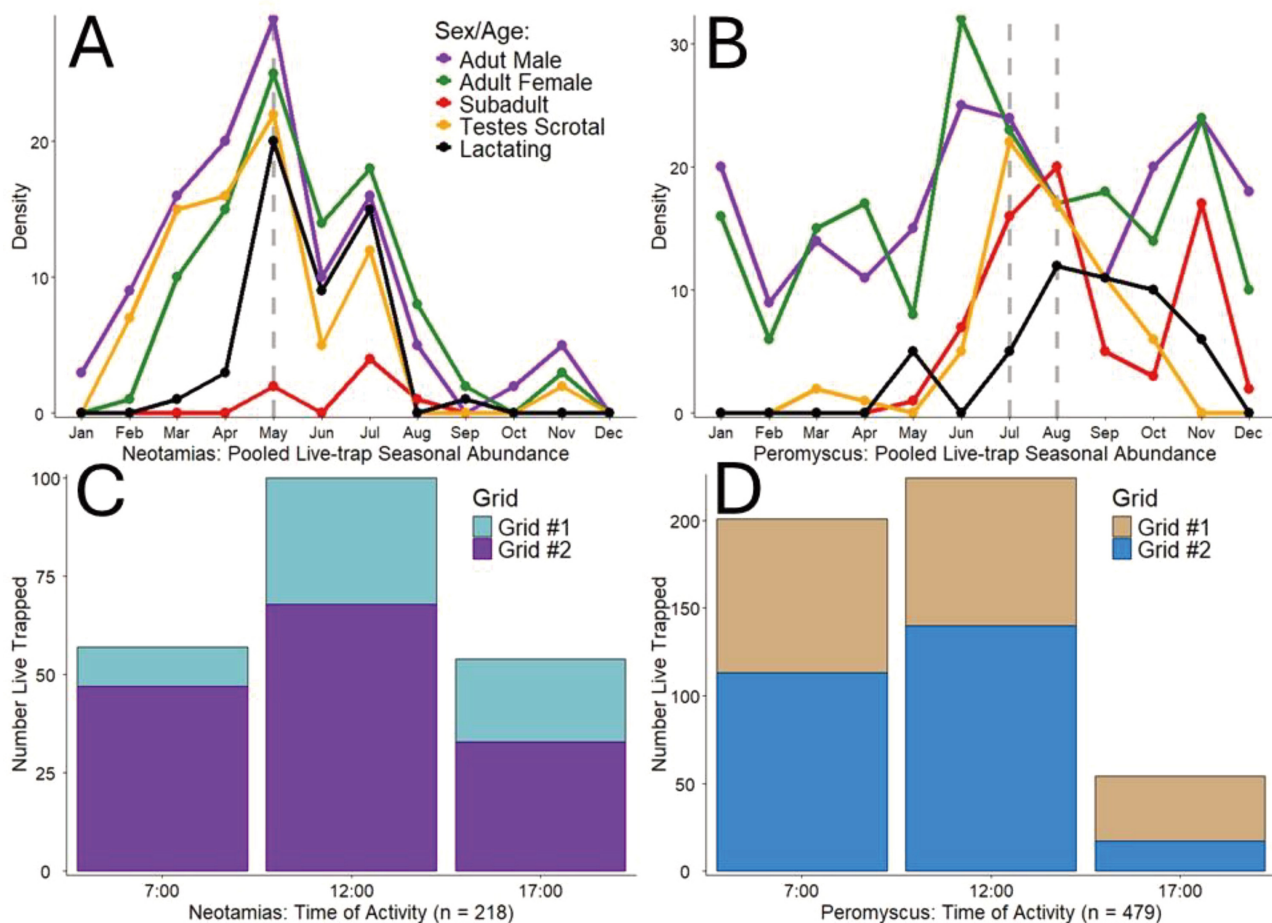


Fig. 3. Seasonal (monthly) activity of individual, age, sex, and reproductive condition for pooled grids (A = *Neotamias*, B = *Peromyscus*) based on live-trap data. Dashed vertical lines colored gray in figure 3A and 3B index months for which each species was most reproductively active based on live-trap data. Histograms of theoretical density distributions based on diurnal activity patterns for C = *Neotamias* and D = *Peromyscus*.

significantly larger EBS than did males, the difference between sexes was barely significant ($KW = 4.4$, $d.f. = 1$, $p = 0.040$; Table S4). Additionally, there was no significant difference in either ARL or EBS between sexes of brushmice for pooled grids ($KW = 0.01$, $d.f. = 1$, $p = 0.930$ and $KW = 0.81$, $d.f. = 1$, $p = 0.370$; Table S4). Average ARL for adult female brushmice was 78.8 m (12–120 m) and for adult males it was 81.1 m (30–140 m) and average EBS for adult female brushmice was 0.14 ha (0.015–0.34 ha) and for adult males it was 0.15 ha (0.050–0.34 ha).

Microhabitat descriptions for live-traps on grids

We found no significant difference ($V = 304$, $p = 0.700$) between grids based on paired percent use values of microhabitat variables (Table S5), as these two vectors were highly correlated ($r_s = 0.910$, $p > 0.001$, $n = 35$). Principal components analysis of microhabitat parameters accounted for a cumulative 55.7% and 71.5% of the total dispersion among attributes on the first two vectors for chipmunks and brushmice, respectively (Table 1). Vector loadings, variable relationships, and direction of each arrow showed that distance to the nearest tree, shrub, and escarpment-cliff

edge, and rocky, loaded positive for chipmunks along Dimension 1 and Dimension 2 (Fig. 5A). Conversely, in brushmice, slope, substrate, ground cover, and rocky habitat loaded positive along these same two vectors (Fig. 5B). Additionally, tree species composition for Grid 1 was 49.0% pinyon and 51.0% juniper but on Grid 2 it was 64.0% pinyon and 35.0% juniper. The two most common species of shrubs on Grid 1 were mountain mahogany (*Cercocarpus montanus*, 40.0%) and ashy silktassel (*Garrya flavescens*), but on Grid 2 they were mountain mahogany (33.0%) and Gambel oak 26.0%.

Climatic variables and redundancy analysis

A check for variance inflation factors in our climatic predictors found that only 62.5% (5/8) of the climatic covariates had inflation values below 10 (humidity = 2.9, solar radiation = 6.5, temperature = 4.4, wind direction = 3.5, wind speed = 3.2), which indicated that multicollinearity was not a major problem for these remaining variables for use in our RDA model (Zuur et al. 2010). Results of our RDA showed a total of 75.4.0% of the variance in the monthly presence of chipmunks and brushmice in the study area was

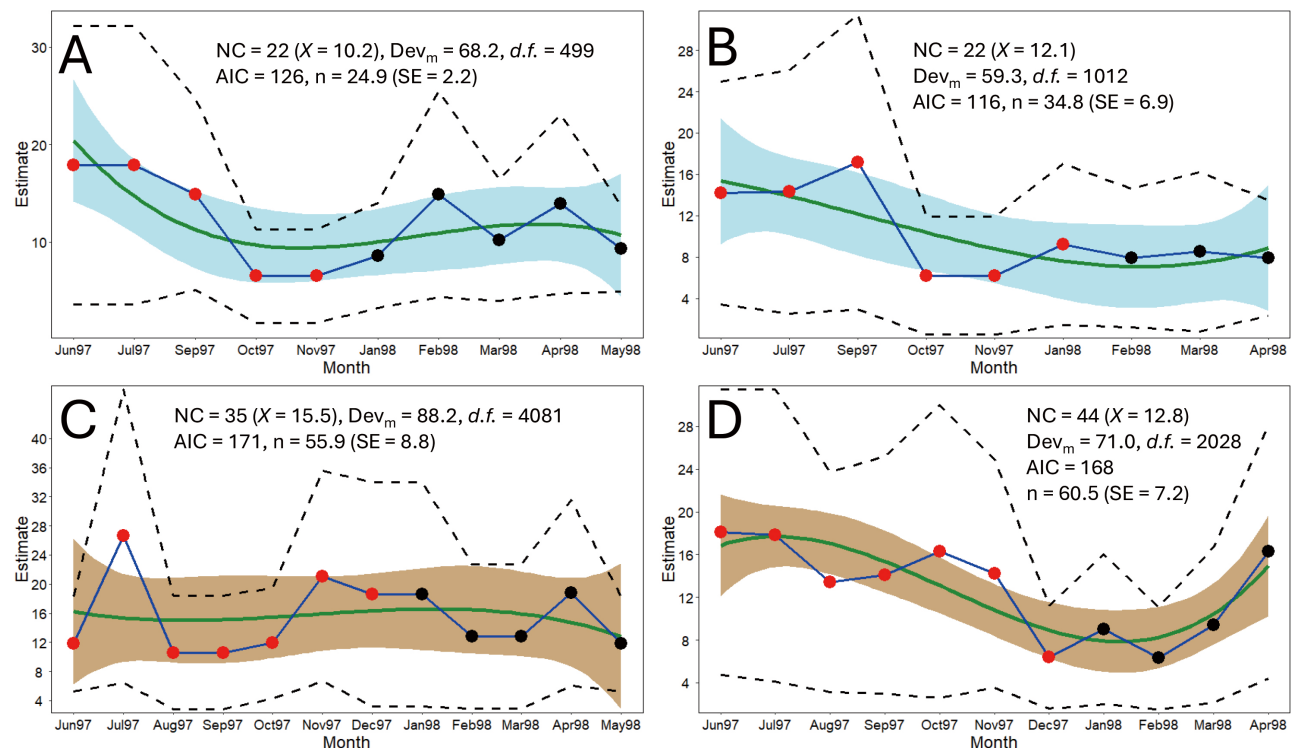


Fig. 4. Monthly capture-recapture totals (1997 = red, 1998 = black points) for *Neotamias* (Grid 1 = A, Grid 2 = B) and *Peromyscus* (Grid 1 = C, Grid 2 = D); n = predicted total number of individuals that “ever” inhabited each grid (X = average), NC = total individuals (standard error [SE]) captured, AIC = Akaike’s goodness of fit criterion, Dev_m = fitted model deviance, dashed line = 1 SE around population size estimate, and ribbons = 95% confidence band around green colored smoothed spline.

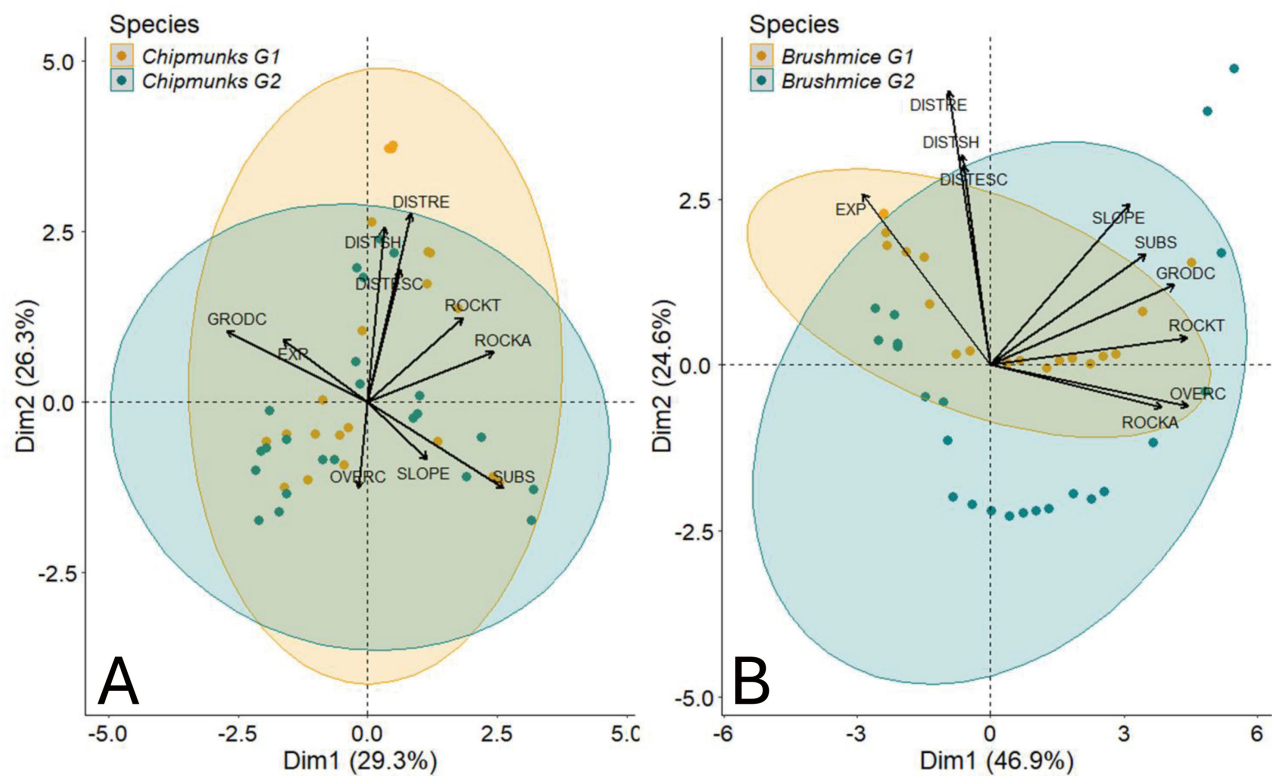


Fig. 5. Principal Components Analysis of microhabitat values associated with A) *Neotamias* and B) *Peromyscus* (grids pooled). EXP = exposure, GRODC = ground cover, DISTESC = distance to escarpment-cliff edge, DISTRE = distance to nearest tree, DISTSH = distance to nearest shrub, ROCKA = rock abundance, ROCKT = rock type, and SLOPE. Areas shaded = 95% confidence ellipses.

Table 1. A) Eigenvalues, percent variance, and cumulative variance explained for each species on the first two vectors each Principal Component axis (Dim). B) Loading derived from the PCA are provided for each microhabitat variable on each component axis

A) Eigenvalues, percent, and cumulative variance				
Eigenvalues	Chipmunks		Brushmice	
	Dim1	Dim2	Dim1	Dim2
Variance	2.9	2.6	4.7	2.5
Percent variance explained	29.3	26.3	46.9	24.6
Cumulative percent variance explained	29.3	55.7	46.9	71.5
B) Loadings				
Microhabitat variables	Chipmunks		Brushmice	
	Dim1	Dim2	Dim1	Dim2
Slope (%)	0.368	-0.269	0.666	0.444
Exposure (%)	-0.519	0.290	-0.615	0.378
Substrate type (%)	0.839	0.407	0.746	0.556
Rock abundance (%)	0.776	0.234	0.820	0.673
Rock type (%)	0.586	0.395	0.943	0.889
Overstory vegetation cover (%)	-0.056	-0.407	0.947	0.897
Ground cover (%)	-0.869	0.328	0.884	0.781
Distance to nearest tree (m)	0.265	0.881	-0.198	0.039
Distance to nearest shrub (m)	0.102	0.886	-0.135	0.018
Distance to escarpment-cliff edge (m)	0.200	0.620	-0.128	0.016

explained by the constrained set of average monthly climatic variables (Table 2A). The remaining 24.6% of the total variance in the dataset was unconstrained and could not be explained. Given that the constrained variance was higher than the unconstrained variance, our analysis suggests that most of the variation in monthly abundance of species was accounted for by the monthly climatic attributes retained above. Importantly, we note that the total variance in the dataset that formed the constrained proportion (75.4%) was not the overall importance of each axis compared to the total variance in the dataset. Rather, it was the proportion of the variance in the accumulated constrained eigenvalues in the rescaled environmental explanatory variables for

RDA1 (57.5%) and RDA2 (42.5%).

Multiplying those two values by the proportion of total constrained variance (75.4%) yields 43.4% (RDA1) and 32.0% (RDA2), which was the relative amount of variance explained (contribution) by our RDA model along RDA1 and RDA2 (Table 2B). Nonetheless, this cumulative proportion also gives a value of 75.4% of the variance explained in our model for the first two axes. Given that there is a relatively large proportion of unconstrained variation (24.6%) in the dataset, our results should be interpreted with caution.

Relative importance of the axes for both constrained and unconstrained models shows that the two RDA axes are constrained to maximize the

Table 2. Redundancy Analysis (RDA) and eigenvalue and permutation tests (999 permutation tests) for RDA model. RDA1 and RDA2 = constrained axes; PCA 1 and PCA2 = unconstrained axes; *d.f.* = degrees of freedom. Bold indicates $p < 0.05$

A) Redundancy Analysis				
Partition of total variance in dataset		Accumulated constrained eigenvalues		
Components	Proportion	Components	RDA1	RDA2
Total	1	Eigenvalue	246.5	195.3
Constrained	75.4%	Proportion explained	57.5%	42.5%
Unconstrained	24.6%	Cumulative proportion	57.5%	100%
B) Eigenvalues contribution to variance in RDA model				
Importance components	RDA1	RDA2	PC1	PC2
Eigenvalue	264.5	195.3	120.4	29.6
Proportion explained	43.4%	32.0%	19.7%	4.9%
Cumulative proportion	43.4%	75.4%	95.2%	100%
C) ANOVA for overall RDA model				
	<i>d.f.</i>	Variance	<i>F</i> -value	<i>p</i> -value
Model	5	459.7	3.8	0.013*
Residual	6	150		
D) ANOVA for each RDA model term				
Variables	<i>d.f.</i>	Variance	<i>F</i> -value	<i>p</i> -value
Average temperature (C°)	1	158.5	6.3	0.010*
Humidity (%)	1	100.1	4.0	0.041*
Peak wind speed (kts)	1	16.2	0.6	0.588
Solar radiation (Ly)	1	166.0	6.6	0.014*
Wind direction (degrees)	1	19.0	0.8	0.502
Residual	7	150.0		
E) ANOVA for RDA model by canonical axis				
Axes	<i>d.f.</i>	Variance	<i>F</i> -value	<i>p</i> -value
RDA1	1	264.5	15.9	0.016*
RDA2	1	195.3	11.7	0.184
Residual	9	150.0		

correlation between the response and explanatory variables, as each axis was a multiple regression model based on all explanatory variables, that yield fitted values for the response. Unconstrained axes resulting from PCA on residuals shows the amount of variation not related to the set of explanatory variables, but that was not a topic of interest in our analysis. Although the overall solution of our RDS analysis was statistically significant, compared to a null model (Table 2C), only average monthly temperature, percent humidity, and solar radiation (Table 2D), and the first canonical axis (Table 2E) were significant in the RDA model. Additionally, the canonical relationship adjusted for the number of explanatory variables ($R^2_{\text{adj}} = 0.549$) showed a rather weak linear relationship between the predictor matrix (X) and the response matrix (Y).

The coefficient associated with explanatory variables showed a relatively broad distance between species on both RDA axes (biplot, Type II scaling; Fig. 6). Measurements of temperature and solar radiation clustered together and loaded positively along RDA1; whereas measured humidity, peak wind speed, and wind direction clustered together, but loaded negatively along RDA1. Length of the arrow for humidity was heavily influenced by winter compared to wind direction and peak wind speed. Collectively, the covariant relationship between temperature, solar radiation, and humidity

strongly drove variation in the seasonal climatic matrix, consistent with seasonal trends in abundance for both species being most active during the warmest seasons (summer, spring, early fall) and less active during winter and inclement freezing weather.

DISCUSSION

Spatiotemporal variance

Our analysis of archival data showed considerable variance in the spatial patterns of syntopic populations of chipmunks and brushmice associated with limestone escarpment-cliff edges within pinyon-juniper woodlands. Live-trapped animals showed highly aggregated and nonrandom spatial distributions for both species. Chipmunks used NW-facing limestone escarpment-cliff edges shaded by thick stands of pinyon-juniper woodland disproportionately compared to brushmice, while brushmice were significantly more widespread in their spatial distribution, which included interior woodlands away from limestone escarpment-cliff edge habitats.

Variance in diurnal and monthly activity patterns of both species was determined largely by seasonal area climate. Chipmunks especially altered activity periods

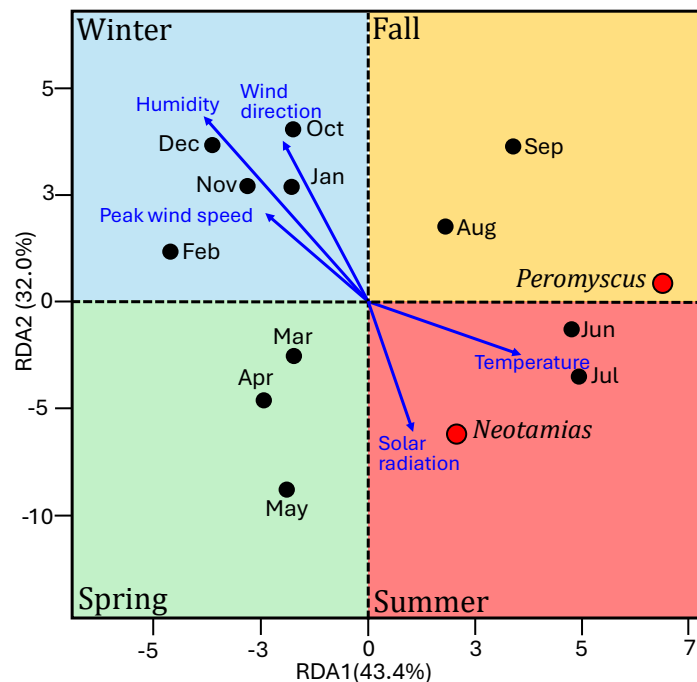


Fig. 6. RDA model biplot of species seasonal presence on monthly climatic vectors (scaling type = 2). Length of arrows show relative strength of each predictor and their correlation with each ordination axes. Longer arrows show variables that strongly drive variation in the community matrix (a measure of fitness for species). Arrows pointing in opposite directions have a negative relationship and those pointing in same direction have a positive relationship. Vectors show direction of each explanatory variable most strongly associated with each axes. Months are abbreviated.

according to daily and seasonal climatic conditions even during harsh weather, as activity patterns tended to be more reduced during cooler climate centered on the middle part of the day and season. Chipmunks were not particularly active during the most severe winter period, except at lower elevations downslope and within the ecotone between pinyon-juniper woodlands and montane scrub (mountain mahogany, and wavyleaf oak (Sullivan and Wilson 2001). Brushmice diverged from this pattern somewhat, in that they were generally active year-round.

Reproductive activity (scrotal testes in males, lactation in females) and grid-based estimates of population size showed seasonal trends based on heterogeneity in climate. For these two life-history parameters, both species responded positively to equitable temperature regimes as reflected in our RDA model; warmer temperature and solar radiation were the primary drivers of reproduction and estimates population sizes. In terms of carrying capacity and grid size within the sample area, contemporary comparisons of habitat quality could use our information as an historical baseline estimate for management. Viewed collectively, contemporary and future monitoring of variance in climatic parameters would seem critical in maintaining a healthy escarpment-based pinyon-juniper woodland ecosystem, when managing for co-occurring heterospecific species, particularly in the context of continued climate change.

Reproductive patterns

Throughout much of its range, the Colorado chipmunk breeds in late spring; however reproductive activity of the Organ Mountains subspecies is bimodal (late winter/early spring vs. July-early October), coincident with the summer monsoon season (Patterson 1980). Yet we found no sign of a bi-modal pattern of reproduction in the Oscura Mountain subspecies. Instead, our analysis showed that chipmunks breed in early spring, as lactation begins in early March and extends through early September. Females with embryos (4–11 mm) were collected in early April and development of testes in males varied from 4 mm in mid-September to 12 mm in mid-April (Sullivan 1996). The Oscura Mountains chipmunk, therefore, appears to have a pattern of reproduction intermediate between the subspecies to the north (*N. q. quadrivittatus*) and the Organ Mountain subspecies to the south (Patterson 1980; Sullivan and Wilson 2001).

Population dynamics of desert rodents is hypothesized to be driven chiefly by resource pulses induced by rainfall events (Shenbrot 2014). Yet timing of early spring conception and lactation in the Oscura

Mountains subspecies appears coincidental with periods of reduced water stress and increased primary productivity (Patterson 1980; Sullivan and Wilson 1991; Sullivan 1996), as procurement of foodstuffs during the most productive growing season enhances reproductive output. Still, our RDA analysis found no strong covariance between seasonal rainfall frequency and activity of chipmunks (or brushmouse). Alternatively, both the Oscura and Organ mountains subspecies may initiate breeding early in the season in response to the onset of precipitation during the summer monsoon season.

An alternative hypothesis, however, suggests that both the Oscura and Organ mountains subspecies may start breeding early in the season in response to the onset of precipitation during the summer monsoon season, thus extending reproduction as long as possible to increase success of early season litters (Fry and Kopp 2013). Although the breeding regime of these two subspecies of chipmunk remains unresolved, both explanations are likely interconnected and warrant further research. Viewed in the context of historical rainfall data, monitoring for reproductive optimization in relic heterospecific semi-arid communities of focal species should be considered a priority management strategy.

Microhabitat analyses

Our study found that microhabitat use was highly correlated with the distribution of limestone escarpment-cliff edges, especially characteristic of chipmunks. Brushmice used different resource vectors within the microhabitat spectrum, as reflected in their expanded spatial distribution into interior of woodland habitat. Modeled estimates of the number of chipmunks to have “ever” inhabitant the study area were much higher for Grid 2 than Grid 1, likely based on variance in the multifaceted resource base. For example, on Grid 2: 1) average distance to the nearest pinyon tree and escarpment-cliff edge were smaller, 2) percentage of rock abundance was somewhat larger, 3) density of pinyon trees was greater, and 4) diversity of shrubs included an added mast crop (Gambel oak) virtually absent on Grid 1. These microhabitat characteristics indicate a more diverse habitat/resource base available on Grid 2 than on Grid 1. Thus, providing a potential explanation for discrepancy in estimated population size between grids (24.9 vs 34.8), a further indication that the “quality” of suitable habitat is not evenly distributed across the woodland-escarpment landscape.

Cashes of mast foods are an essential part of total primary production in woodland ecosystems, which function as primary food sources primarily for

overwintering chipmunks (Sullivan and Wilson 2001; O'Connell and Frey 2023 2024). Seeds of juniper, pinyon, and oak are the only source of tree recruitment, which function as a vital food staple for numerous taxa (Chambers 1999; Zlotin and Parmenter 2008). Similarly, brushmice are also heavily dependent on rocky refuges within this woodland community for shelter, nesting, which provide multiple food storage sites year-round. Even when snow or ice blankets the ground, there are still terrestrial non-insect arthropods under leaf litter, rocks, and within decaying wood, mast crops, mistletoe, ash silk-tassel, and fruits-seeds of prickly pear cactus (*Opuntia* spp) lying about the landscape (Jameson 1952; Smartt 1978). Nevertheless, productivity of pinyon-juniper-oak mast (cones, seeds, berries, acorns) can be highly variable (Zlotin and Parmenter 2008; Gibson 2023; O'Connell and Frey 2023). Pinyon trees reproduce only by seed and crops of cones produced every two to six years, followed by multiple years of low cone production (Betancourt et al. 1993). On average, mast crops occur in one to three out of every ten years, and juniper mast crops (berries/seeds) may cycle production of large volumes of mast only every two to five years (Gori and Bate 2007).

Because the quality of rocky escarpment-cliff edge is limited in area, has a patchy distributed, and occurs within a highly fragmented landscape, it represents a "critically" important habitat type within communities of woodland species. As such, the biotic and physical characteristics of the local environment constitutes critical habitat for co-occurring taxa because it provides the primary source of: 1) food, 2) cover, 3) shelter, and 4) nesting site microclimate necessary to sustain continued survival and reproduction during severe inclement weather. No other concomitance of environmental factors appears to be more important to the survival of this endemic subspecies of chipmunk, or potentially other unique disjunct population or species (terrestrial snails, woodrats (Sullivan 1997), which also co-occur with chipmunks and brushmice in the Oscura Mountains (Sullivan 1994; Sullivan and Smartt 1995). Continued management for optimal suitable habitat for communities of syntopic species, relative to baseline conditions, is an issue for long-term conservation in relic limestone edge ecosystems.

CONCLUSIONS

Many contemporary landscapes have departed fully from historical conditions making it difficult to determine if they should be managed as novel environments, or landscapes in transition or under recovery (Cissel et al. 1994; Laughlin et al. 2004).

Importantly, historical representations may describe entirely functional or healthy ecosystems key to understanding current or potential future disturbance impacts, thus facilitating sound ecosystem management long-term (Wiens et al. 2012; Loehman et al. 2014). Moreover, knowledge of historical spatiotemporal patterns of syntopic species assemblages may afford a level of guidance that allows managers to track multifaceted ecological variance over time within a particular focal landscape (Alagona et al. 2012). In the North American Southwest, a goal of resource management must be to preserve biological diversity in these relic, mountaintop ecosystems, which represent unique-biogeographic links to the evolutionary history of the region. Within these fragmented woodland and montane forest environments, special effort must be made to preserve as much of the heterospecific community pool as possible. This process plays a crucial role in shaping ecosystems and promoting and maintaining biodiversity in an era of rapid climate change.

Our findings underscore the need to formally understand the spatiotemporal regime (Parrott et al. 2008), habitat preferences, and seasonal climatic drivers of biological diversity within these semi-arid woodlands nourished by episodic rainfall. As intra-island habitat patches become more isolated, through intervening habitat degradation and fragmentation, there are distance thresholds beyond which searching for seasonal foods make species vulnerable to starvation, exposure, and predation. Of specific concern for conservationists are species with patchy distributions that use a variety of microhabitats. These species are particularly vulnerable to extinction in a fragmented landscape (Wilcove et al. 1986). By understanding the relationships among co-occurring species, resource managers may gain insights into how diverse taxonomic groups coexist, how they interact to survive within a given habitat, and how these heterospecific relationships contribute to the complexity of a fragmented semi-arid ecosystem in an era of rapid climate change.

Thus, resource managers should make every effort to acquire archival data, that when combined with contemporary information and long-term monitoring, may reveal nuances in how variability in heterospecific communities disentangle the influence of variance in seasonal climate as relates to: 1) fluctuations in population cycles, 2) reproductive output, and 3) viability among resident taxa. Use of archival data can also assist managers in landscape management for retaining high-quality multi-age enclaves of woodland and relic forest by: 1) prioritizing area treatment and permit issuance for disturbances (fire management, maintenance, positioning of anthropogenic structures,

conversion of land for agricultural purposes; 2) design of feasible restoration, 3) development of monitoring plans to evaluate treatment results, and 4) identification of drivers of change associated with ecosystem transition (Aplet et al. 2000; Andersen et al. 2009; Alagona et al. 2012; Dickinson 2014). Specific and DOD WSMR management recommendations, based on detailed environmental compliance for the Oscura and Organ mountains subspecies of chipmunks, are found elsewhere (Sullivan and Willson 2001).

List of abbreviations

ARL, Adjusted Range Length.
AIC, Akaike's goodness of fit criterion.
EBS, Exclusive Boundary Strip.
GAM, Generalized Additive Model.
NOP, North Oscura Peak.
PCA, Principal Components Analysis.
RDA, Redundance Analysis.
WSMR, White Sands Missile Range.

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Supplementary materials

Table S1. Standard statistics for climatic variables used in our Redundance Analysis (RDA), minus precipitation as it occurred too infrequent during our study period; n = sample size for each month. Actual data for precipitation is presented but it occurred so infrequently that we used average monthly values obtained at Carrizozo, NM (~43 km from NOP; 1981–2010) in our analysis of this variable. (download)

Table S2. Raw data used to generate histograms of theoretical density distributions, NG1 = *Neotamias* Grid#1, ND1 = *Neotamias* Density Grid#1, NG2 = *Neotamias* Grid#2, ND2 = *Neotamias* Density Grid#2; PG1 = *Peromyscus* Grid#1, PD1 = *Peromyscus* Density Grid#1, PG2 = *Peromyscus* Grid#2, PD2 = *Peromyscus* Density Grid#2. (download)

Table S3. Seasonal distribution of numbers and percentages of age, sex, and reproductive condition of A) *Neotamias* ($n = 218$) and B) *Peromyscus* ($n = 479$) live-trapped in mark-recapture studies on Grid 1 and Grid 2 combined. Percent testes scrotal and percent lactating were calculated by summing for all months and dividing by total number of each sex. (download)

Table S4. Raw recapture data, and exclusive boundary strip (EBA [ha]) and adjusted range length (ARL [m]) estimates for both species. (download)

Table S5. Comparison of the percentages of site-specific microhabitat structural use for each grid where *Neotamias* and *Peromyscus* were live-trapped. (download)

Fig. S1. Box plots of seasonal climatic variables. A = average temperature (C°), B = solar radiation (Ly), C) dew point (C°), D = humidity (%), E = pressure (mb), F) = peak wind speed (kts), G = wind direction (°), and H) precipitation (mm); red colored points = means, black colored points = outliers. Sample sizes are provided in table S1. (download)

Fig. S2. Histograms of theoretical density distributions of live-trapped individuals on each quadrant for each grid by species (A, C, E, G) and Generalized Additive Models and statistics for each corresponding histogram (B, D, F, H); W = Shapiro–Wilk’s statistic. Quadrates closest to the escarpment-cliff edge in each grid were represented by quadrates 90 through 100 (A, C, E, G). (download)