



Original Investigation

Variation in habitat use of coexisting rodent species in a tropical dry deciduous forest

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ABSTRACT

Use of habitat is a critical component related to structure of small-mammal communities, with partitioning occurring primarily along dimensions of microhabitat, although use of microhabitat often does not explain fully use at a macrohabitat level. Through grid studies of small mammals in coastal Colima, Mexico (during January 2003–2005), we appraised influence of available habitat, species richness, abundance, and cumulative abundance of other small mammals on variation in habitat used by species. We evaluated 14 habitat variables (reflecting ground cover, slope, canopy, and vegetation density on vertical and horizontal axes) and developed a composite variable (principal component 1) reflecting general openness of habitat through which we addressed habitat use. For the four most common mammalian species (*Sigmodon mascotensis*, *Heteromys pictus*, *Baiomys musculus*, and *Oryzomys couesi*), two measures of variation in habitat used were employed to estimate niche breadth, one of which assessed variation in habitat use relative to variation present on a grid. *Sigmodon mascotensis* and *B. musculus* preferred areas that were more open, and *H. pictus* and *O. couesi* occupied less-open areas; breadth of habitat use did not differ interspecifically. Habitat use was more variable on grids with more variability in habitat, although not greater than chance expectations. Findings do not lend support to the resource-breadth hypothesis as an explanation for population densities of species at a local level or the habitat-heterogeneity hypothesis as a predictor of species richness. Variation in habitat used by *S. mascotensis* did not proportionally increase when diverse habitat was available but was greater when the species was more abundant. For *H. pictus*, when cumulative abundance of other small mammals was greater, breadth of habitat used was greater. Intraspecific density-dependent habitat selection may result in *S. mascotensis* selecting a greater variety of habitats, while greater interspecific abundance is related to a greater range in use of habitats by *H. pictus*. *Baiomys musculus* used a higher proportion of habitat relative to that available when more species were present on a grid. Variation in habitat used by *O. couesi* was unrelated to any factor examined. Overall, the four species responded in notably different ways with respect to availability of habitat, abundance, and presence of other species.

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Introduction

Use of resources by species is a critical component related to community structure (Bradley and Bradley, 1985). For small-mammal communities, early studies by Schoener (1974),

Rosenzweig et al. (1975), and Grant (1978) suggested resource partitioning primarily occurs along dimensions of microhabitat rather than of food. For example, Lambert et al. (2006), studying in tropical Amazonia, obtained evidence that abundances of many species of small mammals were not responding directly to resource (food) levels, but rather to habitat features. For an assemblage of small rodents in the Valley Thicket of South Africa, vegetation structure correlated with abundance, number of species, and turnover of species, while no evidence was found that morphological

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structuring or hierarchical sets of ecological relationships existed among species (Kryštufek et al., 2007). Microhabitats sustain important resources for small mammals, and analyses of use of habitat may provide at least indirectly information on how such resources are used by different species and how this influences community structure. At the same time, there is evidence of macrohabitat characteristics being better predictors than microhabitat features of densities of two rodents in a temperate area (*Peromyscus leucopus* and *Microtus pennsylvanicus*; Morris, 1987).

Niche breadth frequently has been employed as an index of habitat use (e.g., Roughgarden, 1974; Paine et al., 1981; Seagle, 1985; Swihart et al., 2006). The concept of niche breadth underlies numerous hypotheses in evolutionary biology (Feinsinger et al., 1981), including those relating to optimal foraging and niche overlap, and theories have been developed to enable broad generalizations about niche breadth. Evaluation of these theories generally has taken the form of interspecific comparisons not involving investigations of potential factors driving niche breadth nor including information on possible intraspecific variation in niche breadth. For example, species with higher and lower values of niche breadth have been deemed generalists and specialists, respectively (Pandit et al., 2009). The resource-breadth hypothesis by Brown (1984) is another generalization positing that species with broader niches have larger geographical ranges and larger populations as a result.

Small mammals are relatively easy to mark and recapture and thereby one can track their movements in the environment; as a result, they provide good subjects for investigating niche breadth in terms of variation in use of habitat. Studies in the tropics are of particular interest in that seasonality with respect to important aspects of the environment often is less pronounced than in temperate regions. As emphasized by Lacher and Mares (1986) and still largely true today, empirical data on processes at the community level are meager or lacking, particularly for the Neotropics.

Several hypotheses attempt to address questions concerning which factor or factors affect habitat use by small mammals, though it is still not clear what drives niche breadth. Variability of surrounding resources is a feature said to permit coexistence of species via mechanisms based on habitat selection in time and space (Brown, 1989). Various aspects of competitive interactions also can result in differential use of habitat among rodents (Grant, 1972; Holbrook, 1979). The theory of island biogeography has linked number of species in an assemblage to niche breadth based on the idea that intense competition narrows niches, allowing more species to coexist (MacArthur and Wilson, 1967). Population size and interspecific abundance are additional factors purported to drive competition and affect use of habitat. Competition within a single species may force use of a wide variety of habitats, but in the presence of interspecific competitors, species are restricted and specialize on habitat (Rosenzweig, 1991). Habitat selection can have notable influence on a variety of ecologically relevant factors, including population regulation, species interactions, and community composition (Morris, 2003), with the possibility that selection of different habitat components by organisms can occur at different scales (Mayor et al., 2009). Furthermore, evolution of species in heterogeneous environments involving both habitat choice and local adaptation has been shown to promote specialization, which in turn can result in differentiation and increased biodiversity (Ravigné et al., 2009).

Through studies of small mammals on grids in Colima, Mexico, we evaluated habitat use by species within assemblages. Our study can shed new light on how habitat factors and niche breadth relate to community assemblages. Our objective was to determine the influence of available habitat, species richness, abundance, and cumulative abundance of other small mammals on variation in habitat used by focal species. Potentially, all of these factors could affect habitat use. In addition, we evaluated the null prediction

based on neutral theory that species within community assemblages respond in a similar manner to ecological factors associated with niche breadth.

Material and methods

Study area and trapping

Data were collected in January 2003–2005 in coastal habitat less than 1 km from the Pacific Ocean at Playa de Oro, Colima, Mexico. Average January temperature (for Manzanillo, 21 km east-southeast of study site) was 24.7 °C, and monthly rainfall was 31.3 mm (average 1961–2005; Instituto Nacional de Estadística, Geografía e Informática, 2006). Trapping locations were in tropical dry deciduous forest with thorn-forest and mangrove elements (Table 1); elevation was less than 10 m above sea level. Prominent trees and shrubs in the area included *Coccoloba barbadensis*, several *Acacia* including *A. hindsii* and *A. farnesiana*, *Senna pallida* and *S. occidentalis*, *Pithecellobium lanceolatum* and *P. dulce*, *Hyperbaena ilicifolia*, *Crataeva tapia*, *Prosopis juliflora*, and *Guazuma ulmifolia* (Schnell et al., 2008b). Grazing occurred in the region, but most of our study grids were not accessible to livestock due to some fencing and to density of vegetation. Prominent agriculture in the vicinity included groves of coconut palms (*Cocos nucifera*) and production of corn (*Zea mays*), sweet potatoes (*Ipomoea batatas*), and beans (*Phaseolus vulgaris*).

Five non-overlapping trapping grids were established each year (15 grids total). Adjacent grids were never closer than 500 m to one another in a given year. Between years, adjacent grids typically were 200 m or more apart, which as indicated by Morris (1989) is expected to be a distance sufficient to overcome pseudo-replication and autocorrelation when trapping small mammals. Having 15 different grids enabled us to sample the area more thoroughly. In addition, given that we took some voucher specimens at the end of trapping sessions to verify field identifications of species, we did not resample the same sites because we were concerned that in some cases this might have an influence on species present and numbers of individuals in a subsequent year.

Each grid of 100 stations (10 × 10 square with adjacent stations 10 m apart) had two Sherman live traps (7.5 cm × 9.0 cm × 23.0 cm; H.B. Sherman Traps, Tallahassee, Florida) at each station baited with rolled oats. One trap was on the ground, and the second was supported by a thin plywood platform (12.5 cm × 34.5 cm) attached to a tree or a shrub 1–2 m above ground. Grids were sampled for eight nights (Table 1), with the exception of grid 5 in 2004 (9 nights) and grid 1 in 2005 (7 nights), for an overall sampling effort of 24,000 trap-nights. Relatively few “new” animals were captured at the end of a given sampling period, so extending an additional night or having one less night had relatively little effect. Traps were checked each morning, re-baited as needed, and opened for the full 24-h period. Informal checks of traps at other times indicated that only rarely did animals enter traps during the day. We had low trap mortality throughout the study. For each capture, we recorded the species and trap location, tagged the animal in both ears using uniquely numbered Monel No. 1 ear tags (National Band and Tag Company, Newport, Kentucky), and released it at the site of capture.

Measuring habitat

Following Schnell et al. (2008a), we quantified habitat structure by evaluating 14 characteristics, most reflecting vegetation structure (Table 2). For 2004 and 2005, measurements were made at points 1 m from each trapping station (1000 points total). Percentage of ground cover was estimated (to nearest 5%) for a 1-m square (first 7 variables in Table 2). Number of shrub stems hitting a 1-m

Table 1

Description of vegetation on each grid at Playa de Oro, Colima, Mexico, with sampling dates indicated (descriptions from Schnell et al., 2008a).

Grid number (January dates)	Description
2003	
1 (2–5, 9–12)	Thorn forest with some palm trees close to mangroves
2 (2–5, 9–12)	Thorn forest with some palm trees close to mangroves
3 (3–5, 9–13)	Thorn forest next to palm plantation
4 (3–5, 9–13)	Thorn forest next to palm plantation
5 (3–5, 9–13)	Mixture of grassy plots and palm trees associated with undergrowth of thorn forest
2004	
1 (3–5, 9–13)	Mixture of thorn forest and mangrove, with some palm trees
2 (2–5, 9–12)	Mixture of thorn forest and mangrove, with some palm trees
3 (2–5, 9–12)	Thorn forest close to palm plantation
4 (3–5, 9–13)	Mixture of grassy plots, palm trees, and thorn forest next to agricultural fields
5 (2–5, 9–13)	Mixture of grassy plots, palm trees, and thorn forest next to agricultural fields
2005	
1 (4–6, 10–13)	Dense thorn forest with abundance of woody vines
2 (3–6, 10–13)	Thorn forest mixed with mangrove and palm trees with dense undergrowth
3 (2–6, 10–12)	Mixture of thorn forest, grassy plots, and xerophilous shrubs
4 (2–6, 10–12)	Mixture of grassy plots, palm trees associated with dense undergrowth of thorn forest, and patches of mangrove
5 (3–6, 10–13)	Mixture of grassy plots, palm trees, and thorn forest

bar at 1-m height was determined four times (once in each cardinal direction from the central point), and the average calculated (variable 8). Canopy cover (i.e., percent closed, variable 9) was estimated using a spherical densitometer (model C, Forest Densimeters, Bartlesville, Oklahoma), as was slope (variable 10) with a clinometer. Using a 7.5-m vertical pole marked at each decimeter, we determined number of decimeter intervals within which vegetation touched the pole; resulting data were summed for 0–2.5 m (maximum of 25 hits; variable 11) and for 2.5–7.5 m (maximum of 50 hits; variable 12). Maximum height of canopy was estimated to the nearest 0.5 m (variable 13). Distance to nearest tree (≥ 10 cm dbh; diameter at breast height) was determined in each of four quadrants (with edges being cardinal directions) and the average taken (variable 14); distances 10 m or greater were tabulated as 10 m.

Similar measures were taken in 2003 but at 25 evenly spaced points on a grid instead of 100 points. For each variable, we estimated values at each trapping station from these 25 measurements using ordinary and point kriging (computer program Surfer, version 8; Golden Software Inc., 2002). Resulting values (500 total) from the five grids were then treated the same as those for other years.

In a partial evaluation of possible effects of kriging with respect to estimating values of variables at specific trapping stations in 2003, we selected 25 uniformly spaced trapping stations for grid 1 in 2005 and used kriging to estimate variables for the other 75 trapping stations. We employed two measures of fit of kriged values with those recorded during sampling at the 75 stations for

each of the 14 variables—product–moment correlation of the kriged and actual values, and average percent deviation (i.e., for the 75 stations, absolute average deviation of kriged values from actual measurements divided by average value of actual measurements, with result multiplied by 100). Correlations of kriged and actual values for the 14 variables ranged from 0.053 to 1.000, with the average being 0.430. The percent deviations show a range from 0.0 to 151.2%, with an average of 56.7%. Thus, for this grid and for some variables, kriging was effective in reflecting the measurements we actually took at sites, while for others it was not. Conducting a limited number of evaluations of some variables on other grids suggested that the results for grid 1 in 2005 were indicative of what would be found for other grids. In general, low correlations and high average percent deviations were associated with variables where there was little variation on the grid and where average values were small. General differences among grids were maintained when using kriging within grids. Overall, we concluded that kriging provided adequate results for inclusion of 2003 data in the study.

Assessing variation in use of habitat

To obtain a composite variable reflecting overall habitat variation, a principal components analysis (NTSYSpc; Rohlf, 2009) of the 14 habitat variables was performed based on the 1500 trapping stations. We standardized variables (mean 0, standard deviation 1), calculated product–moment correlations among variables, extracted the first principal component (PC1), and projected trapping stations onto this component.

For each of the four most common species of small mammals (*Sigmodon mascotensis*, west Mexican cotton rat; *Heteromys pictus*, painted spiny pocket mouse; *Baiomys musculus*, southern pygmy mouse; and *Oryzomys couesi*, Coues' rice rat), we calculated two measures of variation in habitat use for each grid where the species was captured at more than one trapping station. Both measures may be considered estimates of niche breadth. First, we estimated variation in habitat used by calculating standard deviation of projections on PC1 of stations where the species was captured (hereafter referred to SD Habitat Used). August (1983) employed a similar measure as an assessment of heterogeneity of habitat.

We also analyzed a relative measure of niche breadth because, as emphasized by Feinsinger et al. (1981), it is important to have measures of niche breadth that take availability of resources into account. Relative variation in habitat used (i.e., Relative SD Habitat

Table 2

Loadings on principal component 1 based on 14 habitat measurements for 1500 trapping stations on grids at Playa de Oro, Colima, Mexico (2003–2005).

Variable	Principal component 1
Percent woody plants	0.07
Percent forbs	0.39
Percent grasses	0.64
Percent leaf litter	-0.66
Percent dead wood	-0.30
Percent rocks	-0.12
Percent bare ground	0.12
Average vegetation hits at 1 m	0.24
Percent canopy closed	-0.73
Slope (degrees)	-0.23
Total vegetation hits from 0 to 2.5 m	0.32
Total vegetation hits from 2.5 to 7.5 m	-0.44
Maximum canopy height (m)	-0.66
Average distance to nearest tree (m)	0.58

Bold values indicate relatively high positive or negative loadings on component.

Used) assessed variation in habitat used relative to variation present on the grid. It was calculated as:

$$\frac{\text{SD Habitat Used} - \text{SD Habitat Grid}}{E_s}$$

where SD Habitat Grid is the standard deviation of PC1 on a grid and E_s is the estimated standard error of SD Habitat Used with the number of stations used by the species drawn at random from the 100 grid stations. Using this denominator, adjusted for there being differences in variation among grids and differences in the number of individuals of a species on the grid, enabled us to assess across grids the degree to which available habitat was used by a given species. With the program SYSTAT (version 13; Systat Software Inc., 2009), we calculated E_s by randomly sampling (without replacement) 5000 times from a grid's 100 PC1 values, determining the standard deviation of each sample drawn, and calculating the standard error of the standard deviations. Size of each sample was number of stations for that grid where a given species was captured.

For each species, we calculated Spearman rank correlations (r_s) of both SD Habitat Used and Relative SD Habitat Used with: (1) variation in habitat on grid (i.e., SD Habitat Grid); (2) species richness (i.e., total number of small-mammal species captured on grid); (3) abundance (number of individuals captured) of species being considered; and (4) abundance of individuals comprising all other species (i.e., cumulative abundance of other species). Each of these factors potentially could influence habitat use. Ranked data were analyzed to minimize any undue influence of outliers. Previous more detailed studies of individual species—for example *S. mascotensis* (Schnell et al., 2010) and *B. musculus* (Schnell et al., 2008b)—have shown that numbers of individuals captured and abundance estimates based on encounter histories produce very similar results.

SigmaPlot 11 (Systat Software Inc., 2008) was used to generate plots, calculate correlations, and conduct analyses of variance (ANOVAs). We employed the Holm–Sidak adjustment to take into account that multiple comparisons were made (Systat Software Inc., 2008).

Due to autocorrelation, we resampled (a Monte Carlo simulation procedure) to determine significance of rank correlations between SD Habitat Used and SD Habitat Grid. The program Resampling Stats Add-in for Excel (version 4; Statistics.com, LLC, 2009) was used in a two-step process to create an expected distribution of rank correlations against which we compared the correlation obtained. A species occurred at a given number of trap stations on a particular grid. For that grid we randomly drew that number of stations and calculated the standard deviation of PC1 (i.e., simulated SD Habitat Used); this procedure was repeated 5000 times to create an expected distribution of SD Habitat Used given the number of stations at which the species was caught on the grid. This was repeated for each grid where the species occurred. As the second step in the overall procedure, we randomly drew one simulated SD Habitat Used from each of the grid distributions for that species and calculated the rank correlation of SD Habitat Used with SD Habitat Grid. This was repeated 5000 times, after which we compared the actual rank correlation from our data with the created distribution of rank correlations to determine the probability (one-tailed) of our obtaining the given value simply by chance.

Results

During the three years of study, 1040 individuals from 12 species of small mammals were captured on grids. Abundances of *S. mascotensis*, *H. pictus*, *B. musculus*, and *O. couesi* were 96, 106, 135, and 573, respectively (Table 3). Other species encountered less frequently were *Heteromys spectabilis*, *Nyctomys sumichrasti*, *Oligoryzomys fulvescens*, *Osgoodomys banderanus*, *Peromyscus perfulvus*,

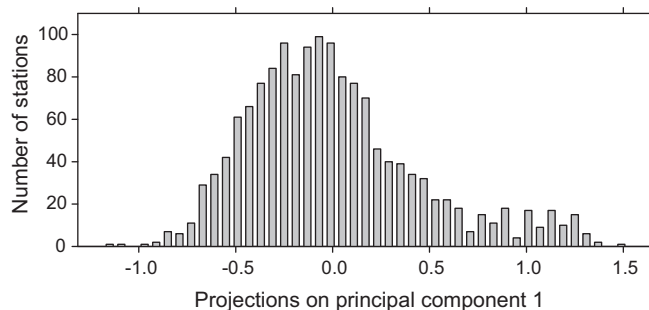


Fig. 1. Histogram depicting projections of 1500 trapping stations on principal component 1. Low values reflect more closed habitat (relatively less grass, more leaf litter, a closed tall canopy, and trees close-by) and high values more open habitat (more grass, little leaf litter, an open low canopy, and trees more distant).

Reithrodontomys fulvescens, *Tlacuatzin canescens*, and *Xenomys nelsoni*.

Principal component 1 (based on the 14 habitat variables) explained 20.2% of observed variation and characterized habitat as ranging from closed to open. Purposely, we chose initial habitat variables that were not highly correlated and, thus, not redundant. As a result, the relatively low percent explained by component 1 is not surprising. Nevertheless, the component overall reflects important variation in habitat structure among trapping stations. Loadings of variables on principal component 1 are provided in Table 2. Stations with low projection values for PC1 tended to have relatively less grass, more leaf litter, a closed tall canopy, and trees close-by, while stations with high projection values for PC1 can be characterized as having more grass, little leaf litter, an open low canopy, and few trees in the immediate vicinity. Projections on principal component 1 ranged from -1.1 to 1.5 with most being from -0.5 to 0.2 (Fig. 1).

The standard deviation in PC1 values of stations where species were captured (i.e., SD Habitat Used) did not differ among the four species; however, average values on PC1 of stations where species were captured on grids varied significantly interspecifically (one-way ANOVA; $F_{3,45} = 9.34$, $P < 0.001$; Fig. 2). Multiple-comparison tests indicated that *S. mascotensis* and *B. musculus* were not different statistically ($t = 0.37$, $P = 0.715$) in their projections on PC1. *Sigmodon mascotensis* and *B. musculus* differed significantly from *H. pictus* ($t = 4.37$, $P < 0.001$ and $t = 3.51$, $P = 0.001$, respectively) and *O. couesi* ($t = 3.79$, $P < 0.001$ and $t = 2.99$, $P = 0.005$, respectively), with *H. pictus* and *O. couesi* not differing from one another ($t = 0.70$, $P = 0.490$). *Sigmodon mascotensis* and *B. musculus* had relatively high projection values, indicating they frequented more open areas, while *H. pictus* and *O. couesi* had relatively low values, signifying they were in more closed areas. Abundance of *O. couesi* on a grid was negatively correlated with abundance of *H. pictus* ($r_s = -0.570$,

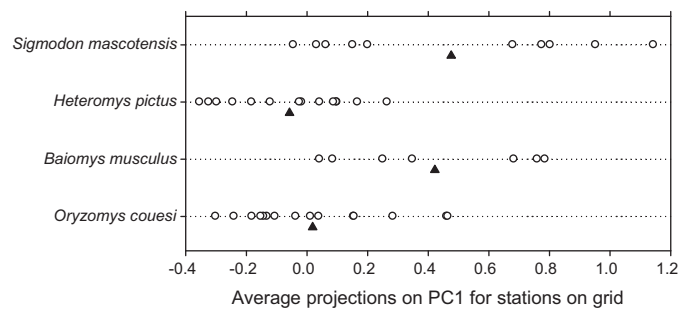


Fig. 2. Habitat used by four mammal species at Playa de Oro, Colima, Mexico (2003–2005). Circles represent averages for individual grids of projections on principal component 1 of trapping stations where species was captured. Triangles indicate mean values, weighting individual grids equally.

Table 3

Abundance (numbers of individuals captured) of four most common species on 15 grids at Playa de Oro, Colima, Mexico (2003–2005). Number of recaptures indicated in parentheses followed by total number of trapping stations where species was present.

Grid	<i>Sigmodon mascotensis</i>	<i>Heteromys pictus</i>	<i>Baiomys musculus</i>	<i>Oryzomys couesi</i>	Species richness	Cumulative abundance of all small mammals
2003						
1	3(3; 5)	27(23; 40)	40(51; 36)	11(6; 17)	8	92
2	–	3(8; 8)	–	35(32; 45)	5	41
3	–	14(13; 23)	–	9(12; 14)	7	31
4	1(3; 3)	8(2; 9)	2(0; 1)	15(10; 15)	7	39
5	–	7(5; 9)	29(31; 31)	38(97; 43)	5	83
2004						
1	17(41; 31)	2(1; 2)	–	63(109; 68)	5	84
2	9(12; 17)	2(0; 2)	–	98(142; 73)	6	128
3	3(4; 5)	11(13; 20)	–	22(10; 20)	7	46
4	25(32; 34)	3(0; 3)	33(32; 36)	75(67; 69)	7	156
5	30(64; 37)	6(9; 9)	18(15; 20)	76(100; 71)	7	134
2005						
1	4(9; 8)	8(10; 15)	5(1; 5)	51(55; 49)	8	76
2	1(0; 1)	6(1; 5)	8(4; 6)	17(14; 21)	8	40
3	–	7(9; 11)	–	6(3; 9)	4	19
4	3(10; 8)	2(4; 5)	–	27(25; 32)	6	41
5	–	–	–	30(22; 33)	1	30

Taxonomy follows Wilson and Reeder (2005) except *Liomys* treated as part of *Heteromys* (Hafner et al., 2007). Two grids where a given species was captured at only a single trapping station could not be included in analysis of SD Habitat Used.

$P=0.025$), but positively correlated with abundance of *S. mascotensis* ($r_s=0.663$, $P=0.007$).

SD Habitat Grid was not significantly correlated with number of species of small mammals present on a grid ($r_s=0.000$, $P=0.995$). In addition, no association was detected between SD Habitat Grid and total abundance of small mammals on a grid ($r_s=0.200$, $P=0.465$), nor with abundance of *S. mascotensis* ($r_s=0.364$, $P=0.176$), *H. pictus* ($r_s=-0.245$, $P=0.374$), *B. musculus* ($r_s=0.223$, $P=0.418$), or *O. couesi* ($r_s=0.321$, $P=0.235$).

There were positive correlations for each species between SD Habitat Used and SD Habitat Grid (Fig. 3A–D), indicating that on grids with more variation, all four species used a wider breadth of available habitat. However, after taking into account inherent auto-correlation resulting from comparison of standard deviations of PC1 for all stations on a grid (i.e., SD Habitat Grid) with a subset of those stations where a species was captured, these rank correlations were not greater than expected simply by chance.

For *S. mascotensis*, SD Habitat Grid and Relative SD Habitat Used were strongly and negatively associated (Fig. 4A and Table 4), suggesting that as more diverse habitat was available on a grid, habitat used by *S. mascotensis* did not proportionally increase but stayed about the same or increased only slightly. There was no evidence of decreased habitat use in that the relationship between SD Habitat Used and SD Habitat Grid was positive. In addition, abundance of *S. mascotensis* on a grid was correlated positively with SD Habitat Used by the species (Fig. 4B). Abundance of *S. mascotensis* was not associated with Relative SD Habitat Used ($r_s=-0.203$, $P=0.580$) or SD Habitat Grid ($r_s=0.364$, $P=0.176$).

For *H. pictus*, when cumulative abundance of other small mammals was greater, SD Habitat Used was greater (Fig. 5A). The correlation between cumulative abundance and Relative SD Habitat Used was not significant ($P=0.084$), although the positive association persisted (Table 4). The correlation of SD Habitat Grid and cumulative abundance of other mammals was not statistically significant ($r_s=0.271$, $P=0.319$).

For *B. musculus*, Relative SD Habitat Used was positively associated with number of species on a grid (Fig. 5B), implying that on grids with more species, *B. musculus* used a higher proportion of the grid (relative to available habitat) than expected. For *O. couesi*,

none of the factors examined were correlated with SD Habitat Used or Relative SD Habitat Used.

Discussion

Although different factors were associated with habitat use within species, we detected no difference in breadth of habitat used (SD Habitat Used) among species. Taking niche breadth as a quantification of tolerance of species to differing environmental conditions (Gregory and Gaston, 2000), our results suggest that the four species are relatively similar in tolerance of habitat heterogeneity. We did find significant differences between occupancy of microhabitats among species, with *S. mascotensis* and *B. musculus* being captured in areas that were more open, while *H. pictus* and *O. couesi* occupied less-open areas. For coastal Colima in 2004, Poindexter et al. (2012) noted that *S. mascotensis*, *B. musculus*, and *H. pictus* were caught primarily in ground traps, with *O. couesi* being captured about equally in ground and elevated traps. Typical habitat of *S. mascotensis* is grasslands (Matson and Baker, 1986) or, more specifically, areas with dense low vegetation, little leaf litter, sparse trees, and an open canopy (Schnell et al., 2010). *Baiomys musculus* primarily resides in grassy areas where cover is provided by brush, rocks, or dense vegetation (Packard and Montgomery, 1978), or at sites with low thick vegetation (mostly forbs, grasses, and woody plants) and few trees (Schnell et al., 2008b). Castro-Arellano (2005) reported that *S. hispidus* and *B. taylori*, congeners of *S. mascotensis* and *B. musculus*, respectively, were closely associated with each other in open grassy areas with little canopy cover and low tree density.

Heteromys pictus occurs most often in lowland dry forest along rivers and streams, although it also has been recorded in xerophytic montane vegetation (McGhee and Genoways, 1978). In fieldwork in other areas, we have found *H. pictus* to be the only species of small mammal remaining in xerophytic areas during some dry periods. *Oryzomys couesi* was in mesic habitats with dense shrubbery and tall grass along streams in Nicaragua (Genoways and Timm, 2005) and in dense, thorny, secondary deciduous brush on Isla Cozumel, Mexico (Engstrom et al., 1989). The species has arboreal nesting habits and semiaquatic behavior, often residing in

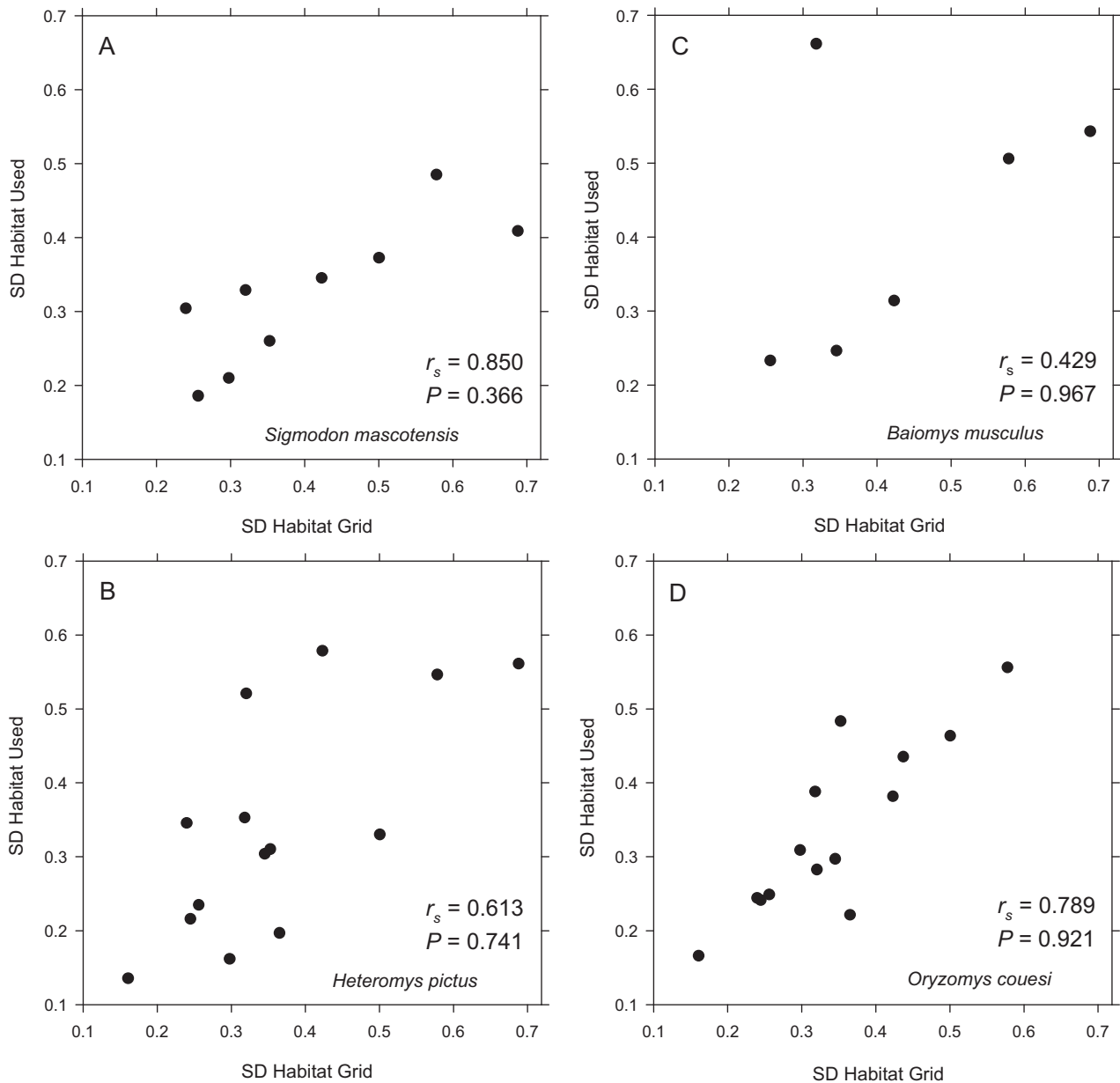


Fig. 3. Standard deviation of principal component 1 for stations where (A) *Sigmodon mascotensis*, (B) *Heteromys pictus*, (C) *Baiomys musculus*, and (D) *Oryzomys couesi* were captured on a grid (i.e., SD Habitat Used) plotted against standard deviation of principal component 1 for all stations on a grid (i.e., SD Habitat Grid). Points represent individual grids.

Table 4
Spearman rank correlations (r_s) of two measures of habitat use for the four most frequently encountered species with SD Habitat Grid, species richness, abundance, and cumulative abundance of other small-mammal species.

Variables correlated	<i>Sigmodon mascotensis</i>	<i>Heteromys pictus</i>	<i>Baiomys musculus</i>	<i>Oryzomys couesi</i>
SD Habitat Grid				
SD Habitat Used	0.850	0.613	0.429	0.789
Relative SD Habitat Used	-0.750*	-0.072	-0.429	-0.196
Species richness				
SD Habitat Used	-0.184	0.395	0.062	0.315
Relative SD Habitat Used	-0.316	0.200	0.926*	0.193
Abundance				
SD Habitat Used	0.712*	-0.324	-0.543	0.368
Relative SD Habitat Used	-0.203	-0.277	-0.429	-0.161
Cumulative abundance of other species				
SD Habitat Used	0.444	0.705**	0.086	0.372
Relative SD Habitat Used	-0.209	0.473	-0.486	-0.259

Asterisks indicate statistical significance of correlations: $P < 0.05$; **, $P < 0.01$; no asterisk, $P > 0.05$.

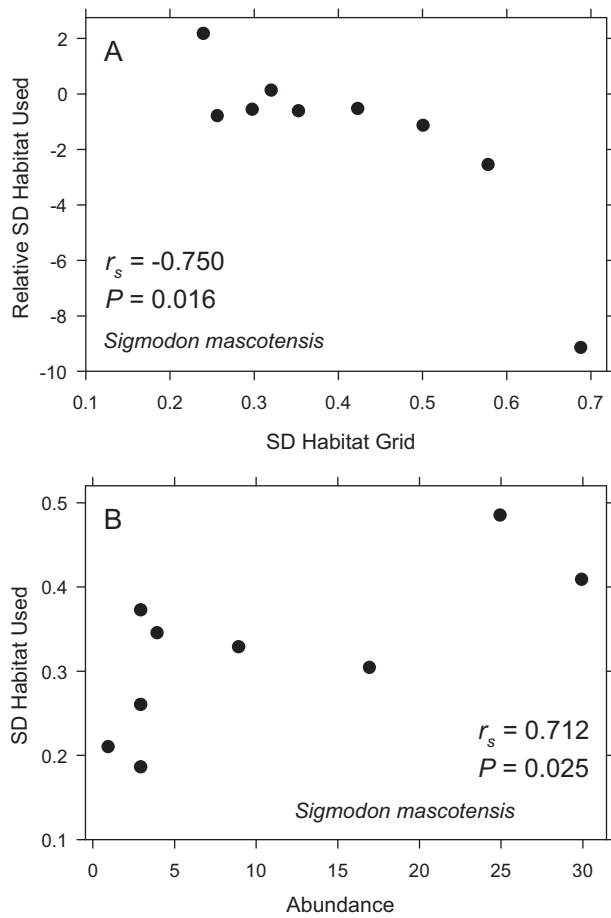


Fig. 4. (A) Relative standard deviation of principal component 1 for stations where *Sigmodon mascotensis* was captured (i.e., Relative SD Habitat Used) plotted against standard deviation of principal component 1 for all stations on a grid (i.e., SD Habitat Grid). (B) Standard deviation of principal component 1 for stations where *S. mascotensis* was captured on a grid (i.e., SD Habitat Used) plotted against abundance of the species. Points represent individual grids.

marshy environments (Benson and Gehlbach, 1979). Thus, habitats reported for *H. pictus* and *O. couesi* are highly variable, but the two species regularly inhabit moist areas, a connection likely responsible for our finding these species inhabiting similar microhabitats.

Abundance of *O. couesi* on a grid was negatively correlated with abundance of *H. pictus* but positively with abundance of *S. mascotensis*. *Oryzomys couesi* and *H. pictus* occurred in similar habitats based on grid averages, while *O. couesi* and *S. mascotensis* differed. However, an analysis of co-occurrence of species at the trapping-station level demonstrated that *O. couesi* shared significantly fewer trapping stations with *H. pictus* than expected by chance but more than expected with *S. mascotensis* (as well as with *B. musculus*; Poindexter et al., 2012). *Sigmodon mascotensis* also shared fewer stations than expected with *H. pictus* and more than expected with *B. musculus*.

Our study does not lend support to the resource-breadth hypothesis (Brown, 1984) in that the four species had similar niche breadths but differed in local abundance. The habitat-heterogeneity hypothesis (MacArthur and MacArthur, 1961) predicts that an increase in number of habitats available leads to an increase in diversity of species. Stevens and Tello (2011) found that both structural and resource heterogeneity (two components of environmental heterogeneity) significantly accounted for rodent species diversity in Mojave Desert communities. When they examined unique and shared effects, resource heterogeneity was

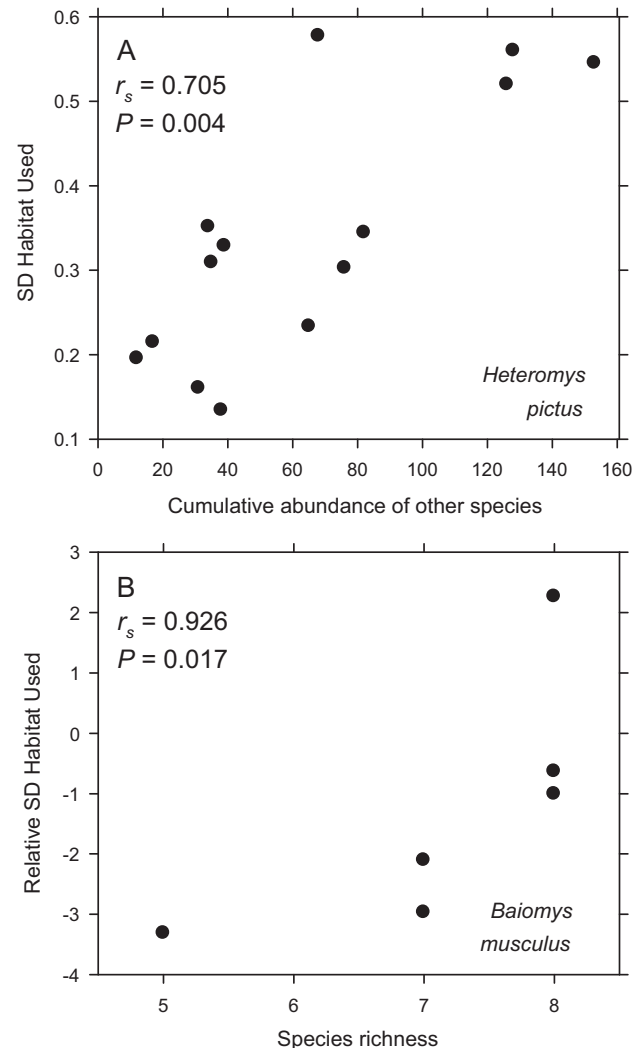


Fig. 5. (A) Standard deviation of principal component 1 for stations where *Heteromys pictus* was captured (i.e., SD Habitat Used) on a grid plotted against cumulative abundance of individuals of all other small-mammal species. (B) Relative standard deviation of principal component 1 for stations where *Baiomys musculus* was captured (i.e., Relative SD Habitat Used) plotted against species richness. Points represent individual grids.

significant and accounted for more variation than structural heterogeneity. Our results do not support the habitat-heterogeneity hypothesis in that no correlation was evident between variation in use of habitat on a grid (SD Habitat Grid) and species richness. All of our grids had relatively equal heterogeneity in habitat structure (i.e., we did not sample grids that ranged from homogeneous to highly heterogeneous); the fact that the range of heterogeneity was small likely explains at least in part why no relationship was found between habitat heterogeneity and species richness.

The strong negative correlation for *S. mascotensis* between Relative SD Habitat Used and SD Habitat Grid suggests that it uses a specific subset of the habitat, irrespective of whether additional habitat is locally available. Additionally, we documented a strong positive correlation between abundance of *S. mascotensis* and SD Habitat Used, suggesting breadth of habitat used is related to the number of individuals present. As a result of intraspecific competition, some species exhibit density-dependent habitat selection, occupying a broader range of habitats when densities are high and being more narrowly focused when densities are low (Rosenzweig, 1991). Rosenzweig and Abramsky (1985) have demonstrated intraspecific density-dependent habitat selection by gerbils

(*Gerbillus allenbyi* and *G. pyramidum*). Degree of habitat selectivity tended to be constant over low densities (<100 individuals/6.75 ha) but was sharply lower at densities >200. In a study of habitat use by *Mus musculus* and *Peromyscus leucopus*, Scott and Dueser (1992) suggested that selection of habitat and intraspecific interactions were more important determinants of habitat occupancy by the species than were interspecific interactions, and Fretwell and Lucas (1970) proposed a mechanism for density-dependent habitat selection based primarily on intraspecific competition. Density-dependent habitat selection within species has been demonstrated in a variety of terrestrial organisms, as well as in fishes (Lindberg et al., 2006). Our results for *S. mascotensis* (preference for a specific subset of habitat and breadth of habitat used being correlated with abundance) fit together well and provide support for the presence of density-dependent habitat selection.

Abramsky et al. (1990) found that interspecific and intraspecific densities, influenced habitat preferences in gerbils (*G. allenbyi* and *G. pyramidum*). Indeed, as modeled by Grant (1975), intraspecific and interspecific competition are proposed to have counteractive effects on occupancy of habitat by mammals. The model specified that individuals select preferred habitat when population density is low but exploit a progressively greater variety of habitats when density increases; however, this exploitation is counteracted by inhibitory effects of interspecific competitors, which occupy the marginal habitats into which expansion is occurring. Rosenzweig (1979) hypothesized that interspecific competition may both reinforce the tendency for habitat selection and serve to stabilize relationships between species. The importance of considering competition and density-dependent habitat selection has been emphasized for evaluations of resource selection using resource-selection functions (McLoughlin et al., 2010). We detected that SD Habitat Used by *H. pictus* was positively correlated with cumulative abundance of other small mammals, suggesting that this species is responsive to abundances of other species.

Habitat partitioning is purported to allow more species to coexist within an assemblage, with species narrowing niche breadths and, thus, decreasing overlap in resources used. While studies of microhabitat generally indicate that coexisting species partition available habitat (Jorgensen, 2004), our results for *B. musculus* were somewhat contradictory. We detected a positive correlation between Relative SD Habitat Used and species richness; in assemblages with more species, *B. musculus* used a higher proportion of the available habitat. Trapping results by García-Estrada et al. (2002), while not reaching statistical significance, suggested *B. musculus* exhibited differential use of habitat depending on the site-specific degree of disturbance.

We found variation in habitat used by *O. couesi* not to be related to any of the factors examined. Of the four species examined, *O. couesi* had the greatest overall abundance and was present on all 15 grids. In 2005, it was the only species present on one grid. August (1983) determined *O. bicolor*, a congener of *O. couesi*, was the only species occupying a grid in a savanna of Venezuela. In the preferred nesting and foraging habitat of cattail-bulrush (*Typha, Scirpus*) marsh, Benson and Gehlbach (1979) judged it unlikely that any other rodent could compete seriously with *O. couesi*. *Oryzomys couesi* is widespread, and its ability to occupy a range of habitats likely is facilitated by it being an omnivore (Medellín and Medellín, 2005).

Overall, microhabitat occupancy differed among the four species in our study. Breadth of habitat used was similar among the four species, but different factors were associated with habitat use within species. When abundance of *S. mascotensis* was greater, they selected a greater variety of habitats, while greater interspecific abundances may have influenced *H. pictus* to use a greater variety of habitats. *Baiomys musculus* expanded the proportion of habitat used relative to what was available when more species were present on a

grid. It would be of interest to determine whether similar patterns hold at other times of year. Also instructive would be an exploration of influence of scale on habitat use, evaluating macrohabitat as well as microhabitat features particularly to address potential factors creating differences in habitat use among species.

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