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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.

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