Desert Rodent Communities of the Canyon Country Province, Colorado Plateau

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Abstract. From 1988–1991, I studied desert rodent communities of the Canyon Country Province, Colorado Plateau. Study areas were located in Capitol Reef National Park, Utah and represented grassland, shrubland, and woodland habitats. I examined species richness, guild structure, body size, and microhabitat use, testing predictions based on patterns documented in other North American desert rodent faunas. Rodent assemblages were relatively simple with respect to species richness and number of taxonomic/foraging guilds. Among coexisting species, only the numerically dominant omnivores exhibited non-random body size. Co-occurrences of species representing three taxonomic-foraging guilds were significantly different from expected and, in one case, correlated with microhabitat use. Desert rodents of the Canyon Country have evolved patterns of morphology and resource use similar to those documented in other North American deserts that may minimize competition and facilitate coexistence.

Key words: Body size, community structure, desert rodents, microhabitat.

Desert rodent communities have received considerable attention from ecologists because of their relative simplicity and ease of study. Research conducted in North American deserts has greatly expanded understanding of small mammal community structure, particularly patterns of species richness, morphology, and resource use. Most previous studies have been conducted in the Great Basin, Mojave, and Sonoran deserts and have largely focused on members of the family Heteromyidae (kangaroo rats and pocket mice). Consequently, prevailing views of desert rodent community structure have a distinct taxonomic and regional bias (Reichman 1991). In contrast, small mammal communities of the Colorado Plateau have received much less attention. It is unknown to what degree they share structural patterns documented in more well-studied arid ecosystems. Variability in species

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richness is a fundamental attribute of desert rodent assemblages, a consequence of historical and ongoing evolutionary, biogeographic, ecological, and population processes (Brown and Kurzius 1989, Brown and Zeng 1989, Whitford and Steinberger 1989, Brown and Heske 1990). Brown and Kurzius (1987) examined desert rodent species richness at regional scales, synthesizing results of studies conducted across the western United States, but largely excluding the Colorado Plateau. They reported three underlying patterns: (1) a large number of species combinations, most of which occurred only a few times; (2) species richness lower than expected if species combinations were random; and (3) greater than expected occurrence of assemblages containing relatively few species. Similar results have also been found at microspatial (plot and trapsite) scale (Brown and Kurzius 1989).

The Canyon Country Province of the Colorado Plateau is characterized by tremendous topographic and vegetative diversity, and a high degree of habitat interspersion. Consequently, a large number of desert rodent assemblages can be found within a relatively small geographic area (Rosenstock 1992). This represents a unique opportunity to test patterns of species richness and co-occurrence in an area that has received little previous attention and at a scale intermediate to that considered in previous studies.

Differences in body size among coexisting, potentially competing species are a common structural characteristic of North American desert rodent faunas (Brown 1987). Coexisting species tend to exceed critical ratios of body mass, often termed Hutchinson's ratios. This pattern is most evident (and well-studied) among granivorous Heteromyids (Bowers and Brown 1982). Body size relationships among other taxa have received much less attention. Canyon Country rodent communities are often dominated by omnivorous Cricetids and Sciurids. Coexisting species in this ecoregion might also exhibit non-random patterns in body size, differences that should be most apparent among species using similar resources.

Because members of a given guild (sensu Root 1967) use similar resources, the potential for competition is high. Brown (1987:193) proposed that coexisting desert rodents tend to belong to different taxonomic and functional groups. However, members of the same guild that coexist must partition available resources. Such partitioning is often reflected in microhabitat use. Among sympatric granivorous Heteromyids, there is strong evidence of microhabitat segregation (Kotler 1984, Price and Heinz 1984, Price and Waser 1985, Reichman 1991). However, understanding of such relationships among other desert rodents is limited. Coexisting rodents of the Canyon Country Province might also be expected to show similar separation.

Hypotheses

I examined patterns of species richness, body size, guild structure, and microhabitat use in desert rodent assemblages of the Canyon Country Province, Colorado Plateau. I tested four sets of predictions based on structural patterns documented in other North American desert rodent communities. Stated in null form, these were: (1) species richness and guild size are random variables; (2) species coexistence and body size are independent; (3) members of taxonomic-foraging guilds co-occur at random; and (4) guilds that co-occur more or less frequently than expected do not show dissimilarity in microhabitat use.

Methods

Study Area

This study was conducted in Capitol Reef National Park (CARE), in Wayne County, south-central Utah, USA (38° 15' N 111° 15' W), an area that typifies the Canyon Country Province of the Colorado Plateau. Topography of CARE is complex, composed of intricate canyon systems, slickrock cliffs and slopes, mesas, talus, benchlands, and alluvial floodplains. Elevations range from 1,195 to 2,690 m. A wide variety of edaphic conditions are present, including soils derived from volcanic, aeolian, and sedimentary parent materials. The climate is arid, temperate continental. Precipitation is distributed between winter snowfall and summer thunderstorms and averages 17 cm per year.

With respect to mammalian biogeography, CARE lies within the Canyonlands Province of the Colorado Plateau faunal area. The majority of species are drawn from Cosmopolitan and Chihuahuan aerographic faunal elements (Armstrong 1977). Distribution patterns within the Canyon Country Province largely reflect physical boundaries to animal movements, primarily major river systems and their canyons.

Rodent and Habitat Sampling

I sampled rodents and habitats at 104 study sites, representing grassland, shrubland, and woodland plant community types within the cold-temperate lowland zone (Spence et al. 1995). All sites were within a 40-km radius of CARE Park Headquarters and not isolated by significant barriers to rodent movement and dispersal, such as major rivers or mountain ranges. Therefore, I assumed that local biogeographic effects were minimal and that the rodent fauna at each study site was drawn from a common species pool.

Sampling was conducted in the fall of 1988–1991 (September–October). At each site, I established a rectangular 2 x 25 trap grid, with stations spaced

10 m apart. Three snap traps (two Museum Specials™ and one Victor™ rat trap) were placed within a 1 m radius of each station, and baited with a mixture of peanut butter, whole oats, and birdseed. Each grid was sampled for two days, with traps checked morning and evening. Analyses of preliminary trapping data indicated that this level of sampling effort was adequate to detect both species richness and relative abundance. Captured small mammals were identified to species, aged by pelage condition, and weighed using a hand-held Pesola™ scale. Voucher specimens were deposited with the Resource Management Office at CARE.

I described microhabitat characteristics at each small mammal capture location, by recording the presence or absence of microhabitat components within a 1 m radius of the trap. These components represented the primary structural habitat features present across the study area: herbaceous vegetation, low shrubs (<50 cm height), medium-stature shrubs (50–100 cm), tall shrubs (>100 cm), deciduous trees, evergreen trees, downed woody material, and rock outcrops.

Statistical Analysis

I followed Brown's (1973) criteria to minimize the influence of rare or transient individuals on estimates of rodent community parameters. Only common species (those comprising >5% of total individuals at a site) were included in the analyses, except for large rodents (>80 g), which are often under-represented because of trapping bias. I assigned each captured species to one of five guilds, based on taxonomy (Family) and diet (following Morton 1979).

Distributions of community parameters (numbers of species and guilds) were assessed by fitting observed values to a Poisson distribution. I used a chi-square goodness-of-fit test to detect significant ($P \leq 0.05$) deviations from randomness.

Body sizes of coexisting rodents were tested with null-model simulations, using the modified 2 x 2 contingency table procedure of Bowers and Brown (1982). Separate simulations were conducted for the subset of omnivorous species and for all species combined. I used a critical mass ratio value of 1.5, originally proposed by Brown (1973) as a conservative estimate of Hutchinson's ratio. I classified all coexisting and non-coexisting species pairs as having a mass ratio ≥ 1.5 or <1.5, calculated from the mean mass of adult individuals captured in this study. The simulation randomly shuffled observed data to create a new 2 x 2 table with the same marginal totals, from which I calculated:

$$Y^2 = \Sigma\, (S - E)^2/E,$$

where S was the number of pairwise occurrences in each cell and E was the expected value based on the marginal totals. This process was repeated 5,000 times to obtain a randomization distribution of Y^2 under the null hypothesis of independence. The locations of observed Y^2 values (calculated from capture data) within their respective randomization distributions, yielded an approximate probability of obtaining the observed values by chance alone.

I also used a null-model simulation to examine pairwise coexistence of desert rodent guild members. The simulation drew a random set of rodent pairs, equal in size to the original data set, by sampling with replacement from a pool containing all guilds, weighted by their respective number of members. Random pairs contained representatives of one or two guilds, except that single guild pairs could only be drawn from guilds containing >1 species. Occurrences of 13 possible guild pairs were tabulated and the process repeated 5,000 times, to derive randomization distributions of expected occurrence, under the null hypothesis of random association. The location of observed pairwise guild occurrence values within their respective randomization distributions reflected the approximate probability of occurrence by chance alone (Manly 1991). I applied a Bonferroni correction to maintain an overall Type I error rate of $P \leq 0.05$ for the 13 pairwise tests.

I tested for differences in microhabitat use among "significant" guild pairs (i.e., those that occurred more or less frequently than expected). I calculated pairwise microhabitat dissimilarity for all species, using the Bray-Curtis coefficient (Ludwig and Reynolds 1988). Differences in mean coefficient values between significant and non-significant guild pairs were compared with a randomization test (Manly 1991). I again applied a Bonferroni correction, to maintain an overall Type I error rate of $P \leq 0.05$.

Results

Species Richness

Species composition varied considerably across the 104 study sites. A total of 52 different species combinations were observed, the majority occurring only once or twice, and few occurring >3 times (Fig. 1). Species richness ranged from one to five per site, $\bar{x} = 2.1$. The majority of observed combinations contained two or three species (Fig. 2). This distribution approached non-randomness ($X^2 = 7.1$, $P < 0.10$).

Guild Structure

Five taxonomic-foraging guilds were represented: omnivorous Cricetids (5 species), omnivorous Sciurids (4 species), herbivorous Cricetid (1 species), insectivorous Cricetid (1 species), and granivorous heteromyid (2 species) (Table 1). Omnivorous Cricetids and granivorous heteromyids were most widely distributed, appearing in 83% and 44% of the observed species combinations, respectively (Table 1).

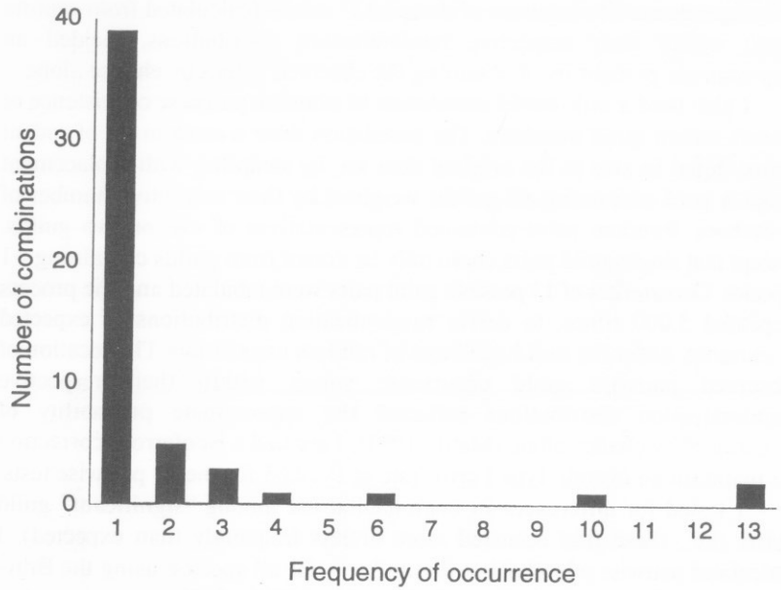

Fig. 1. Frequencies of occurrence of 52 desert rodent species combinations found at 104 sample sites in the Canyon Country Province, Colorado Plateau.

Most assemblages contained members of two guilds (Fig. 3). This distribution was significantly non-random ($X^2 = 10.89$, $P < 0.025$). There was considerable repetition of guild members, with 38–50% of all assemblages having >1 representative of a given guild.

Of 13 possible guild pairings, one occurred more frequently than expected and two occurred less frequently than expected. Omnivorous Cricetids occurred together more frequently than expected ($P < 0.0001$), while omnivorous Sciurids occurred together and in combination with omnivorous Cricetids less frequently than expected ($P < 0.0001$).

Body Size

Body size and coexistence were not independent among omnivorous species ($Y^2 = 3.59$, $P = 0.02$). Species of similar body size (mass ratio <1.5) coexisted less frequently than expected, while species of dissimilar size (mass ratio ≥1.5) occurred more frequently than expected. This relationship disappeared when all other guilds (granivore, herbivore, and insectivore) were included in the analysis ($Y^2 = 0.06$, $P = 0.59$).

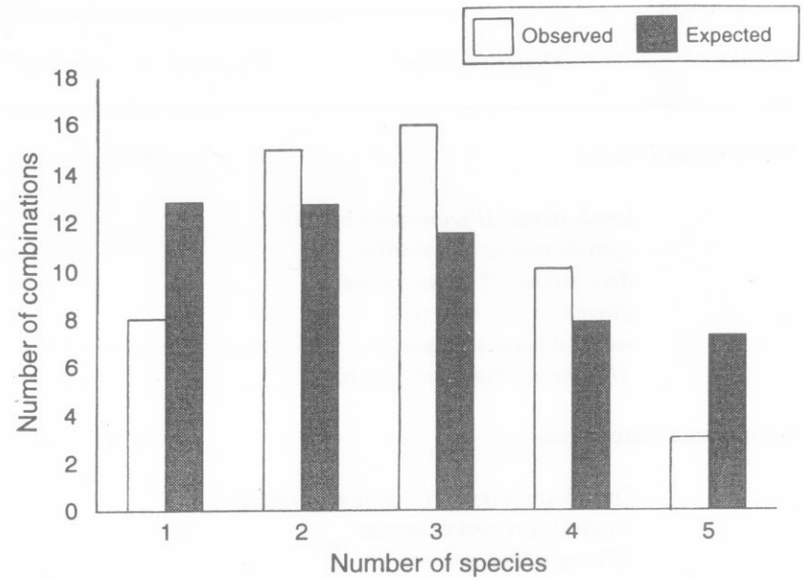

Fig. 2. Desert rodent species richness in 52 observed species combinations in the Canyon Country Province, Colorado Plateau. Expected values derived from Poisson distribution.

Microhabitat Use

Among the three guild pairs with observed occurrences significantly different than expected, only one showed differences in microhabitat use. Pairs of omnivorous Cricetids, which occurred together more frequently than expected, had significantly greater microhabitat dissimilarity ($P = 0.01$) than guild pairs with nonsignificant frequencies of co-occurrence (Table 2).

Discussion

Species Richness

Desert rodent assemblages of the Canyon Country Province showed a range of species richness similar to that reported from neighboring biogeographic regions, including the Chihuahuan Desert (Brown and Kurzius 1989), Mojave Desert (Hafner 1977), and Great Basin (Brown 1987), although mean values for my study sites were lower. I found spatial variation

Table 1. Taxonomic/foraging guilds represented in 52 observed small mammal assemblages in the Canyon Country Province, Colorado Plateau.

Guild	Member species	Frequency of occurrence[a]
Omnivorous Cricetid		83%
	brush mouse (*Peromyscus boylii*)	
	canyon mouse (*P. crinitis*)	
	deer mouse (*P. maniculatus*)	
	pinyon mouse (*P. truei*)	
	western harvest mouse (*Reithrodontomys megalotis*)	
Granivorous Heteromyid		44%
	Ord's kangaroo rat (*Dipodomys ordii*)	
	Great Basin pocket mouse (*Perognathus parvus*)	
Omnivorous Sciurid		35%
	cliff chipmunk (*Tamias dorsalis*)	
	Hopi chipmunk (*T. rufus = quadrivittatus*)	
	least chipmunk (*T. minimus*)	
	white-tailed antelope squirrel (*Ammospermophilus leucurus*)	
Herbivorous Cricetid		17%
	desert woodrat (*Neotoma lepida*)	
Insectivorous Cricetid		10%
	northern grasshopper mouse (*Onychomys leucogaster*)	

[a]Across all 52 observed species combinations.

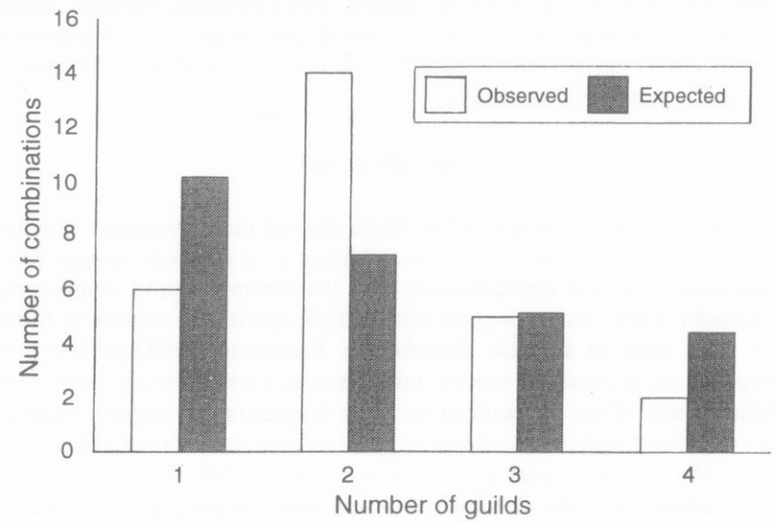

Fig. 3. Number of desert rodent taxonomic/foraging guilds represented in 52 observed species combinations in the Canyon Country Province, Colorado Plateau. Expected values derived from Poisson distribution.

Table 2. Microhabitat dissimilarity (Bray-Curtis coefficient, mean ± SE), of Canyon Country desert rodent guild pairs with occurrences significantly different than expected, compared to nonsignificant pairs. Asterisk indicates significant differences ($P \leq 0.05$).

Guild pair	Dissimilarity
Omnivorous Cricetids together	0.74 ±.02*
Omnivorous Cricetids + Sciurids	0.66 ±.02
Omnivorous Sciurids together	0.58 ±.03

Canyon Country desert rodent assemblages do have deterministic aspects. The number of observed species combinations was large, but much smaller than the total number possible. Observed combinations were also non-random

with respect to the number of species and taxonomic/foraging guilds represented. These patterns are likely a consequence of processes documented in other desert rodent communities; for example, competition and responses to patchily distributed resources.

Guild Structure

Canyon Country desert rodent fauna showed more consistent structure when viewed at the guild level. Assemblages were relatively simple, often with more than one representative from the dominant guild (omnivorous Cricetids). These results suggest that multiple species are capable of filling the same roles in different assemblages. Functional similarity has been proposed as a cause of species mixes across various desert ecosystems (MacMahon 1976). In contrast to other biogeographic regions, Canyon Country desert rodent assemblages appear to have considerable redundancy of guild members, perhaps a consequence of the high macro- and microhabitat diversity. I found evidence both supporting and rejecting Brown's (1987) hypothesis that coexisting species tend to belong to different taxonomic and functional groups. The morphologically similar Cricetid rodents of the Canyon Country Province have apparently evolved mechanisms facilitating successful coexistence, while the Sciurids may not have.

Body Size

Cricetid-dominated desert rodent assemblages of the Canyon Country show body size relationships similar to those found among Heteromyid rodents in other North American deserts (Bowers and Brown 1982, Brown 1987, Reichman 1991). These results are in contrast to Price and Brown's (1983) observation that Cricetid rodent assemblages do not show distinct size divergence. My differing conclusions may reflect the fact that the assemblages they considered had too few Cricetids for such patterns to be detected. As in other North American deserts, morphological patterns of coexisting Canyon Country desert rodents are closely tied to guild structure and are most evident among the most abundant taxonomic group.

Microhabitat Use

Microhabitat use appears to be an important aspect of community organization among Canyon Country desert rodents. Dissimilarity was apparent only among sympatric omnivorous Cricetids. These differences likely serve to minimize competition and facilitate coexistence among a group of taxonomically related and morphologically similar species. Similar resource partitioning has been documented in other rodent assemblages with a large Cricetid component (Meserve 1976, Hallett 1982). Coexisting omnivorous Cricetids and Sciurids did not show significant microhabitat separation. However, these species likely avoid interference competition by temporal separation, the former group being nocturnal, and the latter primarily diurnal. In contrast, omnivorous Sciurids did not show significant differences in microhabitat resource use, nor did they co-occur at any study sites.

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