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Michael A. Bowers; James H. Brown

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BODY SIZE AND COEXISTENCE IN DESERT RODENTS: CHANCE OR COMMUNITY STRUCTURE?¹

MICHAEL A. BOWERS AND JAMES H. BROWN²

*Department of Ecology and Evolutionary Biology, University of Arizona,
Tucson, Arizona 85721 USA*

Abstract. We use a simple test to evaluate the null hypotheses that desert rodent communities are composed of species assembled at random with respect to body size. This hypothesis is unequivocally rejected for species in the granivore guild: species of similar size (body mass ratios <1.5) coexist less frequently in local communities and overlap less in their geographic distributions than expected on the basis of chance, suggesting that their co-occurrence is precluded by interspecific competition. When granivore species and members of other guilds are combined in the same analysis, the patterns apparent in granivores diminish or disappear. These results indicate that ability to detect community structure depends to a large extent on thorough knowledge of the organisms and choice of appropriate statistical tests. We suggest that recent claims that many communities are indistinguishable from random associations of species are premature.

Key words: *body size; coexistence; community; competition; desert rodent; geographic range; guild; Hutchinson's ratio.*

INTRODUCTION

Recently the theoretical and empirical foundations of evolutionary and community ecology have been subjected to increasingly critical re-evaluation. Much of this attention has focused on concepts and data suggesting that communities are composed of species assembled in nonrandom patterns determined primarily by availability of limited resources and by competition among species for these resources (e.g., Hutchinson 1959, Grant 1968, Mac Arthur 1972, Cody 1974, Cody and Diamond 1975). Critics have argued that models implicating competition in community structure are based on questionable assumptions and that empirical observations purporting to demonstrate a significant role of competition usually consist of indirect, circumstantial evidence which is subject to alternative explanations (e.g., Connell 1975, Ricklefs 1975, Bedard 1976, Wiens 1977, Connor and Simberloff 1979, Strong et al. 1979). Several recent studies have claimed that characteristics of coexisting species, including several examples which purportedly demonstrate the influence of interspecific competition, can be equally well and more parsimoniously accounted for if the species are assumed to have been assembled at random from some appropriate species pool (Sale 1977, Connor and Simberloff 1979, Hubbell 1979, Strong et al. 1979). In fact, few investigators have tested rigorously and rejected the null hypothesis that observed associations of species do not differ significantly from those expected from an appropriate model of random processes (but see Hendrickson 1981).

Over the last decade, studies of seed-eating desert rodents have contributed increasingly to our under-

standing of interspecific interactions and community structure. Several investigators have concluded that coexistence of species is determined in large part by interspecific competition for limited food resources (Brown et al. 1979, and references cited therein). Perhaps the most striking patterns are in body size. The significant differences in body size among coexisting species of seed-eating rodents were discussed by the early naturalists (e.g., Grinnell and Orr 1934) and investigated in some detail in several recent studies (e.g., Rosenzweig and Sterner 1970, Brown 1973, 1975, Brown and Lieberman 1973, MacMahon 1976, Hafner 1977, Price 1978*b*). Brown (1973: 780) claimed that seed-eating rodent species of similar body size occurred together less frequently than expected on the basis of chance on local sand dunes, but did not give details of his analysis. Despite these studies, the functional significance of body size in rodent ecology remains unclear, and the relationship between coexistence and body size is worth re-examining in the light of the recent criticisms of studies purporting to demonstrate an important role of competition in determining community structure.

THE HYPOTHESES

In the present paper we test the null hypothesis that coexistence of desert rodent species is independent of their body sizes. Using primarily data from the literature, we examine the relationship between body size and coexistence on two levels: within local habitats, and within much larger geographic areas. We use a simple model of statistical independence to obtain expected frequencies of co-occurrence of pairs of species, and then test whether deviations of these expected values from observed frequencies of co-occurrence are independent of the ratios of body sizes between the species.

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² Order of authors was determined by toss of a coin.

An alternative hypothesis is that body sizes of coexisting species present nonrandom patterns which reflect the operation of deterministic ecological processes in structuring communities. It has often been suggested that the ecological and evolutionary responses of species populations to interspecific competition influence the distribution of body sizes observed in associations of closely related, coexisting species. If interspecific competition has influenced the ecology of desert rodents, we can make three specific, a priori predictions about the patterns of body size we expect to be revealed by our analyses.

Prediction 1: Species in the same guild which coexist in the same local habitats will show nonrandom patterns of body size, because species of similar size should occur together less frequently than expected on the basis of chance. A guild is defined as a group of species which use similar resources in similar ways (Root 1967). We employed Morton's (1979) classification of desert rodents into guilds of species which use similar food resources, to test this prediction for the diverse granivore guild.

This prediction follows from some longstanding observations and conjectures in evolutionary ecology. Phylogenetically related species often are so constrained by similar morphology, physiology, and behavior that they can avoid competition for the same resources only by selecting different habitats, so they do not really coexist on a local scale, or by differing significantly in body size, so they have different energy requirements and different capacities for searching for, harvesting, and processing food resources. Hutchinson (1959; see also Lack 1947, Brown and Wilson 1956) noted that coexisting congeners often appear to exhibit body size ratios which were more constant than expected by chance, because they seemed to be constrained to exceed some minimum value. Many subsequent studies have claimed that body size ratios of closely related, coexisting species (often termed Hutchinson's ratios) are nonrandom and that ratios for the most similar species normally exceed 1.25 for linear dimensions or 2.0 for body mass. Such patterns are often cited as evidence that interspecific competition plays a major role in structuring ecological communities. Unfortunately, the null hypothesis that body size ratios can be accounted for equally well by random assemblage of species from some appropriate species pool, as by some deterministic process such as interspecific competition, is seldom tested rigorously (Connor and Simberloff 1979, Strong et al. 1979, but see Brown 1973, Hendrickson 1981, Pearson and Mury 1979).

Prediction 2: If species in the same guild show nonrandom patterns of body size within local communities, they should show similar but perhaps less precise associations on a geographic scale; geographic ranges of species of similar size should overlap less

than expected on the basis of chance. This prediction follows directly from the previous one. If competition precludes local coexistence of species of similar size and resource requirements, it might also limit overlap in their geographic distributions. However, since species can occur in the same geographic area but avoid competition by selecting different habitats, body size patterns on a geographic scale might be less precise than those within local habitats.

Prediction 3: Inclusion of species in different guilds will diminish or obliterate nonrandom patterns of body sizes expected on the basis of Prediction 1, because species which do not interact should coexist essentially at random. Membership in different guilds implies that species do not compete severely. Since these rodent species are neither mutualists nor major predators of each other, coexistence of species in different guilds should not be influenced appreciably by deterministic interactions between them. Consequently, when an entire community is examined without regard to guild structure (e.g., Connor and Simberloff 1979), apparently random associations between species in different guilds may obscure deterministic patterns of coexistence within guilds. Thus we predict that nonrandom distributions of body sizes which may be present within the granivore guild will not be so apparent if desert rodent communities are analyzed without regard to guild structure.

THE TESTS

Local coexistence

From the literature and a few unpublished sources (Chew and Butterworth 1964, Jorgensen and Haywood 1965, Rosenzweig and Winakur 1969, Brown 1973, 1975, O'Farrell 1974, Nichols et al. 1975, Larsen 1978) we obtained data on numbers of individuals by species for samples of desert rodents from 95 local sites in three major North American deserts: Great Basin (33 sites), Mojave (24), and Sonoran (38)³. Sites were selected only on the basis of sample area and habitat uniformity. We tried to include only those studies in which the investigators had attempted to sample thoroughly the rodents in a restricted area (<5 ha) of relatively homogeneous habitat. Shreve's (1942) map of the North American deserts was used to assign specific sites to the three deserts. Localities were widely distributed over these deserts. We included sample areas from the Chihuahuan-Sonoran Desert transition in southeastern Arizona with the Sonoran Desert sites,

³ For a complete list of species recorded at all 95 sites, as well as data on species overlap, consult ESA Supplementary Publication Service Document No. 8103 for 9 pages of supplementary material. For a copy of this document, contact the senior author or order from The Ecological Society of America, Cornell University, Ithaca, New York 14853-0239 USA.

and did not use any localities within the Chihuahuan Desert proper, because there were too few for an independent statistical analysis.

We used objective, a priori criteria for assigning all species of rodents to one of four guilds. We followed Morton (1979), who classified all North American desert rodents as either granivorous, herbivorous (foliage-eating), insectivorous, or omnivorous. We used Brown's (1973) criteria to restrict the analysis to only the common species which occurred at each site. Common species were defined as those which were represented by >5% of the total individuals in the sample, except for the very large rodents (\bar{x} body mass > 80 g) which were included whenever they were present. Such criteria are necessary to exclude from the analysis rare individuals of small species which were transients from other habitats and to correct for underrepresentation of large rodents in the samples because of trapping bias (see Brown 1973). Body masses for each species were obtained from the literature by averaging data for many individuals from many sites. Interspecific geographic variation in body size is not sufficient to affect our analysis, which depends solely on ratios of sizes of coexisting pairs of species.

Our analysis is conceptually and operationally simple. We determined the frequency of occurrence of each species among all of the sample sites in each of the three deserts separately and also in all deserts combined. For each area, we generated an expected frequency of co-occurrence of the two appropriate species by taking the product of the two observed frequencies of occurrence. This procedure is based on the null hypothesis that probability of occurrence of any given species in a local site depends only on its frequency of occurrence in the large universe of sample localities and is independent of the distribution of all other species; consequently species pairs are expected to associate at random. The actual observed frequency of coexistence of each pair of species in the samples was then compared with the expected value and scored as being either greater or lesser than expected (positive or negative association). Each pair of species also was scored as differing in body mass by either more or less than a ratio of 1.5, which was originally used by Brown (1973) as a conservative estimate of Hutchinson's ratio.

Finally, we used 2×2 contingency tables to test the null hypothesis that deviations from expected frequencies of co-occurrence were independent of the ratios of body sizes, employing each pair of species only once in each test.

We performed two tests of the null hypothesis. In the first, we analyzed only species within the granivore guild. In the second, we included all species, both granivores and members of all other guilds, in the same analysis. There were too few species in each of

the nongranivore guilds to test rigorously for a relationship between coexistence and body size within each of these guilds separately.

Overlap of geographic ranges

We used a different data base, but virtually identical procedures, to test the null hypothesis that the geographic overlap of species distributions is independent of the ratio of their body sizes. We measured the frequency of occurrence of each species relative to a sampling universe. This universe was obtained by placing a grid of points over Shreve's (1942) map of the North American deserts. The interval between grid points represented 50 km. A total universe of 619 grid points incorporated the combined area encompassed in the three deserts: Great Basin, Mojave, and Sonoran. Maps of the geographic distribution (from Hall and Kelson 1959) of each species of desert rodent listed in Morton (1979) were projected onto the sampling universe and the numbers of grid points within the range of each species and within the overlapping parts of the range for each pair of species were tallied (see footnote 3). The proportions of all grid points within the range of each of the two species were multiplied to generate expected frequencies of overlap for each pair of species under the null hypothesis of independent distributions. Observed frequencies of overlap were compared with these expected values and scored as either greater or lesser than expected. Only those pairs of species whose ranges came within 200 km of each other were included in the analysis, because it seemed unlikely that distributions of species with more separated ranges had been affected by competition within recent time. We used 2×2 contingency tables to test the null hypothesis that deviations from expected overlap in geographic ranges were independent of the ratio of body sizes, again using the body mass ratio of 1.5. We performed this analysis twice, first using only the species in the granivore guild, and then incorporating all species in all four guilds.

Statistical analysis

A chi-square or Fisher's Exact test frequently is used to assess the probability that the distribution of data in a 2×2 contingency table could be expected on the basis of chance. Although the chi-square test has been used to analyze pairwise associations of species (e.g., Brown 1973: 780; Pielou 1979: 225), it is inappropriate because the assumption that all entries in the table are independent is violated. Since each observation represents a pair of species, and both members of that pair appear in other entries in combination with other species, the observations are not statistically independent. More specifically, with s species there are $\frac{s^2 - s}{2}$ pairs, and each species is represented in $s - 1$ of these.

TABLE 1. 2×2 contingency tables testing the null hypothesis that local coexistence of granivorous rodents and rodents in all guilds in three deserts is independent of body size ratio. See text for details of the Y^2 statistic and its accompanying probability values.

	Granivores				All guilds			
	Body mass ratio	Association*		Body mass ratio	Association			
		-	+		-	+		
Great Basin	<1.5	6	0	<1.5	21	11	$Y^2 = 5.16$	$P = .003$
	>1.5	15	15	>1.5	54	30		
					$Y^2 = 0.02$	$P = .870$		
Mojave	<1.5	3	1	<1.5	18	9	$Y^2 = 0.05$	$P = .652$
	>1.5	11	5	>1.5	49	28		
					$Y^2 = 0.08$	$P = .826$		
Sonoran	<1.5	7	0	<1.5	26	15	$Y^2 = 4.5$	$P = .047$
	>1.5	23	15	>1.5	62	30		
					$Y^2 = 0.20$	$P = .677$		

* Association was scored as either positive (+) or negative (-) depending on whether observed frequencies of coexistence were greater or less than expected on the basis of chance.

To assess the effect of such paired observations, we used a simulation technique to determine the probability of obtaining the observed distribution of entries in our 2×2 contingency tables under the null hypothesis of random species associations. To test each hypothesis we generated $s \times s$ matrices (where s = the number of rodent species in the assemblage), and randomly assigned the sign of association, either + or -, to species pairs in the half of the matrix above the main diagonal (r_{ij} : $1 \leq i, j \leq s$, $i \neq j$) entries and category of body size ratio, either <1.5 or >1.5, to the other half (r_{ji} entries). The marginal totals for the contingency tables (e.g., total number of + associations, etc.) were set equal to the observed values, while the simulation generated joint entries in the tables reflecting pairs of species associating at random. Each simulation procedure was repeated 1000 times. For each simulation we created a 2×2 contingency table and calculated $Y^2 = \sum \frac{(O - E)^2}{E}$, where O is the number of pairwise observations in each cell and E is the expected number determined by taking the product of the appropriate marginal totals and dividing by the total of all observations. The distribution of this Y^2 statistic was significantly different from the chi-square distribution ($P \ll .01$ in all cases). Consequently, we compared the observed value of Y^2 for each rodent assemblage with the expected distribution obtained from the 1000 simulations and thus determined the approximate probability of obtaining the observed value under the null hypothesis. Because of the large number of simulations for each test, the empirically estimated probability level should be very close to the actual one. Interestingly, these probabilities were always very close to those obtained by chi-square tests of the same data, even though the assumption of independent sampling was violated and the expected

distribution of pairwise associations consequently was very different from a chi-square distribution.

RESULTS OF THE TESTS

Granivorous rodent species of similar size occurred together significantly less frequently than expected on the basis of chance on both a local and a geographic scale. This nonrandom pattern was diminished or obscured when species of all guilds were combined in the same analysis.

We first consider coexistence of granivores within local habitats. In both the Great Basin and Sonoran Deserts, pairs of seed-eating rodent species which differed in size by a ratio of <1.5 coexisted less frequently than expected on the basis of chance (Table 1), resulting in a clear rejection of the null hypothesis ($P = .003$ and $.047$ for the Great Basin and Sonoran Deserts respectively). The null hypothesis was not rejected in the analysis of coexistence of granivores in the Mojave Desert (Table 1), but the power of the analysis was impaired by the small number of sample sites and the fact that few of the species were of similar size. When we analyzed data on coexistence of granivore species in all three deserts combined, a much more pronounced nonrandom pattern was observed (Table 2) and the null hypothesis was rejected with great confidence ($P = .008$).

When species in all guilds were analyzed together, the nonrandom pattern apparent within the granivore guild diminished or disappeared. The null hypothesis was not rejected for analyses of any of the three deserts independently (Table 1). When data for all three deserts were combined, there was a marginally significant tendency for species of similar size to coexist less frequently than expected on the basis of chance ($P = .053$), but the pattern was much less pronounced than when only granivores were considered (Table 2).

TABLE 2. 2×2 contingency tables testing the null hypotheses that local coexistence and geographic overlap of granivorous rodents and rodents in all guilds are independent of body size in all deserts combined. See text for details of the Y^2 statistic and its accompanying probability values.

	Body mass ratio	Granivores		Body mass ratio	All guilds	
		Association*			Association	
		-	+		-	+
Geographic overlap	<1.5	44	13	<1.5	65	53
	>1.5	72	60	>1.5	162	176
		$Y^2 = 8.60$	$P = .010$		$Y^2 = 1.64$	$P = .231$
Local coexistence	<1.5	27	0	<1.5	93	15
	>1.5	65	28	>1.5	274	98
		$Y^2 = 10.60$	$P = .008$		$Y^2 = 5.55$	$P = .053$

* Association was scored as either positive (+) or negative (-) depending on whether observed frequencies of coexistence were greater or less than expected on the basis of chance.

Since the number of pairwise comparisons increases as almost the square of the number of species, most of the pairs in this combined analysis represent species in different guilds. Clearly inclusion of species in other guilds obscures the patterns present among granivores and produces associations that appear much more random.

The actual relationship between local coexistence and body size ratios in granivorous rodents may be more precise than suggested by our analysis. Our data on frequency of coexistence are subject to sampling error. Only 1 of 17 pairs of granivore species which differed in size by a ratio of <1.5 coexisted more frequently than expected within a single desert (Table 1). This pair (*Dipodomys ordii* and *D. merriami* in the Mojave Desert) were taken together on only one site³. This same pair of species coexisted less frequently than expected by chance in both of the other two deserts and in the combined analysis (Tables 1 and 2). Not a single pair of granivore species with a size ratio of <1.5 coexisted more frequently than expected on the basis of chance in the analysis of the largest most complete data set: the one for all three deserts considered together. Furthermore (Table 2), we followed Brown (1973) in basing our analyses on an arbitrary body size ratio of 1.5, which was chosen to be a conservative value. Local communities often exhibit apparently regular patterns of body size in which minimum ratios for species pairs are usually approximately 2. When we used objective criteria to select the largest community of species most frequently recorded in each of the three deserts³, the patterns of body sizes were strikingly similar (Fig. 1). Although the identities of these species were often different, each desert supported a community of four species exhibiting remarkably similar distributions of body sizes. In each community, body masses ranged from approximately 7 to 100 g and minimum ratios exceeded 1.75.

Geographic distributions of granivorous desert rodents also overlapped nonrandomly with respect to

body size (Table 2). Pairs of species with size ratios <1.5 tended to be negatively associated, resulting in strong rejection of the null hypothesis ($P < .01$). However, when species in the herbivore, insectivore, and omnivore guilds were combined with the granivores in the same analysis, the pattern present in granivores was totally obscured (Table 2) and the null hypothesis was not rejected ($P = .23$).

Some granivore species of similar size have strikingly displaced geographic ranges. The most obvious cases (Fig. 2) involve rodents of extreme size: the smallest pocket mice (body mass <11 g) and the largest kangaroo rats (>100 g). In comparison, species of intermediate size frequently show much more overlap in their geographic ranges, but many of these species pairs select different habitats and rarely coexist in local communities (e.g., Schroder and Rosenzweig 1975, Hoover et al. 1977). This pattern is apparent from our analysis by comparing observed and expected co-occurrences for local and geographic areas (Table 2). Whereas 13 of 57 pairs of granivore species with body size ratios <1.5 overlapped more frequently than expected by chance in geographic distribution, 0 of 27 pairs coexisted more frequently than expected in local communities.

In order to perform these analyses we have had to make some seemingly arbitrary decisions about community and guild composition as well as what measure of association and ratio of body sizes to use. All of these decisions were made a priori, based on our knowledge of rodent biology and published precedent. We used the same procedures as Brown (1973) to exclude rare species from communities, determine sign of association, and select the critical body size ratio of 1.5. We followed Morton's (1979) assignments of rodents to guilds, because it was even more conservative than Brown's. So far as we have been able to determine, none of these decisions affect the qualitative outcome of the analyses, but of course they influence the quantitative details. Two points deserve ad-

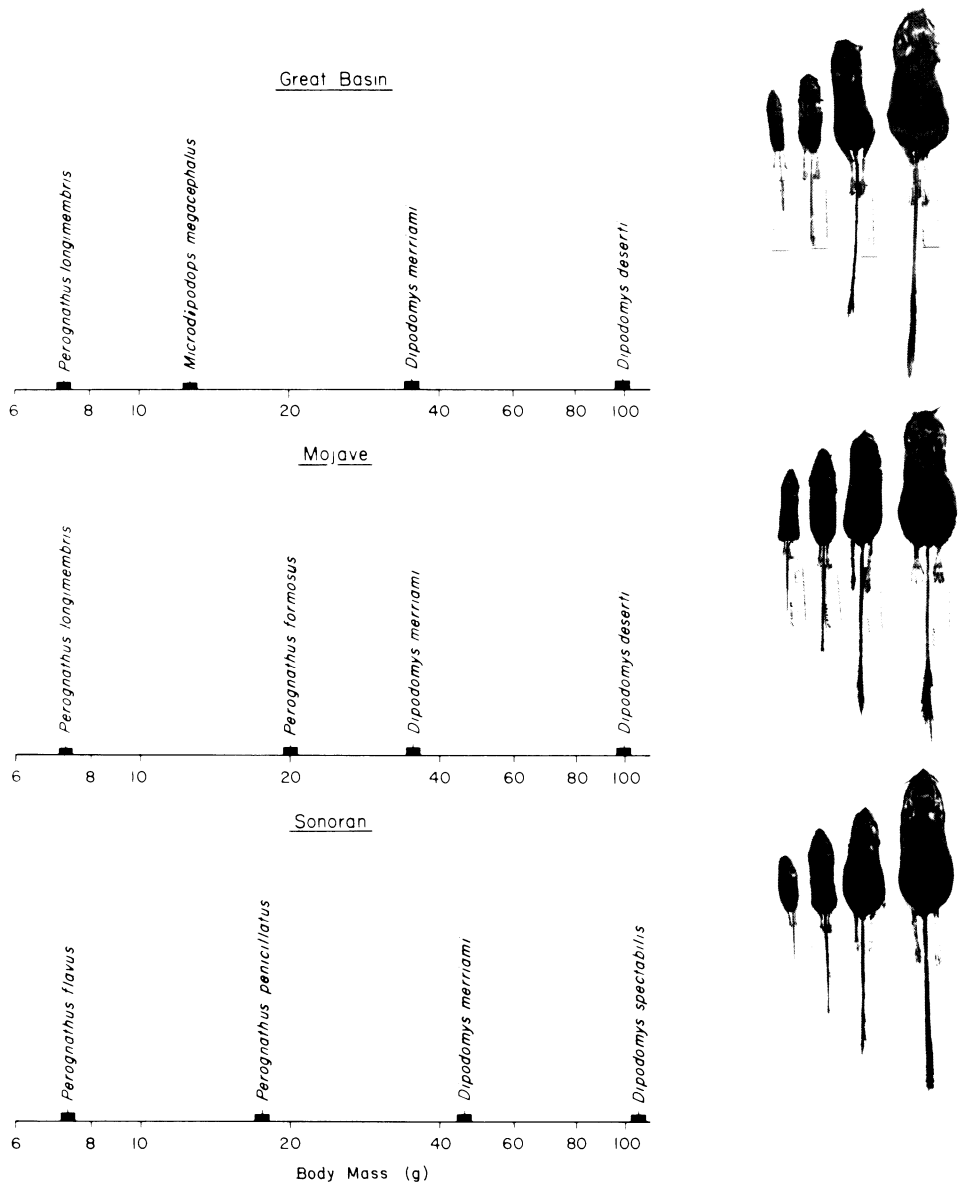


FIG. 1. Distribution of body sizes (plotted on a logarithmic scale so that equal spacing indicates equal ratios) in arbitrarily chosen, diverse communities in three deserts (see text). Note that the size distributions of species are very similar even though the identity of species often differs between deserts.

ditional consideration. First, the body size ratio of 1.5 seems to be surprisingly close to the critical ratio for coexistence (Fig. 3). If the analysis of local coexistence in granivores is repeated using different ratios, the null hypothesis is rejected with decreasing statistical confidence as the ratio becomes much larger or smaller than 1.5. If the analysis is repeated using ratios < 1.5, the statistical power of the test is limited by the small number of species pairs of similar body size. Moreover, some species pairs with body size ratios only slightly greater than 1.5 occur together more frequently than expected on the basis of chance (Fig. 3)

so the nonrandom pattern gradually becomes less clear as the ratio increases above this value. Second, we decided to score associations of species pairs qualitatively as either positive or negative rather than using some quantitative index of association. We assumed that size-dependent competition between two species would be the primary factor determining whether the pair coexist more or less than expected on the basis of chance, but that factors other than competition are likely to influence the extent to which their local and geographic distributions overlap. Third, the null hypothesis implicitly assumes that each species could

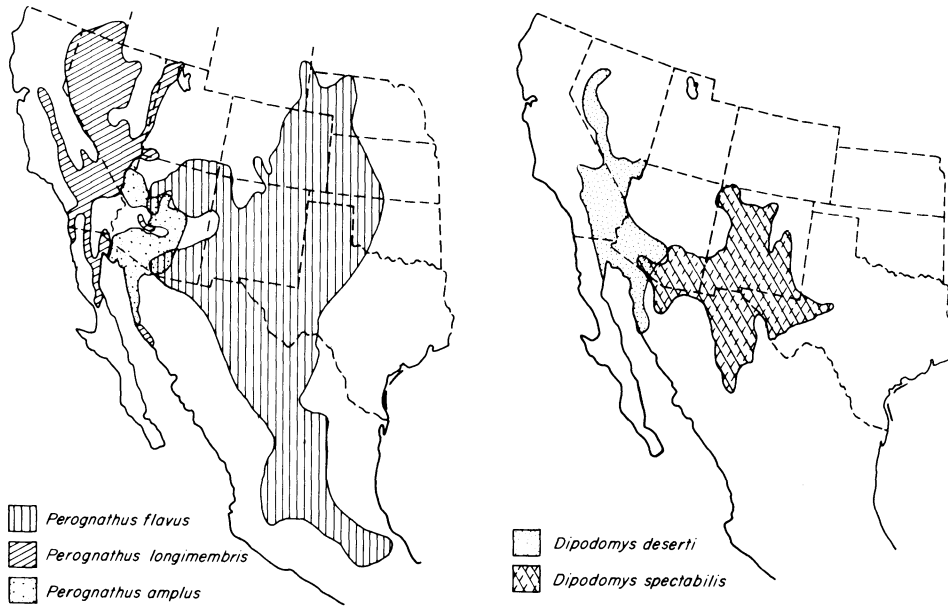


FIG. 2. Geographic ranges of small pocket mice (*Perognathus* spp., body mass <11 g) and of large kangaroo rats (*Dipodomys* spp., body mass >100 g). Redrawn from Hall and Kelson (1959). Note the extremely small overlap in geographic ranges of the species of similar size.

potentially occur at each sample site. If this is not true and the sampling universe is unrealistically large, our method will underestimate the degree of co-occurrence expected under the null hypothesis resulting in an excessive number of positive associations. However, this would not affect the results of our analyses, which show numerous negative associations among similar-sized species. Although we are confident that the nonrandom patterns we have demonstrated in associations of granivorous rodent species are more robust than the arbitrary decisions we have had to make

to perform our analyses, we also believe that we have been able to demonstrate these patterns with such clarity because a great deal is known about the ecology of the rodents and we have been able to incorporate this information in a rigorous, objective analysis.

DISCUSSION

Body size and mechanisms of coexistence

We have demonstrated a significant negative association among some of the species in desert rodent

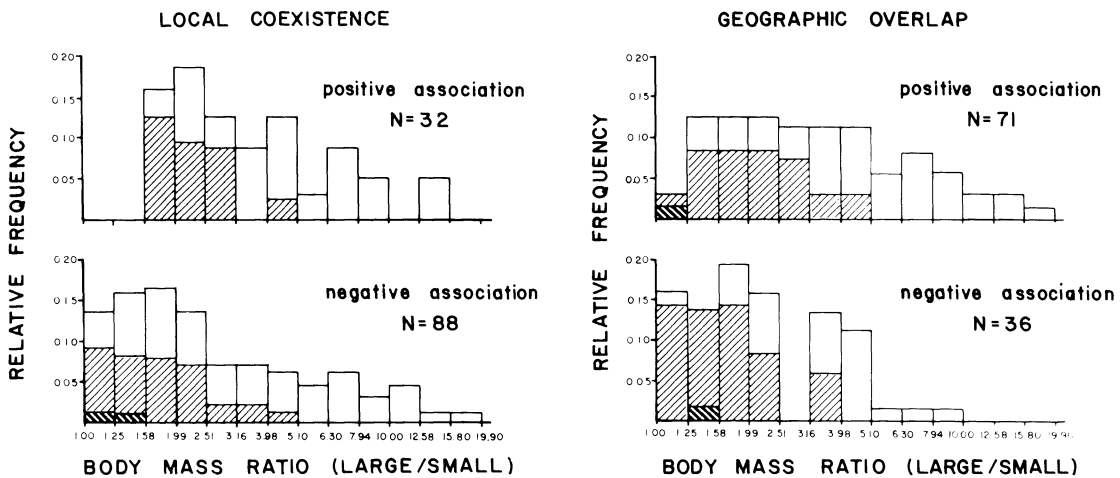


FIG. 3. Frequency histograms of pairwise species associations plotted over body mass ratios on a logarithmic scale. Shading indicates phylogenetic affinities of pairs of species. Unshaded: species in different genera; light hatching: congeneric species in different species groups; dark hatching: members of the same species group (based on taxonomies of Hall and Kelson [1959] and, for *Dipodomys*, Lidicker [1960]). Note that even the negative associations between species of similar size are often for species in different genera or species groups.

communities: granivore species of similar body size occur together much less frequently than expected on the basis of chance. This pattern in itself does not prove that these communities are structured by interspecific competition; however, the pattern is entirely consistent with this explanation. Additional evidence supporting the competition hypothesis is our finding that negative association is observed only among species which, on a priori criteria, we would expect to compete most intensely (members of the diverse granivore guild). Co-occurrence of species in different guilds does not appear to differ significantly from random association.

An alternative hypothesis to competition which could possibly account for this pattern of negative association between similar sized species invokes a model of allopatric speciation. Specifically, if rodent species were formed by geographic isolation we might expect that the most closely related species might still have nonoverlapping geographic ranges; such close relatives also might not have diverged significantly in body size. If this accounts for the pattern we observe, then negatively associated species of similar size should be very closely related (in the same species group or subgenus). This is clearly not the case for granivorous rodents inhabiting the Mojave, Sonoran, and Great Basin deserts (Fig. 3). Furthermore, the fact that nonrandom associations are more pronounced in local communities than on a geographic scale (Table 2) indicates that contemporary ecological interactions among coexisting species rather than an historical legacy of geographic speciation is the more likely explanation for this pattern. Consequently, we can reject the hypothesis of allopatric speciation and focus on the competitive relationships among these species.

These results tend to corroborate numerous recent studies suggesting that interspecific competition plays a major role in determining the structure of communities of seed-eating desert rodents. Although much of the evidence is indirect and circumstantial, the process of interspecific competition provides the only single, parsimonious explanation for numerous, diverse, independent observations (Brown et al. 1979 and included references). In addition, we now have direct evidence from exclusion experiments for competition among granivorous rodent species (Munger and Brown 1981). Because rodent species of similar body size rarely coexist in the same habitat, Munger and Brown's experiments tested for competition between species which differed in size by a ratio of at least 2, yet they demonstrated significant negative interactions. We would expect even more intense competition between species more similar in size.

Although desert rodent ecologists have long recognized that differences in body size appear to reduce competition and thus facilitate coexistence among granivorous species, the mechanism of interaction remains a major unsolved problem. Several hypotheses

have been proposed: (1) Species forage selectively for food packets providing net energy returns that are positively correlated with body size (Brown et al. 1979); (2) Coexistence is mediated in part by interference, and body size affects the outcome of interspecific aggression (Rosenzweig and Sterner 1970, Congdon 1974, Hafner 1977, Hutto 1978, S. C. Trombulak and G. J. Kenagy, *personal communication*); (3) Ability to safeguard food cached in the burrow depends in part on burrow diameter and hence on body size (M. S. Hafner, *personal communication*); (4) Rodents of different body size forage selectively in different microhabitats (Lemen and Rosenzweig 1978, Price 1978b). None of these mechanisms are necessarily mutually exclusive and all might operate to facilitate coexistence.

Although the functional significance of body size differences among coexisting species of seed-eating rodents remains poorly understood despite more than a decade of research by numerous ecologists, the present study reaffirms that nonrandom distributions of body sizes are one of the most striking characteristics of community structure. All available evidence is consistent with the interpretation that species of similar size tend to compete intensely and therefore are unlikely to occur together in the same area.

Competition and community structure

Despite increasingly supportive evidence from studies of desert rodents and a few other systems, the theory that communities are structured in part by limited availability of essential resources and by interspecific competition has received increasingly strong criticism. Most notably, several recent studies (Strong et al. 1978, Connor and Simberloff 1979, D. Simberloff and W. Boecklen, *personal communication*) have re-examined data purporting to demonstrate patterns of community structure resulting from competition. They have claimed that many of the observed patterns do not differ significantly from those expected if species are assembled at random according to an appropriate null model. On this basis Strong et al. (1979: 918) "suggest that apparent randomness would account for a substantial proportion of variation in many real ecological communities were null hypotheses employed that assumed no structure at the outset. Null hypotheses of this sort have not been customary, and for this reason we suspect that more structure and pattern have been deduced by ecologists than actually exist." In a similar vein Connor and Simberloff (1979: 1138) state, "All this is not to say that species *are* randomly distributed on islands, or that interspecific competition does not occur. Rather, statistical tests of properly posed null hypotheses will not easily detect such competition, since it must be imbedded in a mass of non-competitively produced distributional data. Instead, one must make a strong argument for competitive exclusion via observed active replacement of one species

by another, experiment, or very detailed autecological study." We suggest that such a negative viewpoint is unwarranted.

A major point at issue here concerns the nature of null hypotheses and the importance that is attached to failure to reject them. There are numerous tests of null hypotheses that might reasonably be applied to almost any community. Failure to reject one or more of these is hardly evidence that the community is not structured by deterministic biological processes such as interspecific competition. The kinds of information used in the test and the statistical form of the test itself strongly influence the sensitivity of the test to nonrandom patterns and hence its capacity to reject the null hypothesis. The difficulties of developing analytical procedures that are both biologically appropriate and statistically rigorous and powerful are particularly great when, as in the present case, the relationship between empirical pattern and deterministic process is indirect and complicated by other factors. Processes other than interspecific competition influence the local and geographic distributions of species and thereby affect patterns of coexistence on all spatial scales. Factors other than body size determine the intensity of competition between species, particularly when they are distantly related or members of different guilds. In fact, because competition is a negative interaction which reduces the fitness of participating individuals, over evolutionary time we expect species to evolve and to associate in communities so as to utilize limiting resources more efficiently, thereby reducing the apparent competition with other species. These complications do not necessarily mean that we will be unable to detect deterministic patterns of coexistence and body size which reflect the role of competition in structuring communities; they do imply, however, that we should look for evidence of competition where we expect it to be most severe: between closely related species of similar size in the same guild.

All of this is not to argue that chance does not play a significant role in the association of species to form communities. Random processes probably are particularly important in determining the composition of very small, local, or temporary systems, but they provide rather unsatisfactory explanations for the diversity of nature on a larger scale. Testing community characteristics against null hypotheses is a valuable exercise, but the greatest progress is made when an appropriate null hypothesis can be rigorously and emphatically rejected, because presumably such a rejection indicates a nonrandom pattern caused by deterministic mechanisms. We believe that future work on desert rodents and other organisms will corroborate that interspecific competition plays a substantial role in the organization of ecological communities.

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