Resource Utilization and Coexistence of Seed-Eating Desert Rodents in Sand Dune Habitats
Author(s): James H. Brown and Gerald A. Lieberman
Source: *Ecology*, Vol. 54, No. 4 (Jul., 1973), pp. 788-797
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1935673
Accessed: 20/06/2011 15:28

RESOURCE UTILIZATION AND COEXISTENCE OF SEED-EATING DESERT RODENTS IN SAND DUNE HABITATS[1]

JAMES H. BROWN

Department of Biology, University of Utah, Salt Lake City 84112

AND

GERALD A. LIEBERMAN

Department of Biology, Princeton University, Princeton, New Jersey 08540

Abstract. As many as five species of seed-eating rodents coexist in sand dune habitats in the North American deserts. Among species occurring together the ratio of body weights of adjacent species pairs is usually greater than 1.5. The seed resources of the habitats appear to be apportioned among species chiefly in two ways: (1) rodents differentially harvest seeds of different sizes, and seed size selection is positively correlated with body size; (2) species forage in different areas relative to the cover of perennial shrubs. The species also differ in their annual activity (some are active all year, others may go torpid for short periods or hibernate for several months), but it is difficult to evaluate how these differences affect the utilization of seeds. Our estimates of total overlap in resource utilization between species indicate that competition for seeds has an important influence on community structure in desert rodents. In productive habitats species that are quite similar (overlap values greater than 80%) in resource utilization are able to coexist and species diversity is high, but in less productive habitats ecologically similar species are excluded, resulting in decreased species diversity.

INTRODUCTION

In what ways and to what extent must resource-limited species differ in their use of environmental resources in order to coexist? The early ecologists Lotka (1925), Volterra (1926, 1931), and Gause (1934) demonstrated both empirically and theoretically that differences in resource utilization are a necessary condition for stable coexistence. Recent interest in the structure and dynamics of natural communities has resulted in the investigation of the quantitative aspects of resource utilization by both theoretical and empirical ecologists (e.g., MacArthur and Levins 1967, MacArthur 1958, 1970, Cody 1968, Pianka 1969, Pulliam and Enders 1971). Numerous studies have quantified differences between ecologically similar coexisting species, but only a few have attempted to identify the resources that are in short supply and measure directly the way they are apportioned among the various species.

Rosenzweig and his collaborators (Rosenzweig and Winakur 1969, Rosenzweig and Sterner 1970) have emphasized the suitability of desert rodents for field studies of coexisting, ecologically similar species. Rodents are abundant and diverse in the deserts of North America. It is not uncommon to find 8 or 10 species in a small area of uniform habitat, and 5 or 6 of these species usually are ecologically similar in that they feed largely on dry seeds and their populations fluctuate in response to the seed crop. Most of the granivorous species belong to the family Heteromyidae, which have fur-lined cheek pouches used to collect and transport food. It is easy to sample dietary items in the form and proportions in which they were collected by dead-trapping these species and collecting the contents of the cheek pouches. Because of their abundance, quantitative data on other aspects of the ecology of these species are also relatively easy to obtain.

In a previous paper Brown (1973) described the extrinsic ecological, biogeographic, and evolutionary variables that determine the diversity of seed-eating rodent species in sand dune habitats. The present paper presents data on the use of food resources by these species and attempts to identify the kinds and quantity of differences that permit coexistence.

METHODS

This paper is based on data collected while Brown was sampling the rodent faunas of 18 sand dunes in Nevada, eastern California, and western Utah. The locations of these dunes, dates when they were sampled, descriptions of the habitats, and composition of the rodent faunas are described in the previous paper (Brown 1973). The dunes are hills of wind-drifted sand partially stabilized by isolated perennial shrubs spaced several meters apart. The rodents were collected in "Museum Special" dead traps set in groups of four. In order to test for differential utilization of the habitat in a horizontal dimension relative to plant cover, Brown placed each trap in a particular position relative to an isolated shrub, as follows (Fig. 1): (1) in the center of the plant, (2) at the edge of the plant, (3) 1 m from the plant on the bare sand, and (4) at least 2 m from the plant in the most open area of bare sand. These groups of traps were

[1] Received April 7, 1972; accepted September 11, 1972.

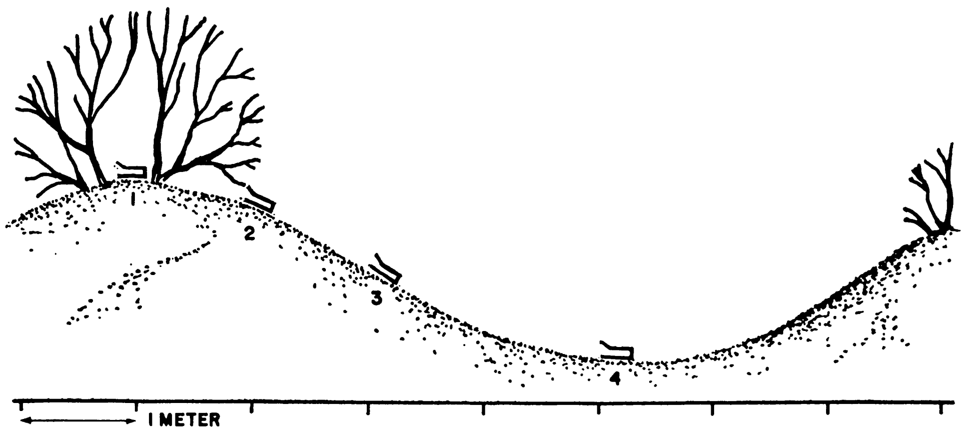

FIG. 1. Placement of traps relative to perennial shrubs to measure horizontal foraging areas.

set 10–15 m apart as 100–200 traps were set each night in an irregular line running through the most uniform habitat on the dune.

The following morning when the traps were collected, the position of each animal caught was recorded and the rodents were weighed and checked for food items in the cheek pouches. About 40% of the heteromyids had seeds or other food in their cheek pouches. The pouch contents of each individual were collected in labeled vials. The vials were returned to the laboratory and the seeds in each were sorted into 13 size categories, using a graded series of Tyler sieve screens (4, 5, 6, 7, 8, 9, 10, 12, 14, 16, 20, and 24 mesh).[2]

RESULTS AND DISCUSSION

A total of 18 species of rodents were captured during the study. Of these species, 3 (*Onychomys torridus, O. leucogaster*, and *Ammospermophilus leucurus*) are not primarily granivorous, and 7 were taken too infrequently (fewer than 10 times) for adequate analysis. The present paper is based largely on the data obtained for the remaining 8 species, which are the important species of seed-eating rodents inhabiting the sand dunes of the Great Basin, Mojave, and Colorado Deserts. Six of these species (*Perognathus longimembris, Microdipodops pallidus, M. megacephalus, Dipodomys merriami, D. ordi,* and *D. deserti*) belong to the family Heteromyidae, the most diverse and specialized group of North American desert rodents, and all have cheek pouches. The other two species (*Reithrodontomys megalotis* and *Peromyscus maniculatis*) belong to the family Cricetidae and are found in mesic grasslands, forests, and marshes as well as in desert habitats. Cricetids do not have cheek pouches, and we have no samples of the natural food items collected by these two species.

The rodents range in size from 7 to 100 g and those species which coexist on the same dune form a remarkably regular array of sizes. This was discussed in detail by Brown (1973: Table 2 and Fig. 3) and will be summarized briefly here. Species of similar size were only rarely common on the same dune, but when a particular species was absent from one or more dunes another species of almost identical size frequently was present. Thus three species in the 12–13 g size range (*M. pallidus, M. megacephalus,* and *P. penicillatus*) "replaced" each other on different dunes; the two smallest species (*P. longimembris,* 7.1 g, and *R. megalotis,* 8.6 g) were never common on the same dune; and the most similar sized kangaroo rats (*D. merriami,* 37.6 g, and *D. ordi,* 48.9 g) were both common on only two of the seven dunes within their common geographic and altitudinal ranges. With the exception of these two kangaroo rats, all pairs of common, coexisting species differed in weight by a ratio (larger/smaller) of at least 1.4. The pairs of bigger species tended to differ in size by a larger factor than did the smaller species. Also, as the number of coexisting species decreased, the differential in body size between adjacent pairs of species increased; the ratio of weights for adjacent pairs was 2.0, 2.3, 2.7, and 2.7 on dunes with 5, 4, 3, and 2 coexisting species respectively.

Seed size selection

The striking regular patterns of body size distributions on dunes with varying diversity and composition of species, indicate that the ability of seed-eating rodents to coexist in these habitats depends on their being of different size. This suggests that the various species of rodents differentially utilize seeds of different sizes according to their body sizes. This is pre-

[2] The millimeter equivalents of these mesh sizes are given in Fig. 3. They form a geometric series, each size being about 19% larger than the one before.—Ed.

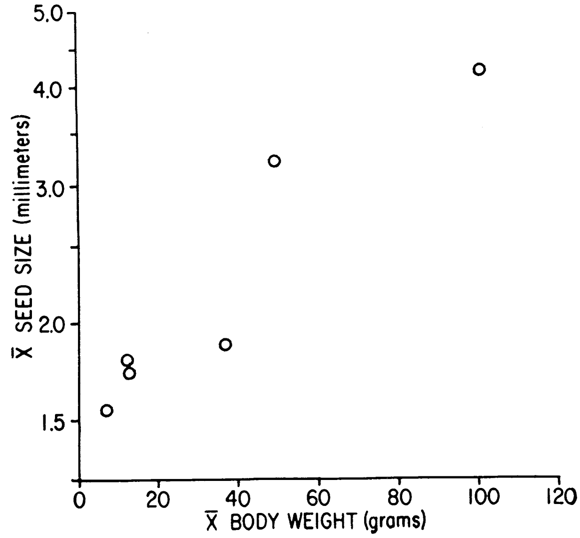

FIG. 2. Relation between diameters of natural seeds in the cheek pouches and body size for six species of heteromyid rodents.

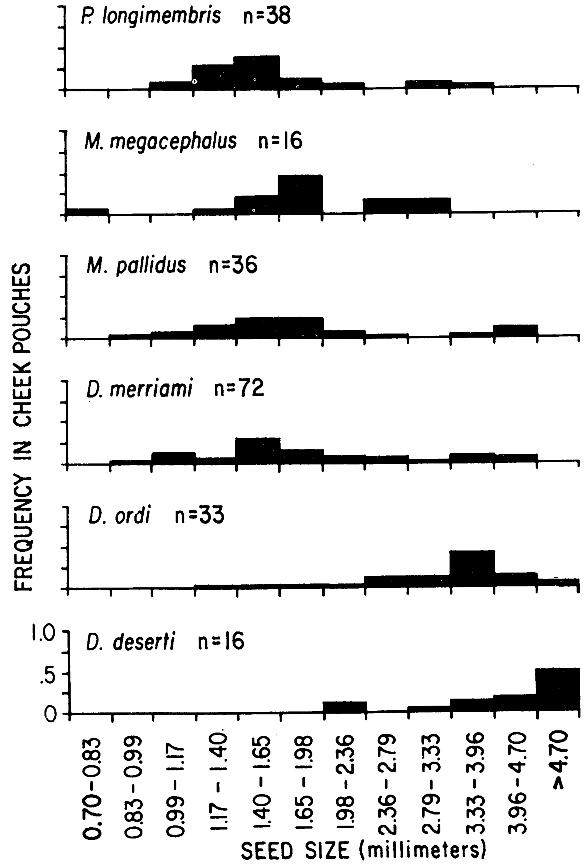

FIG. 3. Frequency distribution of sizes of natural seeds in the cheek pouches of six species of heteromyid rodents. Size categories determined by the Tyler sieves, which form a geometric series. The mean size of all seeds in the pouches of each individual was determined, and then the values for all individuals were plotted.

cisely what happens; the mean size of seeds in the cheek pouches of field-caught heteromyid rodents is closely correlated with the mean body weight of the species ($r = 0.94$; Fig. 2). However, when the mean seed size in the pouches of each individual is plotted to provide a frequency distribution of seed size utilization for each species (Fig. 3), it is apparent that each species uses a wide range of seed sizes and there is a great deal of overlap for species that differ in body weight by a factor of 2 or 3 (e.g., *P. longimembris,* 7.1 g; *M. pallidus,* 12.5 g; and *D. merriami,* 37.6 g).

Two aspects of the way the data on seed sizes were collected might result in artificially large variances in the sizes apparently used by each species. First, since the data are based on seeds collected from cheek pouches, it is possible that the seeds temporarily stored in the pouches are more variable in size than those which are eaten. One phenomenon may be particularly important in this respect. Many seeds are produced in clusters or pods, and so several small seeds may be harvested by a rodent as one large package. However, the rodent may discard the supporting structures and place only the individual seeds in its cheek pouches. We are quite certain that this happens occasionally in some species (e.g., *D. merriami*), and it would have the effect of indicating a mean seed size smaller and a variance larger than the size of particles actually harvested. Second, we sorted seeds into size categories by passing them through a series of graded sieves. This technique separates seeds on the basis of their linear dimensions. Rodents probably find seeds, which are usually buried in the sand, by a combination of olfactory and tactile cues. The probability of tactile encounter should be related to the linear dimensions of a seed, but it is possible that seed size discrimination by the rodents is based on other parameters (e.g., intensity of odor, or weight) that we have not used in analyzing the cheek pouch contents. We do not feel, however, that either of these sources of error has affected our results significantly.

Another problem with the data is that we have no information on the sizes of seeds utilized by the two species of cricetid rodents that occur together with the heteromyids on many sand dunes. Because these cricetids, *Peromyscus maniculatus* and *R. megalotis,* occupy appropriate positions in the body size spectrum when they coexist with heteromyids (Brown 1973, Fig. 3), we have assumed that they select seeds on the basis of size in the same way. Therefore, we have derived hypothetical seed size utilization distributions for these species based on the data for heteromyids. Means for each species were predicted on the basis of body weight from the relationship in Fig. 2, and variances were assumed to equal 4 (an intermediate value for the heteromyids). The resulting distributions are only as valid as the tenuous assumptions on which they are based, but in the absence of empirical information they are useful for discussing probable mechanisms of coexistence of several species of seed-eating rodents. Seed size selection by several species of cricetid and heteromyid rodents is presently being studied under controlled conditions in the laboratory.

In order to assess the significance of seed size allocation in the coexistence of rodent species in sand dune habitats, we examined the situations where the greatest number of species (5) occur together. We converted the data in Fig. 3 to normal curves of unit area and used the hypothetical values for *Peromyscus maniculatus* to derive sets of resource utilization curves for two different groups of coexisting species (Fig. 4). The group of species in the lower graph occur together on two dunes and the group in the upper figure show the most even subdivision of seeds in five species associations. It is apparent that the large kangaroo rats, *D. deserti* and *D. ordi,* and the

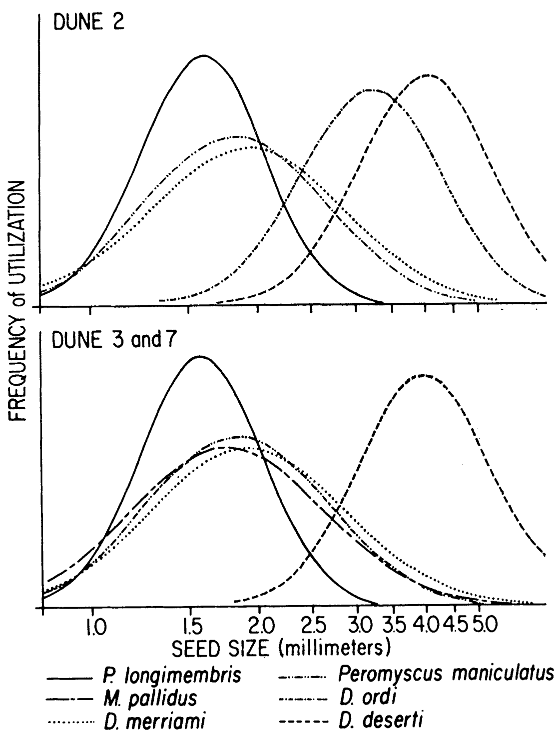

FIG. 4. Seed size utilization curves for communities of five coexisting species of desert rodents. Above, curves for the association of five species which gives the most uniform spacing of utilization curves; below, curves for the most frequently encountered five species community. Curves obtained by normalizing the data in Fig. 3, and computing a hypothetical curve for *Peromyscus maniculatus* (see text).

small pocket mouse, *P. longimembris,* use the smallest range of seed sizes, whereas species of intermediate size, *M. pallidus, D. merriami,* and perhaps *P. maniculatus,* show less tendency for specialization. A great deal of overlap is obvious among the smaller species in the use of small seeds. Overlap can be quantified by taking the proportion of the normalized distribution of frequency of utilization for one species which overlaps with a second species. This produces a symmetrical measure of overlap that can vary from 0 to 1. Table 1 gives a matrix of such overlap values for all possible species pairs, and those pairs which frequently coexist on sand dunes are indicated. Again, it is apparent that small and medium-sized species coexist even though they overlap tremendously in the size of seeds on which they feed.

Unfortunately we know of no information on the abundance of seeds as a function of their size in these or any other desert habitats. The relative abundance of rodent species and some preliminary samples of the distribution of seeds on sand dunes indicate that small seeds are more abundant than large ones. This suggests an exponential distribution of seed sizes that is abruptly truncated at sizes smaller than 1.5 mm. Consequently, we have used a logarithmic scale for seed size in Fig. 4. If seed sizes are exponentially distributed, it fits nicely with our observations that body sizes of coexisting species tend to be distributed as a geometric series. However, when four or five species coexist, pairs of small species tend to have more similar size ratios than do the large species; the small species feed on small seeds and have largely overlapping seed size utilization curves, whereas the large species use larger seeds and have considerably less overlap.

The rodents of each species utilize a narrower range of seed sizes than that available in their environment and apparently do not collect seeds in the proportions in which they are present. It is not hard to imagine the advantages to large species of specializing on large seeds. For seeds below some critical size, it may simply require more energy to locate and harvest them than these seeds contain. It is less obvious why small rodents should specialize on small seeds and apparently avoid the large ones. This is particularly perplexing in the light of the observations of Rosenzweig and Sterner (1970) that small rodents can husk and consume large seeds more efficiently than small seeds. We will advance a very tentative explanation for our observations. In mammals that search for particulate food items, the size of the foraging area or home range (R, in ha) varies with body size (W, in kg) according to the relation $R = 5.1\, W^{0.71}$ (McNab 1963). Thus small rodents must gather their seeds from smaller areas than large ones

TABLE 1. Overlaps in resource utilization between pairs of species of seed-eating desert rodents. Values in parentheses are based on hypothetical curves of seed size selection for *R. megalotis* and *Peromyscus maniculatus*. Asterisks indicate pairs of species that commonly coexist in sand dune habitats

				Seed size			
	R. meg.	*M. meg.*	*M. pal.*	*P. manic.*	*D. mer.*	*D. ord.*	*D. des.*
P. long.	(.81)	.78	.69*	(.69)*	.71*	.20*	.08*
R. meg.		(.87)	(.90)	(.90)*	(.85)	(.29)*	(.17)
M. meg.			.88	(.90)*	.80	.35*	.18
M. pal.				(.95)*	.92*	.38*	.22*
P. manic.					(.96)*	(.40)*	(.22)*
D. mer.						.46	.27*
D. ord.							.70*
				Horizontal foraging area			
	R. meg.	*M. meg.*	*M. pal.*	*P. manic.*	*D. mer.*	*D. ord.*	*D. des.*
P. long.	.76	.76	.62*	.81*	.62*	.58*	.55*
R. meg.		.58	.53	.58*	.45	.42*	.44
M. meg.			.90	.92*	.86	.82*	.79
M. pal.				.86*	.90*	.90*	.85*
P. manic.					.82*	.77*	.74*
D. mer.						.88	.84*
D. ord.							.85*
				Overall: Seed size x horizontal foraging area			
	R. meg.	*M. meg.*	*M. pal.*	*P. manic.*	*D. mer.*	*D. ord.*	*D. des.*
P. long.	(.62)	.59	.43*	(.56)*	.44*	.39*	.04*
R. meg.		(.51)	(.48)	(.52)*	(.38)	(.12)*	(.08)
M. meg.			.79	(.83)*	.76	.29*	.14
M. pal.				(.82)*	.83*	.34*	.19*
P. manic.					(.79)*	(.31)*	(.16)*
D. mer.						.40	.23*
D. ord.							.59*

do. On sand dunes, seeds are probably either randomly distributed or clumped; large seeds are almost certainly rarer than small ones. This means that the number of large seeds within the limited foraging area of a small rodent would be small and unpredictable. In small rodents natural selection would favor behavioral and morphological traits that made the discovery and harvesting of the more abundant and predictable small seeds more efficient, even if it meant that individuals sometimes ignored large seeds. Both large and small rodents should concentrate their foraging activities on those areas of the habitat where seeds of the appropriate size are most likely to be found. This may be particularly important on sand dunes, where it is likely that there is some sorting of seed sizes by the wind and blowing sand. Unfortunately we have no information on the spatial distribution of seed sizes in the field.

Rosenzweig and Sterner (1970) have suggested that coexisting desert rodents of different body size cannot efficiently divide seeds on the basis of size when size selection strategies are based on time and energy budgets. These conclusions are based on experiments in which several species of heteromyid rodents husked commercial seeds in the laboratory. Our data, based on natural seeds in the cheek pouches of field-trapped heteromyids clearly contradict these findings and show that seed size selection does occur and that it is related to body size. Rosenzweig and Sterner were probably misled in using husking efficiency as their criterion for measuring the advantage of seed size selection. It is evident from following the tracks of rodents on sand dunes that they spend most of their active time searching for seeds, and they cover large areas each night in the course of these foraging activities. When heteromyid rodents discover seeds they stuff them into their cheek pouches to be husked and eaten (or stored) later. Apparently it is the energetics of collecting, not husking, seeds which has selected for the observed patterns of seed size selection.

Foraging areas

Resources may be allocated among coexisting species according to intrinsic properties such as their size or shape and according to extrinsic properties such as their distribution in space or time. Observers of ecologically similar species of vertebrates have frequently noted that coexisting species frequently subdivide food resources by concentrating their foraging activities at different heights (e.g., MacArthur 1958, Cody 1968, Pianka 1967). We have no data on the heights at which the seed-eating rodents forage in sand dunes but several sorts of evidence suggest that vertical habitat segregation is not an important means of allocating seed resources. First, seeds, even when they are still on the plants, are distributed over only a narrow range of heights. The tallest plants on the dunes are shrubs that rarely exceed 128 cm in height, and most of the seeds are produced by herbs and grasses only a few centimeters tall. Second, most, if not all, of the rodent species do climb up into the perennials when these are bearing good crops of seeds. We have observed all of the common species except *D. deserti* and *D. ordi* climbing about in the vegetation. Third, most of the time the available seeds are not on the plants but scattered on or buried in the sand. It is obvious from following tracks that all of the species spend most of their time foraging on the surface of the ground.

It is also evident from the tracks that there are important differences between the species in the distribution of horizontal foraging activities in relation to the perennial vegetation. These differences were quantified by measuring the relative success of traps placed in four positions relative to the perennial shrubs (Fig. 1). The proportion of the total habitat sampled by each trap position varied among dunes. The heavily vegetated dunes had approximately equal proportions of horizontal surface corresponding to each trap position, but on some dunes most of the habitat consisted of open areas of bare sand. The total rodent catch was inversely correlated with vegetative cover; about half as many individuals were caught in the shrubs (132 in position 1) as in the most open areas of bare sand (224 in position 4). The distribution of horizontal foraging activity of the various species is shown in Fig. 5. Foraging areas tend to correlate with the type of locomotion employed by the species. The saltatorial, largely bipedal species (*Microdipodops* ,and *Dipodomys*) tended to concentrate their foraging activities in the open areas away from the shrubs, whereas the scansorial, largely quadrupedal species foraged either in and adjacent to the clumps of vegetation (*Perognathus* and *Reithrodontomys*) or with equal intensity in all areas (*Peromyscus*).

Overlaps of foraging areas (Table 1) were obtained by computing the proportion of the site utilization distribution for one species which overlapped with a second species. It is apparent that some of the species using seeds of similar size also forage in similar portions of the habitat. These measures of overlap in horizontal habitat utilization are accurate measurements of seed resource allocation only if the seeds remain in the same positions relative to the shrubs. If the seeds are redistributed between foraging areas then species foraging in one area can reduce the number of seeds subsequently available to another species foraging in another position. Since

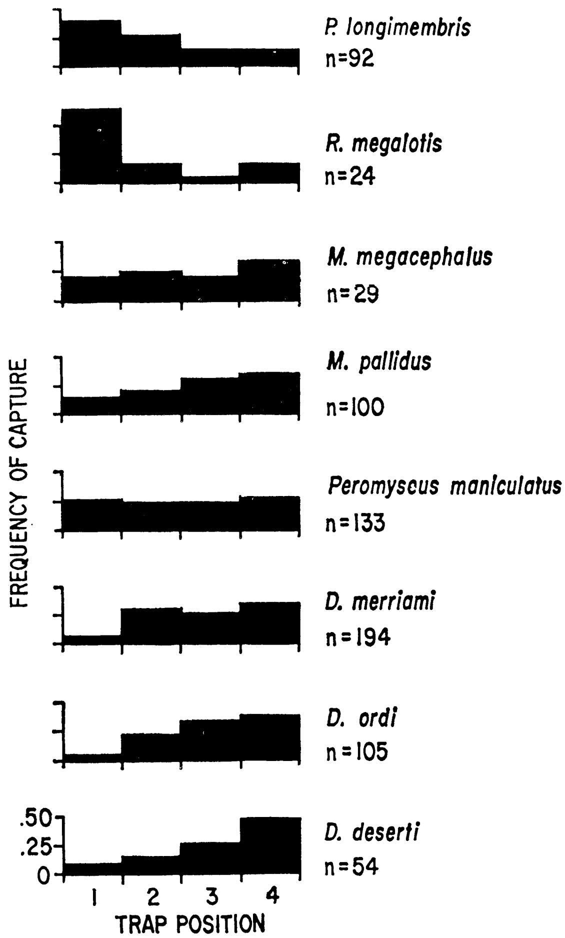

FIG. 5. Use of horizontal foraging areas by desert rodents as measured by frequency of capture in equal numbers of traps set in the 4 positions shown in Fig. 1.

there is certainly some continual redistribution of seeds by the wind, our measures of overlap in horizontal foraging areas probably underestimate the overlap in seed utilization achieved by these foraging patterns. However, because most of the seeds are buried in the sand and even when moved by the wind they probably (for aerodynamic reasons) tend to end up in similar positions relative to the shrubs, we do not think that this is an important source of error.

Foraging times

We know of no important differences between the rodents in diel activity patterns. All species are nocturnal, and all tend to concentrate their foraging activities in the early, warm part of the night unless there is bright moonlight. It is difficult to account for allocation of resources among coexisting rodent species by means of differences in diel activity patterns because on these sand dunes a good crop of seeds is produced only once every year or two. Even if more frequent events, such as heavy winds (which usually blow during the day), made new seeds available, those rodents that forage earlier in the evening would diminish the resources available to those species foraging later. We cannot imagine how foraging later at night would enable a species to coexist with competing species foraging earlier.

There are important differences in seasonal activity between the rodents, but it is difficult to determine how these affect resource allocation and coexistence. The kangaroo rats (*Dipodomys*) are active throughout the year, but all of the other, smaller species are capable of entering torpor. It is likely that this is a strategy for avoiding the stresses of low temperatures and scarce food (Brown and Bartholomew 1969). All of these small rodents can utilize torpor for short periods (a few days), and *P. longimembris* and the two species of *Microdipodops* apparently are capable of hibernating for several months. These species may cease foraging and enter extended periods of torpor during seasons (particularly winter) when few seeds are available and the energetic cost of remaining active is high. When *Microdipodops* and *P. longimembris* are hibernating there are at most one or two species of small and medium-sized rodents (particularly *Peromyscus maniculatus* and *D. merriami*) remaining active to forage and compete for small seeds on the sand dunes.

Unfortunately we have no data on the utilization of torpor by *P. longimembris*, *M. pallidus*, or *M. megacephalus* in the field. Even if we did, it would be practically impossible to evaluate the effect of such seasonal inactivity on the use of the seed crop and the coexistence of these species with their relatives that remain active all year. The situation is further complicated by the fact that *P. longimembris* and the two species of *Microdipodops* do not accumulate large deposits of fat as energy reserves for hibernation; instead they collect and store quantities of seeds before hibernating. While they are accumulating their stores these species certainly must compete for seeds with other species (such as *D. merriami*) which also collect and store small seeds even though they remain active throughout the year. However, hibernation substantially reduces the energetic cost of surviving a cold winter. It is likely that in small rodents such as *Perognathus* and *Microdipodops*, which have small foraging areas and high energetic costs for thermoregulation, the ability to enter extended periods of torpor is an adaptation necessary for existence on most of the northern dunes.

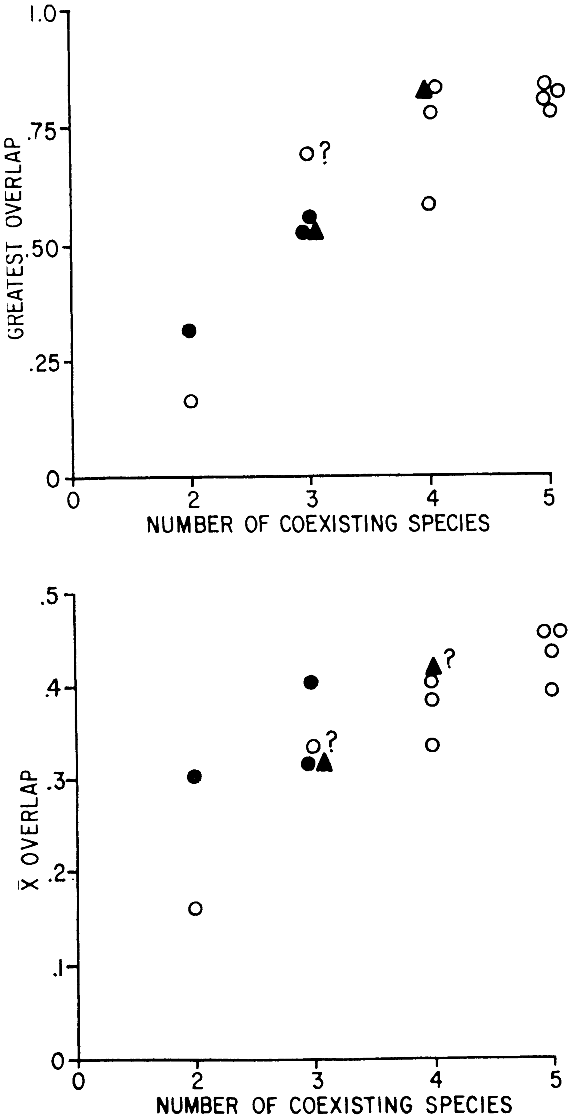

FIG. 6. Relation between values of overlap in overall resource utilization and the number of common rodent species that coexist in various sand dune habitats. Above, relation between maximum value of overlap for any pair of species and species diversity. Below, relation between mean value of overlap for all pairs of species and species diversity. Question marks indicate values for communities containing one species for which there was no reliable data on resource utilization; tentative values of overlap estimated from data for species of similar body size. Each plotted point is drawn from one of the study sites described by Brown (1973); the symbols coincide with those used in Fig. 1 of that paper.

Total overlap in resource utilization

The data on seed size selection and horizontal foraging areas can be combined to quantify the primary overall differences in resource utilization among coexisting rodent species. The product of the overlaps in seed size and foraging areas provides a measure of total overlap which can be computed for each pair of species. This measure of overlap, which can vary from 0 to 1, is essentially a statement of the probability that seeds of appropriate size and location for one species are equally available to the second species. These overlaps are not intended to be estimates of the alphas of Lotka-Volterra competition equations. As shown in Table 1, values of total overlap for pairs of species that normally coexist on sand dunes range from 0.04 to 0.83.

A comparison of the faunas of different dune habitats reveals a relationship between total overlap and species diversity (Brown 1973, Table 2, for the identity and diversity of species on each dune). Both the greatest overlap between any single pair of species and the mean overlap for all pairs of coexisting species are strongly and directly correlated with the number of species that occur together on a dune (Fig. 6). Brown shows that variability in the number of seed-eating rodent species coexisting in sand dune habitats can be attributed largely to the abundance and predictability of seed resources. Apparently dunes that produce larger and more predictable seed crops can accommodate species with greater similarities (overlap) in resource utilization, and hence these dunes can support a greater diversity of rodent species than can dunes having smaller or more unpredictable seed crops. With decreases in predictable seed abundance, species are apparently excluded from dune habitats when they cannot harvest enough seeds to maintain local populations. Usually the excluded species become restricted to other kinds of habitats where their harvesting methods presumably yield better returns. The overlap values, like the distribution of body sizes, suggest that competition for seeds between species with similar foraging habits plays an important role in this exclusion, and hence in the structure and evolution of desert rodent communities. MacArthur (1972) has emphasized the effectiveness of such diffuse competition from several species in producing competitive exclusion.

As Brown (1973) pointed out, when seed production decreases, species are excluded from the dunes in a quite regular order. We do not know enough about the ecology of each species to account for this pattern, but one aspect warrants comment. *D. deserti,* the largest species, inhabits all of the dunes within its geographic and altitudinal range including several southern dunes where it is the only species present. Why should the largest species persist when all of the others have been excluded? This is particularly puzzling because *D. deserti* should have the largest energy requirements and the least dense populations of all the species. Either or both of the following explanations may account for the persistence of *D. deserti* on these dunes. First, *D. deserti* should be favored in habitats where the most abundant or predictable seeds are of large size. In the southern deserts, where *D. deserti* is usually the only species inhabiting dunes, rainfall is low and unpredictable. As a result, the perennial shrubs, which have deep-root systems, may produce more seeds or produce them more predictably than do the small annual herbs and grasses. It is our impression that most of the shrubs produce seeds that are larger and encased in tougher capsules than the seeds of most annuals. Second, situations where a large home range is advantageous should favor the persistence of *D. deserti.* A large home range is a particular advantage when food resources are scarce and clumped. This probably occurs in the southern sand dunes, where there is little rainfall and the wind blows seeds into widely spaced depressions or windrows. In contrast, in less sandy habitats near or adjacent to the southern dunes *D. deserti* is replaced by smaller species *of Dipodomys* or *Perognathus.*

Competitive release and character displacement

The data on body size and seed size selection used in the previous analyses were obtained for all individuals of a species for which data were available, without regard for geographic variation between dunes. However, the absence of particular species from some dunes should affect the distribution of seed sizes available to the remaining species, which could then respond by adaptive modifications of their foraging mechanisms. We might expect a species to take a wider range of seed sizes when it occurs in a habitat containing no coexisting species with similar patterns of resource utilization. In the one case for which we may have sufficient data, they suggest that such competitive release does occur. There was apparently greater variability in the sizes of seeds in the cheek pouches of *D. ordi* from the eastern part of the Great Basin Desert, where it is usually the only *Dipodomys* common in sandy habitats, than in those from the western part, where *D. ordi* frequently coexists with larger (*D. deserti*) and smaller (*D. merriami*) kangaroo rats; variances in sizes of seed in the cheek pouches were 4.56 ($n = 15$) and 0.68 ($n = 18$) respectively ($F = 6.75$; $P < 0.05$). There are two distinct explanations for this apparent difference: *D. ordi* may change its foraging behavior in the absence of sympatric congeners, or it may continue to forage in the same way but encounter and harvest a greater variety of seed sizes because they have not been removed by other species.

Because seed size selection is correlated with body size, local populations of species might evolve somewhat different body sizes depending on what other species occurred in the same habitat. We would expect greater differences in body size when similar species coexist (character displacement) than in the absence of similar species. We have sufficient data in two cases to test for this effect, and in neither case do we find evidence of character displacement in body size. In the eastern part of the Great Basin, where it normally is the only kangaroo rat in sandy habitats, *D. ordi* is no different in size than in the western part, where it occurs together with the larger *D. deserti* and the smaller *D. merriami.* It is questionable whether one would expect character displacement in this case, but most other sand dune habitats in the North American deserts have a large (80–100 g) kangaroo rat, even if that is the only species present. In the second case, *D. deserti* is not significantly smaller on the southern dunes, where it is usually the only seed-eating rodent, than it is on northern dunes, where it is the largest of several species. Thus although differences in body size between desert rodent species are obviously important in resource allocation and hence in coexistence, we can detect no evidence of intraspecific variation in body size in response to differences in the number or identity of coexisting species in sand dunes. Perhaps this is because most of these species also occur in other habitats, where they coexist with other combinations of species and are subjected to different selective pressures.

General Discussion

How similar can species be in the utilization of limiting resources and still coexist? Our data suggest that in predictably productive habitats desert rodents can be extremely similar—80% or more overlap in seed utilization between pairs of species. In fact even greater similarity is probable, because in some cases there are significant overlaps among three or four coexisting species. MacArthur and Levins (1967) have suggested a theoretical limit of similarity beyond which coexistence is impossible and competitive exclusion results. May and MacArthur (1972) argue that this limiting similarity is approached when similar normal distributions of resource utilization for two species have means that are displaced by one standard deviation. Two such distributions would have an overlap value (calculated in the same way as the values obtained for the rodents) of approximately 0.6, which is less than several of the empirical values obtained in the present study. We do not want to stress this discrepancy between current theory and our empirical results, because there are major problems in using our data to test the theory. First, the theory assumes that species with equal carrying capacities complete for resources distributed in a one-dimensional gradient. Clearly these assumptions are not met in our system. Second, we may have ignored some important means of resource allocation in desert rodents. It is disturbing that the highest values of overlap between pairs of coexisting species occur between species in different genera. Generic distinction reflects differences in morphology, physiology, and behavior that could affect seed use in ways we have not measured. On the other hand, Pulliam and Enders (1971) have recently measured the use of seed resources by sympatric species of finches, and they too have obtained extremely high values of overlap.

In general, the patterns of resource utilization and species diversity in desert rodents support current theories of species packing. There is a clear positive relationship between interspecific overlap in resource utilization and the number of coexisting species in a habitat (Fig. 6), and the number of species which coexist is determined by the abundance and predictability of seeds (Brown 1973). This supports MacArthur's (1972) theoretical treatment of species packing and diversity, which showed that more species should coexist in more productive environments because the species should be able to have narrower and more overlapping utilization curves than in less productive habitats. In our system a standard complement of species comprises the most diverse rodent communities; less diverse communities are simply missing some of these species. Since the species involved are the same, the amount of specialization (breadth of utilization curve) does not vary significantly with species diversity, but overlap increases with species diversity as predicted by MacArthur's model. Our data also support May and MacArthur's (1972) prediction that in a sufficiently variable environment the extent of overlap between coexisting species should be inversely related to the variance in resource abundance. In our system variance in seed abundance apparently has some negative effect on species diversity (and hence on overlap in seed utilization), although this is much less pronounced than the influence of productivity.

The literature of ecology is filled with examples of regular differences in body size or the size of trophic structures among coexisting, ecologically similar species use particulate resources (e.g., Hutchinson 1959, Shoener 1965, Rand and Williams 1969, Rosenzweig 1966, McNab 1971). Although a few laboratory studies have attempted to evaluate the effects of size differences on resource utilization (e.g., Kear 1962, Hespenheide 1966, Rosenzweig and Sterner 1970), there is almost no quantitative information on how body size or size of trophic structure influences the use of food resources by free living species in their natural habitats. Rosenzweig (1966), Hespenheide (1971), and Pulliam and Enders (1971) have accumulated data on prey size selection in mammalian carnivores, insect size selection in flycatchers, and seed size selection in finches, respectively. These authors obtained results similar to ours—great overlap in the sizes and kinds of food particles used despite large differences in body size and (in the case of the birds) bill size. These results emphasize the importance of measuring resource utilization directly. There is no doubt that resource allocation on the basis of particle size is one of the important means of coexistence of many species that differ in size. Nevertheless, regular, nonoverlapping distributions of body sizes among sympatric species often conceal broadly overlapping, much more irregular patterns of resource utilization. For many kinds of organisms large differences in body size are probably not sufficient to permit coexistence, and species also differ in other respects, such as habitat or foraging area (Shoener and Gorman 1968). This may be particularly true in organisms such as fishes and reptiles because the young of the larger species are for a long period no bigger than the individuals of the smaller species. It may be less prevalent in birds and mammals because the young are nearly as large as the adults by the time they begin foraging for themselves.

Acknowledgments

We are grateful to numerous colleagues and students for valuable discussions and suggestions. M. L. Rosenzweig, C. D. Barbour, K. T. Harper, H. Horn, W. M. Schaffer, and D. J. Futuyma have kindly read and commented on the manuscript. We are particularly grateful to R. H. MacArthur for numerous discussions, suggestions, and criticisms. A. K. Brown assisted the senior author in many ways. The work was supported in large part by a grant (GB 8765) from the National Science Foundation to J. H. Brown.

Literature Cited

Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology (in press).

Brown, J. H., and G. A. Bartholomew. 1969. Periodicity and energetics of torpor in the kangaroo mouse, *Microdipodops pallidus*. Ecology **50**: 705–709.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. **102**: 107–147.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkins, Baltimore. 163 p.

Hespenheide, H. 1966. The selection of seed size by finches. Wilson Bull. **78**: 191–197.

———. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrranidae. Ibis **113**: 59–72.

Hutchinson, G. E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? Am. Nat. **93**: 145–159.

Kear, J. 1962. Food selection in finches with special reference to interspecific difference. Proc. Zool. Soc. Lond. **138**: 163–204.

Lotka, A. J. 1925. Principles of physical biology. Reprinted 1956 as Elements of mathematical biology by Dover, New York. 460 p.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39**: 599–619.

———. 1970. Species packing and competitive equilibrium for many species. Theor. Pop. Biol. **1**: 1–11.

———. 1972. Geographical ecology. Harper and Row, N.Y. 269 p.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity of convergence and divergence of coexisting species. Am. Nat. **101**: 377–385.

May, R. M., and R. H. MacArthur. 1972. Niche overlap as a function of environmental variability. Proc. Nat. Acad. Sci., U.S. **69**: 1109–1113.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Am. Nat. **97**: 133–140.

———. 1971. The structure of tropical bat faunas. Ecology **52**: 352–358.

Pianka, E. R. 1967. Convexity, desert lizards, and spatial heterogeneity. Ecology **47**: 1055–1059.

———. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. Ecology **50**: 1012–1030.

Pulliam, H. R., and F. Enders. 1971. The feeding ecology of five sympatric finch species. Ecology **52**: 557–566.

Rand, A. S., and E. E. Williams. 1969. The anoles of La Palma: aspects of ecological relationships. Brevoria **327**: 1–19.

Rosenzweig, M. L. 1966. Community structure in sympatric carnivora. J. Mammal. **47**: 602–612.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology **50**: 558–572.

Rosenzweig, M. L., and P. W. Sterner. 1970. Population ecology of desert rodent communities: body size and seed-husking as bases for heteromyid coexistence. Ecology **51**: 217–224.

Shoener, T. 1965. Evolution of bill size differences among sympatric congeneric species of birds. Evolution **19**: 189–213.

Shoener, T., and G. C. Gorman. 1968. Some niche differences in three Lesser Antillean lizards of the genus *Anolis*. Ecology **49**: 819–830.

Volterra, V. 1926. Variazione e fluttuazioni del numer d'individui in specie animali conviventi. Mem. Accad. Naz. Lincei. **2**: 31–113.

———. 1931. Lecons sur la theorie mathematique de la lutte pour la vie. Cahiers Scientifiques 7, Ganthier-Villars, Paris.