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A Mechanism for Resource Allocation among Sympatric Heteromyid Rodent Species

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Summary. Laboratory feeding experiments were conducted with *Dipodomys ordii* and *Perognathus flavus* in an attempt to discover a mechanism which might result in seed size selection. There was no marked difference in the proportions of four seed types collected whether the rodents foraged in the presence or absence of one another. However, analysis of the variability in weight of each of the seed types collected by the two species showed that when alone, the larger kangaroo rat was less effective at harvesting all of a uniformly distributed mixture of seeds. When in the presence of one another both species could harvest enough of the mixed, uniformly distributed seed to coexist indefinitely, but when the food source was presented as four large clumps the kangaroo rat's foraging effectiveness increased tremendously so that the pocked mouse was almost entirely unable to harvest any seed. These data, in light of mobility differences between large and small heteromyids, suggest a mechanism whereby the larger, more mobile kangaroo rats forage for the most readily available (large or clumped) seeds over a relatively large area. The smaller pocket mice, by virtue of their relative efficiency in harvesting seeds can utilize the less detectable seeds which are energetically too demanding for the larger kangaroo rats to harvest. Behavioral dominance of the larger animals may help prevent the smaller from utilizing the most readily available seeds. The patterns of seed size and foraging site selection described in the literature may be easily accounted for by this difference in foraging strategy.

Introduction

The past decade has seen a proliferation of studies related to the problem of coexistence among heteromyid rodents. Researchers have attempted to explain the variance in diversity of heteromyid species and have shown the importance

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of vegetation complexity (Rosenzweig and Winakur, 1969; Brown, 1973), resource productivity and predictability (Brown, 1973, 1975) and historical factors (Brown, 1973, 1975) as determinants of the number of coexisting heteromyid species. For those species which can be found in the same locality, foraging site selection (Rosenzweig and Winakur, 1969; Brown and Lieberman, 1973; Rosenzweig, 1973; Brown, 1975; Rosenzweig et al., 1975; Schroeder and Rosenzweig, 1975) and seed size selection (Smith, 1942; Brown, 1973; Brown and Lieberman, 1973; Brown, 1975) are assumed to be important aspects of resource division and therefore assumed important in promoting the coexistence of heteromyid rodent species (but see Kenagy, 1973). Although the subject of much conjecture in the above studies, a foraging mechanism which might result in seed size and foraging site selection has only very recently been proposed (Reichman and Oberstein, 1977).

This paper describes a series of laboratory experiments which were conducted to determine a mechanism of resource allocation among coexisting heteromyid species. More specifically, the investigation was designed to analyze differences in foraging technique which might be responsible for resource allocation between different-sized heteromyids. *Dipodomys ordii* (49 g) and *Perognathus flavus* (7.2 g) were chosen for experimentation as they are sympatric over a broad geographic range and in some localities (for example Drake, Arizona, where the animals were trapped) they are the only heteromyid species present.

Materials and Methods

Seed selection experiments were run intermittently from October 1972 to February 1973. All experiments were conducted within a 1.2 × 1.2 m arena enclosed by 4 m-high wooden walls. The experimental "box" was placed upon a bare cement floor which was covered with sand to form a mound about 6 cm deep in the middle and 3 cm deep around the edges. In the early experiments single individuals were placed into the box and left to select seeds overnight. In later cases a kangaroo rat and a pocket mouse were both introduced and each was supplied with a refuge area or "house". To prevent the larger animal from killing the smaller, the pocket mouse house had entrances which were too small for the kangaroo rat to enter.

When two animals were used simultaneously the normal procedure began in the evening by placing the pocket mouse into the box first so that it could gain familiarity with the surroundings. This period of time usually corresponded with the time required to weigh seeds to be used in the subsequent experiment (about 20 min). The kangaroo rat was then placed into the box and finally seeds were placed upon the sand. The animals were left in the box overnight during which period they stored seeds in their respective houses. The following morning I removed the animals, separately sifted and weighed the seeds from each of their houses and then sifted and weighed the leftover seeds.

The four seed types used throughout the experiments were clover, millet, milo and husked sunflower seeds. Although the seeds were, on average, larger than those normally encountered by heteromyids, they were within the size range of normally encountered wild seeds and were selected because they were readily distinguished by size. Sunflower seeds were caught in a U.S. Standard Testing Sieve with 5 meshes/in (size 5; 4 mm opening), milo in a size 8 (2.4 mm opening), millet in a size 12 (1.7 mm opening) and the smallest seed (clover) in a size 35 sieve (0.5 mm opening). I retrieved the proportions of each seed type stored by an animal following an experiment by pouring sand and seed through the entire set of sieves which left only the seed to be weighed.

I conducted three types of experiments. The first involved a single individual of either *D. ordii* or *P. flavus* who was introduced into the experimental arena as described above. Five g of each of the four seed types were mixed together then scattered over the entire sand surface. The second type of experiment involved one individual of each of the two species, but was otherwise the same as the first. The third experimental type involved both species but the seeds were introduced as four discrete 5 g piles rather than being mixed and scattered.

In order to reveal between-species differences in the relative variability in amounts of seed taken from one experiment to the next I used the coefficient of variation (*CV*), where $CV = \mathrm{SD}/\mathrm{mean} \times 100$. All similarities in stored or harvested seed were quantified by use of Kulczynski's (in Oosting, 1956) similarity index (*S*), where $S = \sum_{i=1}^{n} 2w_i \,/\, \sum_{i=1}^{n} a_i + b_i$. a_i and b_i equal the proportions of seed type *i* stored or harvested by species *a* and *b*, respectively; $w_i = a_i$ if $a_i \leqq b_i$ or b_i if $b_i < a_i$; and n = number of food items. This measure is identical to the more commonly cited resource overlap index of Schoener (1970). Tests for significance in the difference between the mean weights of stored or harvested seed were conducted using an approximation of the standard *t*-test as described by Sokal and Rohlf (1969, p. 374).

Results

Single-Species Experiments

When a kangaroo rat (*Dipodomys ordii*) or pocket mouse (*Perognathus flavus*) was placed into the experimental box and left to store proportions of the 20 g of seed provided, differences between the species were most apparent in the predictability of their seed storing behavior (Table 1). The pocket mouse was more consistent in the amounts of each type of seed taken throughout the six runs ($CV = 24.8$) than was the kangaroo rat ($CV = 118.9$).

Table 1. The results of six seed selection experiments with the kangaroo rat (*D. ordii*) and six experiments with the pocket mouse (*P. flavus*) when only a single animal was present during a given experiment. The animals were provided with a mixture of 5 g of each of the four seed types. Harvested seed represents the weight of seeds which were stored plus the weight of seeds which were eaten

Seed type	Seed stored[a] (g)	Proportion	*CV*[b]	Seed harvested[a] (g)	Proportion	*CV*[b]
Dipodomys ordii						
Sunflower	3.3 ± 0.97	0.28	29.4	4.4 ± 1.11	0.28	25.2
Milo	4.1 ± 0.35	0.35	8.5	4.1 ± 0.32	0.26	7.7
Millet	1.5 ± 0.75	0.13	50.0	4.2 ± 0.12	0.27	2.9
Clover	2.9 ± 0.90	0.25	31.0	2.9 ± 0.90	0.19	31.1
Totals	11.8 ± 2.42	1.01	118.9	15.6 ± 2.08	1.00	66.9
Perognathus flavus						
Sunflower	4.6 ± 0.23	0.29	5.0	4.6 ± 0.23	0.26	5.0
Milo	4.9 ± 0.15	0.30	3.1	4.9 ± 0.15	0.28	3.1
Millet	2.9 ± 0.21	0.18	7.2	4.3 ± 0.26	0.24	6.0
Clover	3.7 ± 0.35	0.23	9.5	3.9 ± 0.45	0.22	11.6
Totals	16.1 ± 0.05	1.00	24.8	17.6 ± 0.62	1.00	25.7

[a] Given as mean ± SD

[b] CV = SD/mean × 100

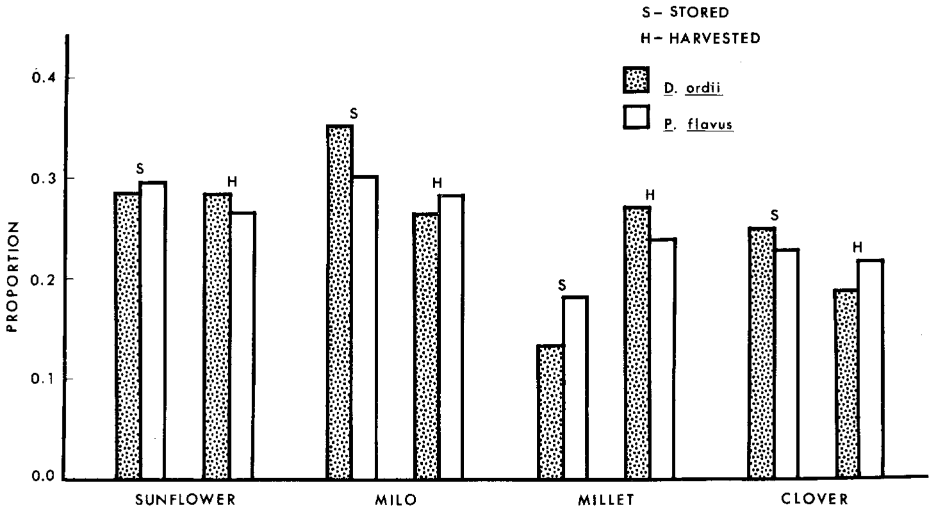

Fig. 1. The relative proportions of four seed types stored and harvested (stored plus eaten) by *D. ordii* and *P. flavus* when in the absence of one another. The results represent averages of six trials for each species. Seeds were presented as a uniformly distributed mixture of 5 g of each of the four seed types

The proportions of the four seed types stored were not substantially different between the two species (Fig. 1). For comparative purposes Kulczynski's similarity index (S) was used to quantify the similarity in proportions of stored seed between the two species and the resultant value equalled 0.94. The pocket mouse stored significantly more food per night on the average than did the kangaroo rat ($t'_s = 3.07$, $t'_{0.05} = 2.57$). However, these values represent stored seed only and since these experiments were run with each species in the absence of the other, the total weight of harvested seed (seeds both stored and eaten) was determined. The amount of seed eaten equalled the amount given less the combined weight of stored seed and seed left untouched after a single run. These values were added to the weight of stored seed to give the total amount of seed harvested. The results (Table 1) show that the pocket mouse was still the less variable food gatherer from one trial to the next. The proportions of harvested (as opposed to stored) seed were still similar between species ($S = 0.95$), and the total amount of food taken by each of the two species was statistically indistinguishable ($t'_s = 1.27$, $t'_{0.05} = 2.57$). The kangaroo rat ate a greater proportion of harvested seed than did the pocket mouse. Kangaroo rats ate an average of 3.8 g of seed per night compared to 1.6 g for the pocket mice.

Two-Species Experiments

When the two species were placed into the box together a number of trends became immediately apparent. First, after eleven trials, the total amount of seed stored by each animal decreased from the amounts recorded when the

Table 2. The results of 11 seed selection experiments with *D. ordii* and *P. flavus* in the presence of one another. The animals were provided with a mixture of 5 g of each of the four seed types

Seed type	Seed stored[a] (g)	Proportion	*CV*[a]
Dipodomys ordii			
Sunflower	2.5 ± 0.33	0.29	13.0
Milo	3.2 ± 0.68	0.37	21.3
Millet	0.9 ± 0.47	0.10	51.8
Clover	2.1 ± 0.76	0.24	36.2
Totals	8.7 ± 1.97	1.00	122.3
Perognathus flavus			
Sunflower	1.4 ± 0.61	0.38	43.4
Milo	1.1 ± 0.46	0.30	42.0
Millet	0.2 ± 0.13	0.05	66.0
Clover	1.0 ± 0.30	0.27	30.4
Totals	3.7 ± 1.45	1.00	181.8

[a] As in Table 1

animals were alone but to a proportionately greater extent in the smaller pocket mouse (Table 2). The amount of stored seed decreased 26% in the case of the kangaroo rat and 77% in the case of the pocket mouse. Secondly, the proportions of the different seed types which were stored by one animal were similar ($S = 0.88$) to those proportions stored by the other so that differential seed selection by these two species was not readily apparent (Fig. 2). Moreover, although the proportions of stored seed types were less similar between the two species for this experiment than when the animals were alone ($S = 0.94$), the differences were not consistent with respect to seed size as one might expect (Brown and Lieberman, 1973; Brown, 1975). Rather, the kangaroo rat took a greater proportion of the two intermediate seed sizes and smaller proportion of the extreme seed sizes than did the pocket mouse. Thirdly, the kangaroo rat was no longer the variable animal with respect to the total amount of

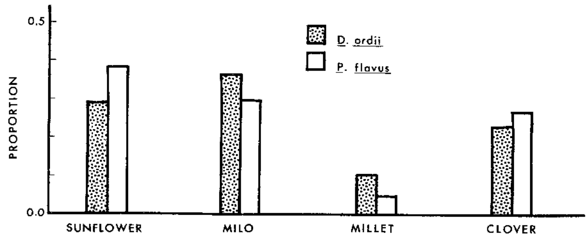

Fig. 2. The relative proportions of four seed types stored by *D. ordii* and *P. flavus* when in the presence of one another. The proportions represent averages of 11 trials. Five g of each of the four seed types were mixed and scattered uniformly in the foraging arena

each seed type stored from trial to trial. The coefficients of variation reveal that the pocket mouse was the more variable seed harvester (Table 2). Finally, the kangaroo rat remained consistent not only in the degree of variability from one experiment to the next, but the proportions of seed types stored were also strikingly similar to the proportions stored when it was alone ($S=0.97$). In general, the kangaroo rat was much less affected by the presence of the other species than the pocket mouse.

In a third experiment the food source was clumped into four piles, each pile containing a different seed type. The kangaroo rat gathered proportions of the four seed types which were similar to the proportions gathered in the first experiment when it was alone and presented with uniformly scattered seed ($S=0.96$) but this time it gathered food much more efficiently (in terms of energy uptake per unit time) and averaged 33% more seed (Table 3). Apparently, the distribution of seeds made it easier for the kangaroo rat to monopolize the food and the pocket mouse averaged only 0.37 g of seed per night (a tenth as much as when the seeds were scattered and both animals were present). Furthermore, this average did not result from the pocket mouse taking consistent proportions of each type of seed. In one case it took only sunflower seed and in another it took 70% clover and 30% sunflower. The summed coefficient of variation for the pocket mouse (468.2) was much higher than the sums derived from the other two experiments (24.8, 181.8). As a result of the relative ease of seed harvesting for the kangaroo rat, its variability in the amount of each seed type stored dropped considerably ($CV=53.2$ compared with 66.9 and 122.3 for the other two experiments).

Table 3. The results of three seed selection experiments where 5 g of each seed type was clumped into a separate pile. Both *D. ordii* and *P. flavus* were present during each experiment

Seed type	Seed stored[a] (g)	Proportion	*CV*[a]
Dipodomys ordii			
Sunflower	4.3 ± 0.35	0.27	8.1
Milo	4.9 ± 0.32	0.31	6.5
Millet	2.3 ± 0.78	0.14	33.9
Clover	4.5 ± 0.21	0.29	4.7
Totals	15.7 ± 0.57	1.01	53.2
Perognathus flavus			
Sunflower	0.10 ± 0.14	0.27	140.0
Milo	0.10 ± 0.24	0.27	240.0
Millet	0.00 ± 0.00	0.00	0.0
Clover	0.17 ± 0.15	0.46	88.2
Totals	0.37 ± 0.09	1.00	468.2

[a] As in Table 1

The two species also stored seed types which were less similar ($S=0.83$) than in the other two experiments. The kangaroo rat stored a mean seed size which was greater than the mean size stored by the pocket mouse.

Discussion

One of the most striking features of an assemblage of sympatric heteromyid species is the distribution of body weights between species. Brown (1973, 1975) has shown that for granivorous desert rodents there exists a logarithmic series of body size categories which remains nearly constant from one sand dune habitat to the next, the largest granivore being about 1.5 times as large as the next smaller, and so on. It seems likely that these weight differences play an important role in the division of resources by, and thus the coexistence of, heteromyid rodents (Brown, 1973, 1975; Rosenzweig et al., 1975). This morphological difference between species very probably results in microhabitat (foraging site) selection and/or foraging strategy differences.

Discussions on the relationship between body size differences and habitat selection have been presented by Bartholomew and Caswell (1951), Rosenzweig and Winakur (1969), Rosenzweig (1973), and Brown and Lieberman (1973) and will not be considered further here.

The most compelling evidence that differences in foraging strategy are associated with differences in body size comes from Brown and Lieberman (1973) who showed a strong positive correlation between mean seed size found in cheek pouches and heteromyid rodent body size (see Rosenzweig and Sterner (1970) and Rosenzweig et al. (1975) for summary of additional evidence for seed size selection in these rodents). Although Brown and Lieberman (1973, p. 792) believe that "it is the energetics of collecting, not husking seeds which has selected for the observed patterns of seed size selection", a mechanism was never proposed to account for the observed pattern. It has been suggested by Rosenzweig et al. (1975) that the large heteromyids might not be able to handle small seeds and the small unable to handle the large seeds. The laboratory data presented herein show that clearly this is not the case, at least for the size range of seeds used in the experiments. Furthermore, although "it is not hard to imagine the advantages to large species of specializing on large seeds ... it is less obvious why small rodents should specialize on small seeds and apparently avoid the large ones" (Brown and Lieberman, 1973, p. 791). It has also been suggested (Brown and Lieberman, 1973) that the smallest rodents should evolve to utilize the most abundant and predictable small seeds and possibly ignore the large seeds. I will show that this is not necessary in order for seed size selection to occur.

Another possibility is that different tendencies toward seed size selection are due simply to differential foraging site selection, superimposed upon a differential seed size distribution. Reichman (1975) found that the seeds available to *Dipodomys merriami* and *Perognathus amplus* in his study area were very similar and their diets (as determined from stomach contents) were also similar. However, although the diets were found to be fairly similar, the seeds harvested (as determined from cheek pouch contents) were much less similar and may have been a result of differences in foraging strategies as described later. In addition, if foraging site selection is the primary factor determining seed sizes harvested by heteromyids then we would expect those animals which overlap strongly in foraging sites to overlap strongly in the sizes of seeds collected. Using Brown's (1975, Table 2) data on foraging site and seed size overlaps for seven species of heteromyids and two species of cricetids, I found a complete lack of correlation ($r = -0.02$, $P \gg 0.05$) between foraging site overlap and seed size overlap. Clearly, another mechanism must be involved in order to produce the observed patterns in seed size selection.

Despite Brown and Lieberman's (1973) findings, data from the laboratory experiments described herein with *D. ordii* and *P. flavus* revealed no seed size selection. A similar lack of seed size selection has been shown by Smigel and Rosenzweig (1974, includes additional references) with *D. merriami* and *P. penicillatus* and by Reichman (1975) with *D. merriami* and *P. amplus*. I believe the key to the solution of this dichotomy lies in the differences between the distribution and size diversity of seeds within the habitat types of rodents which do and those which apparently do not select different seed types.

I now propose a mechanism, based on differences in foraging strategy, which can account for the observed patterns in both foraging site selection and seed size selection in heteromyid rodents (see also Reichman and Oberstein, 1977). As a simple consequence of their increased mobility and home range size (McNab, 1963; Kenagy, 1973) relative to the smaller pocket mice, the larger, bipedal kangaroo rats would operate most effectively by taking seeds which are easily collected (large or clumped seeds) throughout the more open areas of their home range. Seeds which are more difficult to find and/or collect (smallest or non-clumped seeds on average) would be passed over and left for the more efficient havesters (smaller pocket mice) to exploit. Behavioral dominance of the larger animals (Eisenberg, 1963; Blaustein and Risser, 1976) might help prevent the smaller animals from harvesting the most readily available seeds. This would require the smaller species to be highly opportunistic feeders and would allow the larger, more mobile species to become more specialized in their dietary preferences. Meserve (1976) has recently concluded that coexistence of rodents in a coastal sage community depends to a degree upon the subordinate species utilizing generalized feeding strategies during periods when all species are active. This idea runs counter to the suggestion that large generalists and small specialists would be able to coexist (Rosenzweig and Sterner, 1970; Rosenzweig et al., 1975).

My laboratory investigations with *D. ordii* and *P. flavus* provide evidence for the operation of such a mechanism. Although there is a marked size difference between these animals, when they were fed individually (Fig. 1) or together (Fig. 2) on scattered seeds there was little selective difference with respect to seed size between the two species. Because of the similarity between stored and harvested seed proportions (Fig. 1) I have assumed that the use of stored seed is a good indicator of selective tendencies in the later experiments where it becomes impossible to calculate harvested seed for two rodents foraging in the same arena. A more striking difference between the two animals was in their harvesting efficiencies. When alone, the pocket mouse was highly opportunistic in its selective tendencies, harvesting nearly all of each kind of seed (Table 1). The kangaroo rat seemed to concentrate its efforts on the three largest seeds, being especially variable in the amount of small seed taken. This may be a result of the larger animal's relative inability to detect and/or harvest the smallest seeds or a result of a tendency to form search images and skip over smaller seeds which are indeed detected. In either case the smaller animal harvested more of the uniformly distributed seed than the larger during the same time period (Table 1) and in this sense was more efficient. From laboratory data on the seed husking abilities of small and large heteromyids Rosenzweig and Sterner (1970) also concluded that the smaller animals are more efficient seed harvesters and, barring the interference of other variables, should be able to outcompete the larger animals.

When the two animals were placed into the foraging arena together the pocket mouse became the more variable seed harvester, possibly because of restrictions on when and where it could forage. The relatively high harvesting (and possibly detecting) effeciency of the pocket mouse may have enabled it to be successful at opportunistically collecting "leftover" seeds during the periods between the foraging bouts of the kangaroo rat.

The third laboratory experiment involving clumped seeds offers additional support for, and somewhat extends the idea of, feeding strategy differences among heteromyids. The results show that the kangaroo rat gathered nearly all the seed that was available causing the pocket mouse to become extremely variable in the proportions of what little seed it managed to harvest. The kangaroo rat's feeding efficiency increased tremendously. In fact, on average, the kangaroo rat gathered 1.8 times more seed than when the seeds were uniformly distributed. The pocket mouse garnered much less than normal and, over a three night period, indications were that the smaller was being "outcompeted". Evidence in support of this statement comes from the fact that the pocket mouse ate an average of 1.5 g seed per night when alone (determined from Table 1) while the kangaroo rat averaged 3.8 g. In the clumped-seed experiments the amount of seed remaining in the sand after an experimental run was always minute (<1 g). Assuming the kangaroo rat ate normally, the pocket mouse would have eaten 0.5 g on average which supports the possibility that the pocket mouse would eventually have been eliminated from the system through torpor or even starvation. For these animals the implication is that all the food is not clumped to a degree where the kangaroo rat can become relatively efficient and outcompete the pocket mouse in such a fashion. With the relatively high effeciency of the pocket mouse on uniformly distributed seed and the kangaroo rat on clumped seed it becomes tempting to speculate that some of the seed under natural conditions is clumped and that the larger, more mobile kangaroo rat specializes on such clumps, leaving the pocket mouse to the more uniformly distributed seed. Different laboratory experiments and field observations have led Reichman and Oberstein (1977) to just this conclusion.

As seeds become increasingly clumped or patchy in their distribution the rodents would realize an increased abundance of resources and, theoretically, should become specialized in some aspect of their feeding behavior (MacArthur, 1972). By a clumped seed distribution I mean clumps which would be small enough in scale to attract a foraging heteromyid. An example might be seeds which pile up in small depressions in the soil as Reichman and Oberstein (1977) have found. It becomes easy to visualize the larger animal gathering the most readily available (clumped or large) seeds and leaving a portion of the least detectable seeds untouched. This way, because of its mobility, the larger, bipedal heteromyid could get to the next clump and harvest the more easily detectable seeds in the time it would take to get most of the least detectable seeds as well from the first clump. The smaller animal could then capitalize upon the remaining seeds in each clump plus easily detected seeds in the clumps which it encounters first (behavioral interactions and mobility differences keeping the latter to a minimum). The ability of heteromyids to detect and clean out areas of small experimental clumps of seed is remarkable (Lockard and Lockard, 1971; Brown et al., 1975) and suggests that these rodents are specialized to do just that. The length and complexity of their nasal passages may represent an adaptation primarily to seed finding and only concomitantly a physiological adaptation to decreasing water loss as described by Schmidt-Nielsen et al. (1970).

No matter what the distribution of seeds, it still remains possible that, given a high seed size diversity, seed size selection will occur. This follows directly if the largest seeds are the most readily available since they would then be the most abundant component in the large heteromyid's diet. As the diversity of seed sizes decreases, the distribution of seeds becomes increasingly important in influencing whether or not seed size selection will occur. The addition of a clumped seed distribution upon a low range of seed sizes might result in seed size selection which would not have occurred if the distribution were less clumped.

Apparent anomalies of the heteromyid system can now be explained: 1) Overlap in seed sizes taken by different sized heteromyids is considerable (Brown and Lieberman, 1973; Brown, 1975). This makes sense with the animals foraging not for a particular size of seed, but for the most readily harvested seeds which, in the case of the kangaroo rats are, on average, the largest or most clumped seeds and which, in the case of the smaller pocket mice are for the most part leftovers from the larger rodents. This implies that the relative preferences for seed types would be the same for all species regardless of body size. Indeed this was just the finding of Rosenzweig and Sterner (1970) after they conducted experiments on the seed husking abilities of different heteromyid species, and was my finding with the single-species experiments; 2) In the cases where seed size selection is lacking we expect to find the diversity of seed sizes within the habitat to be low or the distribution of seeds to be such that similar size selection occurs (e.g., small seeds clumped to a greater degree than large seeds). Although I have no data on seed distributions, seed samples taken from various localities throughout the Southwest (unpbl. data) revealed that the areas which had the highest diversity of seed sizes contained species which typically show seed size selection via cheek pouch contents (*D. deserti, D. merriami* and *P. longimembris*); the areas with the lowest seed size diversity contained *D. ordii* and *P. flavus*, whose cheek puch contents were similar in their size distribution of seeds; 3) There is a lack of correlation between microhabitat (foraging site) and seed size selection. This follows if the large, bipedal rodents forage only for the most readily available (large, or even clumped small) seeds and cover relatively large areas. They would facilitate coverage of such areas in the least amount of time by spending most (though not all) of their time in open areas. The smaller, quadrupedal heteromyids would be safest spending most of their time near vegetation foraging for the less readily available (small or uniformly distributed) seeds in a more thorough manner over smaller areas.

The most complete utilization of seed resources might be accomplished by the described difference in foraging strategy between the large and small heteromyids. Brown (1975) has shown that an indirect measure of seed productivity is correlated with granivorous rodent species diversity (see also Whitford, 1976). With increased productivity, it would seem possible that the largest kangaroo rat could obtain all its needs with a short foraging bout each night leaving an abundance of seeds which might be utilized in the manner described above by two or three additional species.

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