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Seed Size Selection in Heteromyids
A Second Look

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Summary. The general conclusion of this paper is that heteromyids do not select seed sizes on the basis of their body size. My conclusion comes from the analysis of new data from central New Mexico, analysis of data in the literature on food habits of heteromyids, and a reanalysis of Brown and Lieberman (1973) and Brown (1975). All of these sources agree that no seed size selection exists.

Although no pattern of simple seed size selection was found, interesting differences were noticed among species. First, the tendency to husk appears to be related to the size of the rodent. Second, large heteromyids may depend on fruiting heads made up of small seeds. This mayor may not have significance to the coexistence of heteromyid communities. At present, insufficient data are available to make conclusions along these lines.

Intuitively satisfying hypotheses, such as seed size allocation by heteromyids, are normally very hard to lay to rest. It is my hope that this paper demonstrates the weight of evidence is against seed size allocation in heteromyids, Those who wish to maintain this hypothesis, or reveal that it or related hypotheses have anything to do with heteromyid coexistence, must now produce data to support their position.

Introduction

All workers who have studied heteromyid rodent community structure agree that it is based to a substantial degree on habitat partitioning (Rosenzweig, 1973; Brown, 1973, 1975; Lemen, 1978). However, it has also been suggested that coexistence among heteromyids is partially based on seed size allocation by body size (Fig. 1) (Brown and Lieberman, 1973; Brown, 1975). This paper demonstrates the contrary. In the following sections I shall show that all data collected to date, including those of Brown, lead to the conclusion that no see size allocation exists within the heteromyids. This conclusion is reached by a combination of techniques: new data collected from central New Mexico; collation of all

available data in the literature; and most surprising, the discovery that Brown's conclusions stem from an artifact of his methods coupled with a behavioral pattern by the rodents which has nothing to do with seed size selection.

Three Species in New Mexico

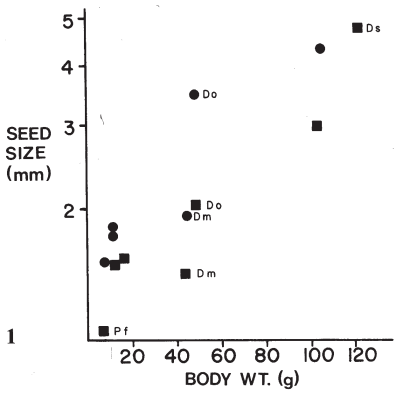
Three heteromyid species can be found commonly on the northern edge of the Jornada del Muerto of central New Mexico. They are: *Dipodomys ordi* (48 g), *D. merriami* (42 g), and *Perognathus flavus* (8 g). Although *D. spectabilis*, *P. intermedius*, and *P. flavescens* can also be found at this locality, they are either too rare or spotty in distribution to be included in this study. *Dipodomys ordi*, *D. merriami*, and *P. flavus* are of particular interest because in Brown (1975) these species showed great differences in seed size selection in the Sonoran and Great Basin Deserts (Fig. 1). Based on that work, one would naturally also predict such a difference in my central New Mexico community.

The area in which this study was conducted is a broad grassy basin. The edges of this basin slope up to low rocky hills and are covered with nearly pure stands of creosote bush (*Larrea tridentata*). The two *Dipodomys* species are macro habitat selectors; *D. ordi* prefers the grass habitat while *D. merriami* is found in the creosote stands. The transition from grass to creosote is sharp, and there is a narrow band of ecotonal habitat a few 100 meters wide where both *D. ordi* and *D. merriami* can be found together (Schroder and Rosenzweig, 1975). The pocket mouse, *P. flavus*, can be found in all of these habitats.

In order to determine the seed size preferences of these heteromyids, independent of possible habitat differences, trap grids were established in the grass, ecotone, and creosote habitats. These areas were trapped with museum specials from the fall to early spring of 1974–1975.

The weight of a species of seed was defined as the average weight of a completely husked sample of that species. Therefore, whether a seed was pouched with or without its husk, it received this same average weight. The weights of all seeds collected by each species of rodent were averaged and are as follows : *D. ordi*, 1.25 mg ($n = 35$ rodents); *D. merriami*, 1.82 mg ($n = 49$); and *P. flavus*, 1.35 mg ($n = 49$). No pattern of seed size selection based on body size exists. Figure 2 shows the same seed weight data broken down by habitat. Because the sample of *P. flavus* in the creosote habitat comes entirely from the fall sampling period (other points are a combination of rodents from both fall and spring) it must be compared not to *D. merriami* as a whole but rather to the sample of *D. merriami* also taken in the fall. That point is the open square in Figure 2, and reveals that *D. merriami* and *P. flavus* are collecting similar size seeds.

Although no pattern of seed size selection by body size exists for these three species, the rodents did appear to be highly selective for the species of seeds taken. In the fall, even though a great many plants were producing seed, 72% of all the seeds taken by *P. flavus* were of only two species of *Euphorbia*. At the same time, 68% of the seeds taken by *D. ordi* and 64% of the seeds tak-



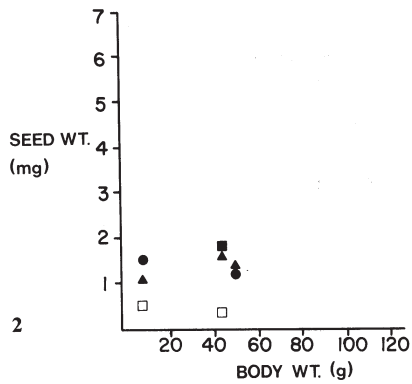


Fig. 1. This graph was originally published in Brown (1975); his analysis used a sieving method to determine seed size. Circles represent species means from data collected in the Great Basin Desert, squares are similar means from the Sonoran Desert. Points labeled are *D. spectabilis* (*Ds*), *D. ordi* (*Do*), *D. merriami* (*Dm*) and *P. flavus* (*Pf*) .

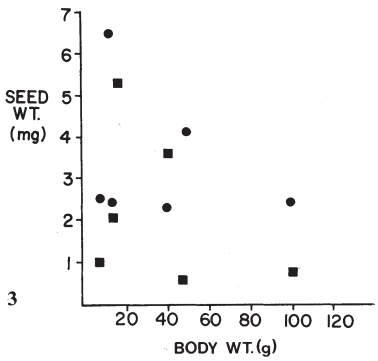
Fig. 2. The central New Mexico data shows a complete lack of positive correlation between the body weight of a rodent and the weight of the seeds it collects. Circles are species means from the grassland habitat, triangles the ecotone habitat, and squares the creosote habitat.

en by *D. merriami* were these same two species of seeds. It appears then that seed selection may be going on; all species simply prefer the same seeds. This is similar to the results of Smigel and Rosenzweig (1974) for two desert heteromyids, *D. merriami* and *P. penicillatus*.

Reanalysis of Brown's Data

Dr. James Brown was kind enough to send me the actual cheek pouch contents upon which both of his seed selection papers were based (Brown and Lieberman, 1973; Brown, 1975). The cheek pouch contents of every individual rodent had been labeled, and individually stored. I counted and weighed the contents of each and determined the average weight for each sample; these values were then averaged to obtain species means. *Dipodomys spectabilis* was deleted from my analysis because, unlike the other species, all of its seed data were from caches instead of cheek pouches.

The results of this reanalysis are presented in Figure 3. As can be seen, there is no positive correlation whatever between seed weight and rodent size. The difference in the results of Brown's analysis and my own is startling. This change is generated because my results are based on seed weights, whereas Brown's depend on sieving to determine seed sizes. In the discussion I shall point out how this difference led to the difference between Figures 1 and 3. I will argue there that the Brown pattern is, indeed, indicative of a real pattern, but that this pattern has nothing to do with seed selection by body size.



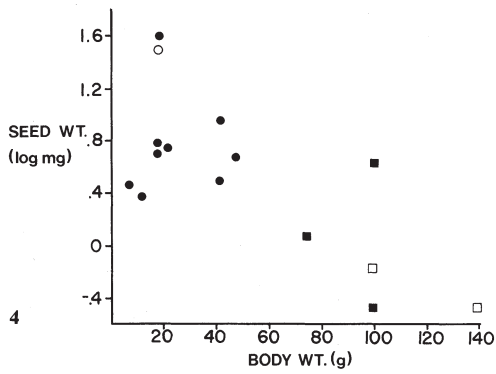


Fig. 3. This plot shows the results of the re-analysis of Brown's data, this time using seed weights instead of sieving. Compare this scattergram to Figure 1.

Fig. 4. Plotted here are the body weights and seed weights for several species of heteromyids; the data collected from published food habit studies. Circles represent cheek pouch data, squares, cache data. The open symbols represent studies where only 85% to 95% of the seed data reported could be used. All other points are represented by at least 95% of the original data.

Data from the Literature

The food habits of heteromyids have received considerable attention by ecologists. This is a valuable source of data for testing seed size selection. Average seed weights were calculated for heteromyid species from these published accounts: *D. spectabilis*: Monson, 1943; Vorhies and Taylor, 1922; Monson and Kessler, 1940; *D. ingens*: Shaw, 1934; *D. merriami*: Franz et al., 1973; Gennaro, unpublished data; Reynolds, 1958; *D. heermanni*: Pitch, 1948; *D. ordi*: Gennaro, unpublished data; *Perognathus penicillatus* : Arnold, 1942; Reynolds and Haskell, 1949; *P. baileyi*: Franz et al., 1973; *P. amplus*: Franz et al., 1973; *P. intermedius*: Franz et al., 1973; Gennaro, unpublished data; *P. flavus*: Gennaro, unpublished data. These average weights were determined by using all the seed species which constituted more than 1% of a species intake. Average seed weights were determined for each species of seed with samples from my own seed collection and the University of New Mexico herbarium.

The results of this analysis are graphed in Figure 4. These results are certainly not indicative of a positive correlation. Instead, they appear to show that larger heteromyids actually prefer smaller seeds (this same trend can be found in Brown's data; Fig. 3). However, this conclusion may be premature. First, all the large species in the literature survey are represented by cache data alone, whereas the smaller heteromyids are all represented by cheek pouch contents. It is not known whether this introduces a bias. Second, the larger species may be living in habitats with smaller seeds, so we cannot be sure if they are discriminating in favor of smaller seeds even if cache contents are comparable to cheek pouch contents.

Two mechanical problems are also involved in Figure 4. First, not all the seed species reported could be found for weighing, these data had to be deleted. In Fig-

ure 4 only those points which could be represented by at least 85% of their reported data were used. Second, because these studies were done by different researchers, the data were reported in a variety of ways: percent occurrence, absolute numbers, volume, etc. I was forced to use the data in whatever form they were reported. Even in view of the possible problems of Figure 4, the pattern definitely does not suggest a positive relationship between seeds taken and rodent body size.

Discussion

There is good evidence of body size character displacement in heteromyid communities (Brown, 1975; Rosenzweig et al., 1975). The rodent communities I worked with in central New Mexico are good examples. In the grassland habitat one can find *D. spectabilis* (110 g), *D. ordi* (48 g), and *P. flavus* (8 g). Syntopic in the creosote habitat are *D. spectabilis*, *D. merriami* (42 g), and *P. flavus*. This kind of body size distribution within guild members of a community would naturally lead one to predict prey allocation by size. However, despite the fact that other desert granivores appear to be allocating seed sizes (ants, D. Davidson, pers. comm.; birds, Pulliam, 1975) heteromyid rodents clearly do not.

To understand why, we must return to the theory of resource allocation (MacArthur and Pianka, 1966; Emlen, 1966; Pullian, 1974; Charnov, 1976). Any allocation by size must be based on "pursuit costs"; seeds large than, say x grams or smaller than y grams have to be prohibitively costly to pursue, and x and y must vary for consumers in proportion to their body size. This condition is certainly fulfilled for granivorous ants. The small *Pheidole* spp. are physically incapable of carrying off the large seeds often taken by bigger ants such as *Pogonomyrmex* spp. It is also fulfilled for birds since large birds are most efficient at shelling and eating large seeds, while small birds are best at small seeds (Mac Arthur and MacArthur, 1972). No such pattern has been found in heteromyids. Indeed, Rosenzweig and Sterner (1970) found that based on husking efficiencies, whatever the size of the heteromyid, all should prefer the largest seeds.

Supposing, even in the face of their drawbacks that Figures 3 and 4 are qualitatively accurate, how then is one to understand why large species should prefer smaller seeds? One cannot. However, large species may be getting smaller seeds (as opposed to preferring them) for several reasons. First, small seeds may predominate in their foraging habitats. Certainly the average seed size available is a function of habitat (Baker, 1972). Second, it may be that the largest kangaroo rats are taking small seeds because they depend heavily on fruiting heads. These fruiting heads are often made up of many small seeds; *Aristida*, *Lepidium*, and *Bouteloua* would be three examples. Thus, the small seeds in the caches may reflect selection for fruiting heads rather than selection for small seeds. Lastly, it is possible that since the data from the larger heteromyids are largely cache data, these rats may prefer to store the smaller seeds and eat the larger seeds on the spot.

It remains to consider the root of the difference between Brown's results and my own. I have already identified this as inherent in the techniques we used to define seed size. Brown dumped the contents of a rodent's pockets on a graded series of soil sieves, and then counted how many seeds were stopped at each level of coarseness of mesh. This makes no allowance for the fact that some of the seeds, but not all, have been husked by the rodents; some have been trimmed of their awns, wings, etc. and some are in whole fruiting heads. In Brown's study such a fruiting head would be counted as a single large seed; with my weight method, the fruiting head would represent many smaller seeds, the weight of each seed determined by an average weight for the husked seed of that species.

The problem with Brown's approach is that different species of rodents handle seeds very differently. The small heteromyids husk more thoroughly and do not pouch entire fruiting heads. A *P. flavus* was found to have carefully clipped the wings from Four Winged Salt Bush (*Atriplex canescens*) while the large *D. ordi* and *D. deserti* (100 g) did not. In the case of husking, the pattern was the same. *Perognathus flavus* would always husk a certain seed species while *D. ordi* often did not bother to husk this same seed species. While these broad patterns of change do exist, much smaller changes in size can also produce changes in husking. *Dipodomys ordi* (48 g) is slightly larger than *D. merriami* (42 g) in central New Mexico. Using skull length as an index of size, *D. ordi*, for this sample, is significantly larger than *D. merriami* (Mann-Whitney U-test: *D. ordi*, $n = 12$; *D. merriami*, $n = 7$; $p = 0.025$). In the early spring data I collected in central New Mexico, both *D. ordi* and *D. merriami* were taking large amounts of *Salsola kali* seeds. These seeds were pouched in one of three ways: unhusked, husked but winged, and completely husked. With the sieving method the size of a Salsola seed is dependent on how completely the seed is husked. The unhusked seed is caught in a 4 mm mesh sieve, the winged seed in a 2 mm mesh, . and, finally, the husked seed is stopped at the 1 mm mesh size. This one seed species can span much of the size range of Figure 1.

To test if *D. ordi* and *D. merriami* were pouching seeds in different condition with respect to husking, I sieved all the *Salsola kali* seeds these rodents had collected and obtained average seed sizes for all individuals following Brown and Lieberman's (1973) methods. The means for the two species are *D. ordi*, $n = 14$, $x = 1.2$ mm; *D. merriami*, $n = 7$, $x = 1.0$ mm. Using a Mann-Whitney U-test I found that *D. ordi* had taken significantly larger seeds than *D. merriami* (*D. ordi*, $n = 14$, *D. merriami*, $n = 7$; $p = 0.01$). But remember, all the seeds sieved were *Salsola kali* seeds; the difference in results were determined exclusively by the difference in husking between these two rodents.

At present there is insufficient evidence to determine why differences in husking behavior exist among rodents of different size. It may be something as simple as space in the cheek pouch, or a more complex interaction between cheek pouch size, husking time, and exposure to predation. Whatever, the pattern exists and makes sieving a poor technique to assess seed size.

The taking of whole fruiting heads is normally restricted to the larger kangaroo rats such as *D. spectabilis* (100 g) and *D. ingens* (150 g) (Monson, 1943; Vorhies and Taylor, 1922; Shaw, 1934). This behavior may well represent a different feeding strategy from the seed gleaning used by smaller heteromyids. The point to be made here is that calling a fruiting head a large seed because it is caught in the top sieve does more to obscure patterns than to reveal them.

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