

Mechanisms of seed harvest by heteromyid rodents: soil texture effects on harvest rate and seed size selection

Mary V. Price and Robert H. Podolsky*

Department of Biology, University of California, Riverside, CA 92521, USA

Summary. Several lines of evidence show that soil texture plays an important role in the distribution of desert-dwelling heteromyid rodents. This is not surprising, since texture influences the energetic cost of digging burrows and of scratching at the soil surface to harvest buried seeds. Texture also may influence the efficiency with which seeds can be separated from the soil particles with which they are mixed. To explore mechanisms of “particle separation” by foraging heteromyids we measured seed harvest rates and size selection in the laboratory for a variety of seed sizes and soil textures. Harvest rate declined with increasing soil coarseness, and the preference for seeds of intermediate size that was apparent in fine soil disappeared when seeds were mixed with soil slightly coarser than the preferred seed size. In addition, there was evidence that particle separation efficiency is sensitive to the relative sizes of seeds and soil. A discontinuity in the function relating harvest rate to soil texture occurred at finer soil textures for small seeds than for large seeds, suggesting that harvest techniques change once soil particle diameter equals or exceeds that of seeds. These results are consistent with the hypothesis that heteromyids use a combination of gravity- and rake-sorting mechanisms for particle separation.

Key words: *Dipodomys* – *Perognathus* – *Chaetodipus* – Foraging mechanisms – Digging

Soil texture appears to be an important factor in the ecology of desert-dwelling heteromyid rodents. Species distributions on geographical and local scales often correspond with particular soil types (e.g. Hardy 1947; Rosenzweig and Winakur 1969; Ghiselin 1970; Hoover et al. 1977; Price 1978; Price and Endo 1989). In addition, soil texture varies among microhabitats that are used nonrandomly by heteromyids as they forage for seeds (Price and Waser 1985; Price and Reichman 1987), and in the laboratory heteromyids discriminate among artificial seed patches that differ in soil texture (Price and Waser 1985; Price and Longland 1989).

Because heteromyids construct underground burrows, it is not surprising that soil characteristics should be critical

to their distributions. Soil texture has a profound effect on burrow humidity and hence on water balance (Hoover et al. 1977). Furthermore, texture and degree of compaction dictate the force that an animal must apply with the forelimbs to cut through, or “shear”, the soil. The force required to shear and subsequently to move the soil affects rates of burrowing and metabolic energy required to excavate a unit length of burrow (Vleck 1979). That such digging costs are not trivial is suggested by the infrequent initiation of new burrows by species like *Dipodomys spectabilis* that have especially extensive burrow systems (Best 1972; Schroder 1972), and by the general correlation in heteromyids between the mechanical advantage of a species’ forelimb for digging and its soil affinities (Heinz 1983; Price unpubl. data).

Texture may influence more than costs of shearing and moving soil, however. This is especially true during foraging, when animals must separate particles of one type (seeds) from a matrix of other particles (soil). A soil texture effect on particle separation efficiency is suggested by the fact that texture influences seed harvest rates even for loose soils that are easily sheared (Price and Heinz 1984), and by the fact that texture of very light substrates can influence both harvest rates (Price and Heinz 1984) and patch choice in the laboratory (Price and Waser 1985; Price and Longland 1989). Why texture should have these effects may become apparent if we consider how heteromyids forage for seeds, and what possible means of particle separation should be available to them.

Possible mechanisms of seed harvest

We know little about mechanisms of seed harvest by heteromyids except that tactile cues are critical (Lawhon and Hafner 1981). Harvesting behavior is easy to observe only under very artificial conditions, e.g., when animals are presented with large seeds on glass plates (Lawhon and Hafner 1981; Nikolai and Bramble 1983; Price and Heinz 1984). Under these conditions each particle is picked up by the forepaws, sometimes is bitten, and then is either rejected or placed into cheek pouches (Lawhon and Hafner 1981; Nikolai and Bramble 1983). In more realistic laboratory experiments and in nature, however, we know that heteromyids harvest buried seeds, and that they do so far too quickly to be testing individually each particle that they touch. Hence they must be using some means of bulk particle separation.

Offprint requests to: M.V. Price

* Present address: Department of Botany, Washington State University, Pullman, WA 99164, USA

By considering in general how a heteromyid harvests buried seeds, we can identify plausible mechanisms of bulk particle separation. Foraging animals move the forefeet forward and then down and back in a raking motion. If digits are spread apart, larger particles should be retained while smaller particles pass through the digits as the forefoot (=manus) is moved backwards, a mechanism we call "rake-sorting". In addition, as the sides of the resulting small excavation cave in, gravity-sorting should concentrate lighter and larger particles on the surface near the bottom of the pit because size and mass affect the angle of repose, i.e., the slope at which loose particles begin to slide downhill under the force of gravity and against frictional resistance.

Both rake- and gravity-sorting mechanisms should be sensitive to the absolute sizes of seeds and soil particles. As any gardener knows, it is harder to rake or shovel gravel than sand, and the dynamics of gravity-sorting should be scale-dependent as well. The relative sizes of seeds and soil also should influence how efficiently they can be separated. For soil particles about the same size as seeds, separation efficiency will be low and many particles will have to be tested individually. For soil particles larger than seeds, a backwards raking motion will no longer concentrate seeds and move them toward the animal, but instead will remove soil, exposing seeds that must be picked up individually. Gravity-sorting also will be less effective in coarse soil, because soil particles rather than seeds will be concentrated at the bottom of a pit. These effects should cause a discontinuity in the relationship between soil texture and harvest rate at the point where soil and seed particles are of equal size.

Several observations suggest that both rake- and gravity-sorting mechanisms may be important for heteromyids. Price and Heinz (1984) found that when soil was coarse, harvest rates were higher in heavy soils, where gravity sorting would be more effective, than in light soils similar in bulk density to seeds. The soil density effect was not observed in fine soil where rake-sorting would be efficient. Price and Heinz also found, as expected, that harvest rates declined rapidly as soil particles approached the diameter of seeds used in the experiments (millet), and declined more slowly once the diameter of millet was exceeded. However, because they kept seed size constant while varying soil texture, it is unclear whether relative or absolute texture was the important factor.

In this paper we discuss experiments that varied both soil particle and seed sizes in an attempt to assess the importance of absolute and relative particle sizes not only for harvest rates, but also for seed size selection. If the size of a seed relative to soil particles affects the efficiency with which it can be harvested, then the value of a given seed size should depend on soil texture, and a change in texture should affect seed size selection.

Methods

(1) Harvest rate measurements

We determined effects of soil and seed particle size on harvest rates in two studies. In both we ground hulled millet in a grain mill and then sieved the mixture through Tyler soil sieves for ten min on a mechanical sieve shaker to isolate two seed-fragment size fractions (seed fragments are referred to as "seeds" in what follows). We isolated soil texture classes by a similar procedure.

Study 1. In the first study, two seed size classes ("large" = 1.68–2.00 mm diameter; "small" = 1.18–1.40 mm) and two soil textures ("fine" = <0.42 mm; "coarse" = 0.85–1.00 mm) were tested in all pairwise combinations. In all cases seed diameter was larger than soil diameter. However, the four treatments formed a gradient in minimum difference between seed and soil diameters: large seeds in fine soil (1.26 mm minimum diameter difference) > small seeds in fine soil (0.76 mm difference) > large seeds in coarse soil (0.68 mm difference) > small seeds in coarse soil (0.18 mm difference). If size of seed relative to soil dictates harvest rate, then rate should rank in the same manner. If soil texture alone is important, then seed size should have no effect on harvest rate, and rates for either seed size in fine soil should exceed those for either in coarse soil.

Seed patches were assembled by filling a 9.3 cm diameter petri dish with either fine or coarse soil, sprinkling a known number of small or large seeds over the surface, and pressing the seeds into the soil with a flat plate. We used seed densities of 1.77, 7.07, and 8.83 seeds/cm².

Harvest rate was measured by a single observer between Jan and Mar for six *Dipodomys deserti* individuals collected as adults from the Kelso sand dunes (San Bernardino County, CA, USA) the previous fall. In the morning before each experimental session, an individual was removed from its home cage and placed into a plastic cage with clean sand as substrate for a five h deprivation period. The cage was then transported to a room with lights dimmed to the point where foraging activity was not inhibited, but observers could see well enough to record behaviour accurately. Trials were conducted as follows. A seed patch was introduced into the cage, and a stopwatch was started when the animal began to harvest seeds from the dish. The watch was stopped and the dish removed if the animal paused for more than 2 sec, began to eat (Heteromyids generally do not eat harvested seeds immediately, but place them into cheek pouches pending transport to a cache), or foraged seeds from the entire area of the dish. The dish was then replaced by another one, and the cycle was repeated until the animal refused to forage. The 12 types of patch (two soil textures × two seed sizes × three seed densities) were presented to each individual in randomized order, and 1–2 complete blocks of 12 measurements were obtained from most individuals. The contents of each foraged patch were sieved and remaining seeds were counted. Seed recovery was almost complete, with only 1–2% error, judging from control trials in which known numbers of seeds were introduced into patches and then immediately recovered.

Harvest rate was calculated by dividing number of seeds removed by time spent harvesting. This procedure yields accurate estimates of harvest rates even though we didn't control time spent harvesting, because heteromyids forage systematically within patches; cumulative number of seeds harvested increases linearly with time in a patch until animals have searched the entire patch (Podolsky and Price, unpublished work). After that, cumulative gain increases very slowly if at all. We remained in the linear portion of the gain curve by terminating trials before animals began to forage areas they had already depleted. On average, animals foraged half of the area of a patch during a trial, which corresponds to a bout duration of approximately 30 s.

Harvest rate data were analysed in a variety of ways. To explore the relationship between harvest rate and seed

density (hereafter “functional response”), we pooled data across individuals and compared the fit of several functions using the NLIN (nonlinear regression) procedure of SAS (SAS Institute, 1982). To determine the relative importance of various sources of variation in harvest rates, we performed a mixed-model factorial ANOVA on log-10 transformed data using the SAS GLM procedure (log-transformation homogenized variances of residuals; by Bartlett’s test $X^2 = 14.5$, d.f. = 13, $P > 0.1$). Finally, we used a nonparametric analysis of variance (Friedman’s method of randomized blocks) to assess whether the ranking of means for the various seed size-soil texture combinations was concordant across seed densities and consistent with those expected if the relative sizes of seeds and soil affect harvest rates.

Study 2. In the second study, two seed size classes (“large” = 2.00–2.36 mm diameter; “small” = 0.85–1.00 mm) and five soil size classes (<0.42 mm, 1.00–1.18 mm, 1.68–2.00 mm, 2.36–2.80, and >4.00 mm diameter) were used. Unlike Study 1, seeds were not always larger than soil particles. Minimum seed – soil diameter differences for small seeds ranged from +0.40 mm (fine soil) to –3.00 mm (coarsest soil), and those for large seeds ranged from +1.58 mm to –1.64 mm.

Seed patches were constructed, harvest rates measured, and analyses of variance were conducted as in Study 1. The only differences were that we used one seed density (1.77 seeds/cm²), so that density wasn’t a factor, and two heteromyid species (*Dipodomys deserti*, three individuals collected from Kelso Dunes; *Perognathus* [= *Chaetodipus*] *penicillatus*, three individuals collected from Pima County, Arizona, USA), so that “species” was a factor. We used a partially-hierarchical ANOVA model that treated seed size, soil texture, and species as fixed effects, and individuals as random-effects nested within species. Once again, log-10 transformation homogenized variances of residuals (Bartlett’s $X^2 = 1.4$, d.f. = 20, $P > 0.9$).

(2) Seed size selection

To determine whether soil texture affects seed size selection, we presented a mixture of three seed sizes embedded in either fine or coarse soil to individuals of six heteromyid species and recorded their patterns of seed consumption using the methods of Price (1983). The six species used were *Dipodomys deserti*, *D. panamintinus*, *D. merriami*, *Perognathus* [= *Chaetodipus*] *baileyi*, *Perognathus* [= *Chaetodipus*] *penicillatus*, and *Perognathus amplus*. Two sizes of soil (<0.42 mm and 1.68–2.00 mm) and three of ground wheat (0.50–1.00 mm diameter and 0.79 mg weight, 1.18–1.40 mm and 2.16 mg, and 2.00–2.36 mm and 12.72 mg) were isolated as described above. Six plastic cages were filled with 1 cm of fine soil and six others with 1 cm of coarse soil, and then a mixture of 5 g of each of the three seed sizes was stirred into the soil in one corner of each cage. One individual of each of the six heteromyid species was placed into a fine-soil cage, and another into a coarse-soil cage, in the late afternoon. Animals were allowed to collect and eat seeds overnight. They were removed from the cages at 0800 h the next morning. The same 12 individuals were retested the following night with the alternate soil texture. Six individuals per species were tested twice, once with each soil texture. All had been

caught as adults from various locations in Arizona and California, USA.

Cage contents were shaken for ten min through four sieves to separate seed sizes from soil and from each other, and each recovered seed size fraction was weighed. Amounts of seed removed (and presumably consumed) were determined by subtracting weights remaining from 5 g, and relative consumption of the three seed sizes was taken as an index of preference. The error associated with this process was on the order of 1–3%, judging from comparisons of weights of seed placed in cages and subsequently recovered in a series of calibration trials without consumers.

If the difference in seed and soil particle diameters dictates harvest efficiency, then in fine soil large seeds should have been highly preferred because they had the greatest diameter relative to soil and also had the highest energy content. In coarse soil, however, large seeds were slightly larger than soil particles but were the most similar (minimum difference = 0 mm), medium seeds were slightly smaller than the soil (minimum difference = –0.28 mm), and small seeds were the most distinct but also had the smallest energy content per seed.

Effects of soil texture on seed size preferences were assessed in several ways. A nonparametric ANOVA (Friedman’s method of randomized blocks) determined, for each soil texture separately, the concordance in consumption rank across individuals within species, and across species. A split-plot ANOVA using the SAS ANOVA procedure treated individuals as unreplicated randomized complete split-plots to see whether individuals changed the grams of each seed size consumed with soil texture. This analysis was backed up with multivariate analysis of variance using the SAS GLM procedure, which treated (arcsin-transformed) proportional consumption of the three seed sizes as nonindependent variables measured on the same individual during a night, and which contrasted proportional consumption by all individuals (and all species) in fine soil with that in coarse soil.

Results

(1) Effects of seed size and soil texture on harvest rate

Study 1. For all soil and seed sizes, harvest rate increased with seed density in decelerating fashion (Fig. 1), producing a Type II or III functional response (Holling 1959). The decelerating nature of the curves is indicated by the fact that negative exponential functions explained slightly more of the variance for all data sets (R^2 values of 0.22–0.29) than did linear functions constrained through the origin (R^2 values of 0.19–0.28).

Analysis of variance (ANOVA, Table 1) indicated highly significant main effects of individual, soil texture, and seed density on harvest rate, but no significant interactions. Although there was no significant effect of seed size on harvest rate, the ranking of mean harvest rate across the four patch types was significantly concordant over all three seed densities (Friedman’s randomized-blocks ANOVA: $X^2 = 8.2$, d.f. = 3, $P < 0.05$). The overall ranking matched an expectation based on relative seed and soil sizes, with mean harvest rate for large seeds in fine soil > small seeds in fine soil > large seeds in coarse soil > small seeds in coarse soil (Fig. 1). These results indicate a slight but

Table 1. Study 1: mixed-model factorial ANOVA for effects of individual ("Indiv"; random effect), seed density ("Dens"; fixed), seed size ("Seed"; fixed), and soil particle size ("Text"; fixed) on log-transformed seed harvest rate by *Dipodomys deserti*. "Error MS" indicates the mean square over which each effect was tested, determined by methods described in Brownlee (1965:530–542)

Source	df	Type IV SS	Error MS	F	P
1. Indiv	5	0.846	16	5.02	<0.01
2. Text	1	1.199	3	35.64	<0.01
3. Indiv × Text	5	0.168	16	1.00	>0.25
4. Seed	1	0.043	5	1.05	>0.25
5. Indiv × Seed	5	0.203	16	1.21	>0.25
6. Text × Seed	1	0.036	7+16	1.11	>0.25
7. Indiv × Text × Seed	5	0.144	16	0.86	>0.50
8. Dens	2	3.161	9	25.96	<0.001
9. Indiv × Dens	10	0.609	16	1.81	>0.10
10. Text × Dens	2	0.167	11+16	2.72	>0.05
11. Indiv × Text × Dens	9	0.228	16	0.75	>0.50
12. Seed × Dens	2	0.430	13	2.74	>0.10
13. Indiv × Seed × Dens	9	0.705	16	2.32	>0.05
14. Text × Seed × Dens	2	0.019	15+16	0.32	>0.50
15. Indiv × Text × Seed × Dens	6	0.107	16	0.53	>0.75
16. Error	16	0.539			

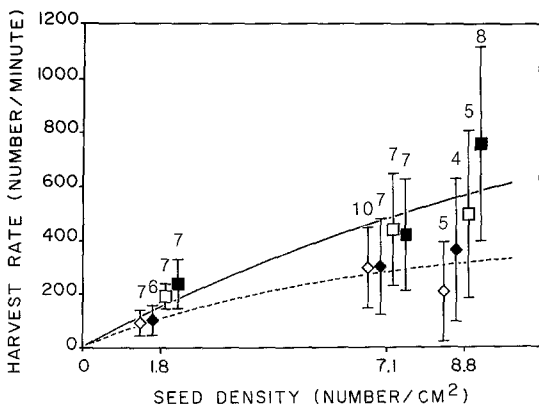


Fig. 1. Effects of soil texture and seed size on the relationship between seed density and harvest rate for *Dipodomys deserti* (Study 1). Symbols depict mean number of seeds harvested per min, $\pm 95\%$ confidence limits, with sample sizes above each bar. Open squares=small (1.18–1.40 mm) seeds in fine (<0.42 mm) soil; filled squares=large (1.68–2.00 mm) seeds in fine soil; open diamonds=small seeds in coarse (0.85–1.00 mm) soil; filled diamonds=large seeds in coarse soil. Solid line=best-fit negative exponential function to pooled fine soil data (rate=1140 $[1 - \exp\{-0.26 \text{ density}\}]$); dashed line=best-fit negative exponential function to pooled coarse soil data (rate=411 $[1 - \exp\{-0.16 \text{ density}\}]$)

consistent effect of relative seed size on harvest rate, over and above a strong effect of soil texture.

(2) Effects of seed size and soil texture on harvest rate

Study 2. As in Study 1, harvest rate decreased significantly with increasing soil particle diameter for both heteromyid species and both seed sizes (Fig. 2, Table 2). Unlike Study 1, however, there was a significant effect of seed size on harvest rate in addition to a soil texture effect (Table 2). Although there was no significant main effect of species on

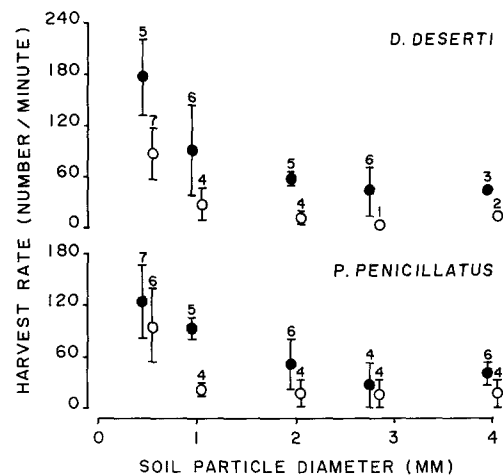


Fig. 2. Effects of soil texture and seed size on harvest rate for two heteromyid species (Study 2). Filled symbols=large seeds (2.00–2.36 mm); open symbols=small seeds (0.85–1.00 mm). Conventions follow Fig. 1

Table 2. Study 2: partially hierarchical ANOVA for effects of individual ("Indiv"; nested within species), species ("Spec"; fixed), seed size ("Seed"; fixed), and soil texture ("Text"; fixed) on log-transformed seed harvest rate by *Dipodomys deserti* and *Perognathus [= Chaetodipus] penicillatus*. "Error MS" indicates the mean square over which each effect was tested, determined by methods described in Brownlee (1954:530–542)

Source	df	Type IV SS	Error MS	F	P
1. Spec	1	0.002	2	0.07	>0.75
2. Indiv (Spec)	4	0.138	12	0.64	>0.50
3. Seed	1	2.384	9	77.13	<0.001
4. Text	4	5.684	10	92.74	<0.001
5. Seed × Text	4	0.410	11+12	2.01	>0.10
6. Spec × Seed	1	0.164	9+12	3.12	>0.05
7. Spec × Text	4	0.043	10+12	0.24	>0.75
8. Spec × Seed × Text	3	0.395	11+12	2.58	>0.05
9. Indiv (Spec) × Seed	2	0.062	12	0.58	>0.50
10. Indiv (Spec) × Text	13	0.199	12	0.29	>0.90
11. Indiv (Spec) × Seed × Text	3	0.030	12	0.19	>0.90
12. Error	51	2.723			

harvest rates, there was a suggestion ($P < 0.1$) that *D. deserti* suffered a relatively greater reduction in harvest rate than *P. penicillatus* with small seeds and with coarse soil (cf. species × seed size and species × seed size × soil texture effects in Table 2).

The effect of soil particle diameter on harvest rate was nonlinear (Fig. 2). Harvest rate showed a rapid initial decrease as soil became coarser, followed by a much slower decrease after soil particle diameter exceeded seed diameter. That the discontinuity occurred at a smaller soil particle diameter for small than large seeds is indicated by pairwise comparisons of least-square means (Table 3; because the overall soil texture effect was significant at the 5% level in all four cases, it was not necessary to control experimentwise error while comparing means subsequently). For both species, harvest rates of small seeds were homogeneous at the 5% level for the four coarsest soils, whereas harvest rates of large seeds were homogeneous only for the three

Table 3. Comparison of harvest rate means for various soil texture treatments. Values are least-square means for harvest rate (numbers harvested per minute). Means that are not different at the 5% level in pairwise comparisons have the same superscript letter. Large seeds=2.00–2.36 mm diameter; Small seeds=0.85–1.00 mm diameter

Species	Seed size	Soil particle diameter (mm)				
		<0.42	1.00–1.18	1.68–2.00	2.36–2.80	>4.00
<i>D. deserti</i>						
	Large	176.40 ^a	89.70 ^b	57.12 ^{b, c}	42.6 ^c	43.8 ^c
	Small	85.71 ^a	26.85 ^b	11.55 ^b	2.4 ^b	13.5 ^b
<i>P. penicillatus</i>						
	Large	124.49 ^a	91.56 ^b	49.5 ^c	25.5 ^c	41.0 ^c
	Small	93.40 ^a	18.84 ^b	16.8 ^b	15.3 ^b	15.9 ^b

coarsest soils. This result is expected if the efficiency of separation changes qualitatively once soil particle size equals or exceeds seed size.

(3) Effects of soil texture on seed size selection

Mean proportional consumption of the three seed sizes by the six heteromyid species is indicated in Fig. 3. For coarse soil, the mean order of proportional consumption over all species was medium seeds (34.9%) > small seeds (32.9%) > large seeds (23.1%). A Friedman's randomized-blocks test, however, indicated no significant concordance among individuals within species in their rankings of the three seed sizes in coarse soil ($X^2 < 5.6$, d.f. = 2, $P > 0.05$ for each species), and no significant effect of seed size on consumption rank when all individuals of all species were combined in one analysis ($X^2 = 4.35$, d.f. = 2, $P > 0.05$). Unreplicated randomized-blocks ANOVA performed on grams of the three seed sizes consumed per night confirmed that there were no significant size preferences when seeds were embedded in coarse soil (Table 4; individuals were treated as blocks in this analysis).

Consumption patterns were different in fine soil. Although the same total amounts of seed were consumed per night as in coarse soil (randomized-blocks ANOVA, with individuals as blocks and total grams consumed in each soil type as the two treatments applied to each block indicated a significant individual effect, $P < 0.001$, but no significant soil texture effect, $P > 0.10$), the mean proportional consumption over all species was medium seeds (61.3%) > large seeds (22.9%) > small seeds (8.9%). For all species except *Dipodomys panamintinus*, there was significant concordance among individuals by Friedman's test ($X^2 > 6.0$, d.f. = 2, $P < 0.05$ for five species). Over all species there was a significant preference for medium seeds ($X^2 = 32.38$, $P < 0.005$), and hence a highly significant overall effect of seed size on consumption in fine soil (Table 4).

Multivariate analysis of variance (MANOVA; SAS Institute 1982) confirmed the difference between consumption patterns in coarse and fine soils. Treating grams of the three seed sizes consumed as nonindependent variables measured on the same individual during a night, MANOVA indicated a highly significant difference between consumption patterns for the two soil textures (Wilks' lambda = 0.70,

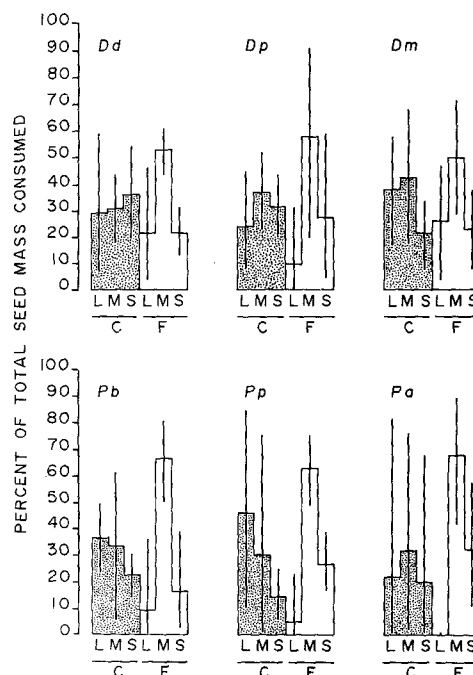


Fig. 3. Effects of soil texture on relative consumption of three seed sizes by six heteromyid species. Bars indicate consumption of large (L; 2.00–2.36 mm diameter), medium (M; 1.18–1.40 mm diameter), and small (S; 0.50–1.00 mm diameter) seeds by individual rodents as percentages of the total mass consumed in a night, $\pm 95\%$ confidence intervals back-transformed from statistics calculated with arcsin-transformed data. Stippled bars indicate coarse (C; 1.68–2.00 mm diameter) soil; open bars indicate fine (F; <0.42 mm diameter) soil. dd = *Dipodomys deserti*; Dp = *D. panamintinus*; Dm = *D. merriami*; Pb = *Perognathus* [= *Chaetodipus*] *baileyi*; Pp = *P. [Chaetodipus] penicillatus*; Pa = *Perognathus amplus*

Table 4. Randomized-blocks ANOVA of grams of each seed size consumed during a night, by soil texture. Individual animals are treated as blocks, and each seed size class is treated as an unreplicated treatment within blocks

Source	df	SS	F	P
A. Coarse Soil				
Individual (block)	35	15.029	2.05	0.005
Seed size	2	0.486	1.16	0.319
Error (block \times size)	70	14.659		
B. Fine Soil				
Individual (block)	35	13.124	3.83	0.0001
Seed size	2	7.231	36.94	0.0001
Error (block \times size)	70	6.851		

$F(3,68) = 9.96$, $P = 0.0001$). The characteristic vector accounting for 100% of the difference between soil types contrasted proportional consumption of medium seeds (weighting coefficient = -0.28) with that of the other two seed sizes (weighting coefficients = 0.14 and 0.18). Hence, there was a pronounced shift in proportional consumption of medium seeds between coarse and fine soil.

Discussion

Results of these studies conform to a model of heteromyid foraging in which soil texture influences the efficiency of

particle separation. If texture influenced only the energetic costs of digging, and not the efficiency of particle separation, we should not have found any evidence that relative sizes of seed and soil particles affect harvest rates, there should have been no effect of soil texture on seed size preferences, and animals should have consumed different amounts of food per night with the two soil types to fuel different digging expenditures (this last effect may, however, be so small as to be undetectable with the loose soils used in our experiments).

Our studies were not capable of distinguishing between gravity- and rake-sorting mechanisms for seed separation. Under both mechanisms soil particle size should have a strong effect on harvest rate because soil size should affect the dynamics of raking and of gravity-sorting regardless of seed size. The observed effect of seed size with soil size held constant is also expected because differences in particle size between seeds and soil should affect the completeness of separation by both methods. As expected, this seed size effect was too subtle to detect statistically when the two seed sizes were similar (Study 1, a minimum diameter differences of 0.28 mm between large and small seeds), and was much more pronounced when large and small seeds were more distinct (Study 2, minimum diameter difference of 1.00 mm). The observed discontinuity in the relationship between harvest rates and soil texture when soil particle diameter approached or exceeded that of seeds is consistent with an expected change in separation efficiency under both mechanisms. The best evidence that animals use both gravity- and rake-sorting mechanisms comes (in hindsight) from Price and Heinz's (1984) observation that substrate density affected harvest rate only when substrate texture was coarse enough to compromise the effectiveness of rake-sorting.

It is interesting in this regard to consider the possibility that the variation in manus morphology that is apparent upon casual observation of heteromyids may reflect variation in ability to use alternative separation mechanisms. Bipedal species tend to have long curved claws on their forefeet that are likely to have a different effectiveness during raking than the shorter claws of quadrupedal species. The fact that *D. deserti* realized much higher harvest rates than the smaller *P. pencillatus* only when harvesting large seeds in fine soil (Fig. 2) could indicate that bipeds are more efficient than quadrupeds at rake-sorting, but not at gravity-sorting. Such subtle differences in seed extraction efficiency could underlie observed differences between bipeds and quadrupeds in utilization of seed patches that vary in seed size and/or soil texture or bulk density (Price 1978; Price and Heinz 1984; Price and Waser 1985; Price and Reichman 1987).

Patterns of seed size selection observed here for fine soil are similar to those obtained by Price (1983). In the earlier study seeds were embedded in fine soil (<0.42 mm diameter), and five species of heteromyid were concordant in preferring ground wheat particles of intermediate (5 mg, ~2 mm) size. Why the largest seeds were not preferred is not yet understood. Perhaps the large auditory bullae of heteromyids so restrict jaw gape that large particles cannot be eaten easily (Nikolai and Bramble 1983). It also is possible that very large seeds must be handled with both forefeet. This would have the effect of halving maximum harvest rates for seeds above a certain size, hence lowering their net value.

The strong effect of soil texture on seed size selection

points to particle separation being a critical component of heteromyid foraging. This effect has some interesting implications for seed selection in different microhabitats. Price and Reichman (1987) noted that at one Sonoran Desert site, seed size distributions were more skewed towards larger seeds under shrubs, where soil is coarser and lighter than in the open. They also noted that average seed densities were higher under shrubs. At first glance it might seem that patches containing more and larger seeds should be most profitable to foraging heteromyids, but it may be that the coarser soil under shrubs instead makes a larger fraction of those seeds effectively unavailable to the rodents. This may have implications for evolution of seed size and microhabitat associations of desert plants.

In this series of studies we have attempted to infer indirectly, from observations of behavior and foraging rates, what mechanisms heteromyid rodents use to extract seeds from the soil. Having a "mechanistic" understanding of processes like foraging is critical for directing our attention towards characteristics of the environment or features of an organism that are ecologically important. Without such understanding we are in danger of wasting time studying relatively insignificant problems or developing models of higher-level phenomena, such as interspecific competition, that are unrealistic, misleading, and/or impossible to test unambiguously (Price 1986; Schoener 1986; Tilman 1987; Arthur 1988; Rothhaupt 1988). We hope the increasing interest in mechanistic approaches will stimulate more studies that elucidate what organisms do, how they do it, and why they don't do something else.

Acknowledgements. We thank all those who assisted, especially Chris Gericke (who collected the data on seed size selection), Laura Snyder (who measured harvest rates for Study 2), Beth Braker and Nick Waser (who helped to clarify our thinking and improve our prose), and an anonymous reviewer (whose extensive comments helped to improve the manuscript). The research was supported by intramural grants from the UC Riverside Academic Senate and NSF Grants DEB-8022164 and BSR-8407602 (to MVP), and by a UC undergraduate Riverside student grant (to RHP).

References

- Arthur W (1988) Mechanisms of coexistence. *Nature* 333:597
- Best T (1972) Mound development by a pioneer population of bannertailed kangaroo rats, *Dipodomys spectabilis baileyi* Goldman in eastern New Mexico. *Am Midl Nat* 87:201-206
- Brownlee KA (1965) Statistical Theory and Methodology in Science and Engineering. Second Edition. John Wiley & Sons, Inc. NY, USA
- Ghiselin J (1970) Edaphic control of habitat selection by kangaroo mice (*Microdipodops*) in three Nevadan populations. *Oecologia* 4:248-261
- Hardy R (1945) The influence of types of soil upon the local distribution of some mammals in southwestern Utah. *Ecological Monographs* 15:71-108
- Heinz KM (1983) Scratch-digging adaptations in kangaroo rats. *Am Zool* 23:890
- Holling CS (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canad Entomol* 91:293-320
- Hoover KD, Whitford WG, Flavill P (1977) Factors influencing the distributions of two species of *Perognathus*. *Ecology* 58:877-884
- Lawhon D, Hafner M (1981) Tactile discriminatory ability and foraging strategies in kangaroo rats and pocket mice (Rodentia: Heteromyidae). *Oecologia* 50:303-309

- Nikolai J, Bramble D (1983) Morphology, structure, and function in desert heteromyid rodents. *Great Bas Nat Mem* 7:44–63
- Price MV (1978) The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921
- Price MV (1983) Laboratory studies of seed size and species selection by heteromyid rodents. *Oecologia* 60:259–263
- Price MV, Endo PR (1989) Estimating the distribution and abundance of a cryptic species, *Dipodomys stephensi* (Rodentia: Heteromyidae), and implications for management. *Conservation Biology* (in press)
- Price MV, Heinz K (1984) Effects of body size, seed density, and soil characteristics on rates of seed harvest by heteromyid rodents. *Oecologia* 61:420–425
- Price MV, Longland WS (1989) Use of artificial seed patches by heteromyid rodents. *Journal of Mammalogy* (in press)
- Price MV, Reichman OJ (1987) Distribution of seeds in Sonoran desert soils: implications for heteromyid rodent foraging. *Ecology* 68:1797–1811
- Price MV, Waser NM (1985) Microhabitat use by heteromyid rodents: effects of artificial seed patches. *Ecology* 66:211–219
- Rosenzweig ML, Winakur J (1969) Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50: 558–571
- Rothhaupt KO (1988) Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature* 333:660–662
- SAS Institute (1982) SAS user's guide. Cary, NC, USA
- Schoener TW (1986) Mechanistic approaches to community ecology: a new reductionism? *Am Zool* 26:81–106
- Schroder G (1979) Foraging behavior and home range utilization of the bannertail kangaroo rat (*Dipodomys spectabilis*). *Ecology* 60:657–665
- Sokal RR, Rohlf FJ (1981) *Biometry*. W.H. Freeman, San Francisco, CA, USA
- Tilman D (1987) The importance of the mechanisms of interspecific competition. *Am Nat* 129:769–774
- Vleck D (1979) The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiol Zool* 52(2):122–136

Submitted March 11, 1989 / Accepted June 12, 1989