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Temporal and Spatial Patterns of Seed Collection
in Four Species of Heteromyid Rodents

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ABSTRACT

This research was designed to provide information on temporal and spatial variation in seed collection by four species of heteromyid rodents. During the summer of 1975, rodents (Dipodomys merriami, Perognathus amplus, P. baileyi, and P. penicillatus) were live-trapped on a series of Sonoran desert habitats at the Saguaro National Monument in southern Arizona. In 1976 and 1977 a single study area containing all four rodent species was live-trapped in order to provide information on microhabitat and seed use among coexisting species. Any seeds contained in the cheek pouches of the rodents were identified and their linear dimensions were measured. Microhabitats were quantified by enumeration of shrubs and measurement of their size.

The appearance and disappearance of certain seed species in the cheek pouches of all rodent species reflects the seasonal production of the seeds. The overlap in seed species collection by rodents is high when common and widespread plants (Larrea divaricata, Opuntia spp., Zinnia pumila, Psilotrophe cooperi, Carnegiea gigantea, Plantago spp., Erodium texanum, and Lesquerella gordonii) produce seeds.

The spatial component of seed utilization of rodents was examined from the viewpoint of seed size collection. Not only do rodent species collect seeds of different size among different habitats, but within a habitat locally coexisting rodent species collect seeds of different size.

As a test of the concept of the independent use of two resources (seed size and microhabitat) by coexisting species, seed size differences were compared to microhabitat differences between all pairs of heteromyid rodents. The results show that the difference between rodent species in the size of seeds they collect depends upon the difference in microhabitat selection of the species. Hence, these two components of the niche (seed size and microhabitat) of coexisting heteromyid rodents reduce to a single dimension.

Many desert rodents rely almost exclusively on the seed supply of habitats for their major source of energy (Beatley 1969; Reichman 1975). Brown (1975) has suggested that seed production is the key determinant of rodent species diversity in desert ecosystems. His strongest evidence is the correlation between long-term mean precipitation and the number of coexisting rodent species in Great Basin and Sonoran Desert habitats of Western North America.

Many environmental parameters probably determine which seeds are collected and stored by heteromyid rodents. In a recent paper (M'Closkey 1978), I noted that four species of heteromyid rodents differ in the size of seeds they collect independent of their body size. These differences are due to both the intrinsic differences among habitats in the production of seeds, and the unequal distribution of different rodent species among the habitats. In addition to differences in seed collection among rodent species there is much variation in seed species and seed size collection for a given species of rodent. Habitats differ in their seed supply (Reichman and Oberstein 1977), and rodent species occupying two or more habitats collect a greater variety of seeds than those restricted to fewer habitats. Brown (1975) shows that the same heteromyid species found in both the Great Basin and Sonoran Deserts collect seeds of different size. The variation in seed collection due to habitat is also confounded by temporal differences in seed production. The biannual pattern of precipitation in the Sonoran Desert results in a seasonal turnover of available seed species.

There are other determinants of the pattern of seed collection by heteromyid rodents. Brown and Davidson (1977) and Reichman (unpublished) have shown that other competing taxa, such as ants, may influence the supply of seeds available to rodents. Reichman and Oberstein (1977) provide experimental evidence that two species of heteromyid rodents, under laboratory conditions, differ in their ability to locate seeds of different distribution and density. This result suggests that topography and habitat structure, by determining seed distribution and numbers, may affect the foraging patterns of rodents and determine which species of rodents coexist.

The purpose of this study is to identify two major sources of variation in the pattern of seed collection in four species of coexisting heteromyid rodents. The temporal component of seed collection demonstrates the ability of rodents to collect seeds when they are produced by the plants. I illustrate this pattern by showing the turnover of certain seed species collected by the rodents. The second major source of variation in seed collection is due to differences in seed availability among habitats or microhabitats. I quantify this spatial pattern by comparing the seeds collected to the microhabitats (defined by shrub density and size) used by coexisting heteromyid rodents. My use of locally sympatric species gives an answer to the problem of the simultaneous use of two resources. Specifically, to what extent does the microhabitat utilization of coexisting species determine their pattern of seed collection?

STUDY AREA, FIELD METHODS, AND DATA ANALYSIS

The field work was conducted in southern Arizona at the Saguaro National Monument during the spring and summer of 1975 and 1976, and during the spring, 1977. The data in 1975 were collected by live-trapping rodents in a variety of habitats and collecting seeds from their cheek pouches. These data provided information on seed utilization by rodent species occupying two or more habitats. In 1976 and 1977 a single study plot (1.8 ha), on a lower bajada, was established on the basis of the trapping results from 1975. I selected this study area because all four species of heteromyid rodents (Dipodomys merriami, Perognathus amplus, P. baileyi, and P. penicillatus) could be caught together.

Depending on the microhabitat, perennial species included palo verde (Cercidium microphyllum) creosote (Larrea divaricata), mesquite (Prosopis juliflora), white thorn (Acacia constricta), white brittlebush (Encelia farinosa), paper flower (Psilotrophe cooperi), desert zinnia (Zinnia pumila), saguaro (Carnegiea gigantea), and prickly pear (Opuntia spp.). The large study plot provided information on the use of microhabitats by coexisting rodents. The home ranges of the four species overlapped and all species were caught at some trap stations. In order to quantify rodent microhabitats, measurements of shrub size (mean of shrub height, greatest and least crown diameters) and shrub density (number of shrubs per 100 m²) were performed at each of the 100 trap stations. This information, combined with data on seeds collected by the rodents, allows an evaluation of the simultaneous use of seeds and microhabitats.

For each rodent species, microhabitats were characterized by accumulating the trap-station records and their associated shrub measurements. An assumption inherent in the analysis is that rodent microhabitats can be represented by measurements of shrub size and density where the rodents are caught. Microhabitat differences among the rodent species were quantified by performing a multiple group discriminant analysis (Dixon 1973) on shrub size and shrub density. Seeds removed from rodent cheek pouches were recorded by species and size (geometric mean of the three major axes; M'Closkey 1978). Seed size differences between pairs of rodent species were quantified by analysis of variance (sum of squares, simultaneous test procedure), and the overlap in seed species collected by pairs of rodent species was computed using a symmetrical, information-theoretic index of overlap. An untested assumption is that either rodents do not eat seeds in the traps, or that the seeds are eaten in the proportion in which they are collected by the rodents. Overall, 6,700 trap-nights results in 524 captures of heteromyid rodents, and 194 seed samples from cheek pouches.

RESULTS

Temporal Patterns of Seed Collection

Due to reduced sample size caused by partitioning data, I treat the temporal and spatial patterns separately, though both are interdependent. The temporal pattern of production of different seeds is reflected by the seed species collected by rodents. Even within a season, definite patterns

of seed collection can be identified. Of the several dozen seed species collected by heteromyid rodents only a few are sufficiently abundant and widespread to show the increase, peak, and decline of seed collection. Although there are microhabitat differences among the rodent species, the plant species I discuss are found within the home ranges of all rodent species, and are at least partly accessible to all rodents. The seed species that I discuss were found in the cheek pouches of all four rodent species though not necessarily with equal frequency.

Annual plants generally appear and disappear in cheek pouches at well-defined times. For example, when I began seed collections in April, 100% of the cheek pouches contained Erodium texanum (storksbill) seeds. In May, only 46.7% of all cheek pouches contained Erodium and this dropped to 4.7% in June. From July through October examination of 130 pouch contents revealed no Erodium. Bladderpod (Lesquerella gordonii) shows a similar pattern of collection by rodents. It appears in cheek pouches in late April and disappears in early June. Some widespread annual plants such as Plantago spp. show interesting differences between years. In 1975, 93.3% of all Plantago records in cheek pouches were in June and July. However, in 1976 and 1977, 85.7% of all Plantago records occurred in April and May. Whatever reasons led to differences in Plantago availability between years, it was reflected in the collection of the seeds by rodents.

Seeds of some perennial plants are collected over a longer period of time than are seeds of annual plants. Many Opuntia spp. (prickly pear and cholla) produce seeds in late July. Maximum occurrence of Opuntia seeds in all cheek pouches is in September with a decline apparent in October

(Table 1). In June, prior to seed production, and in late October, it is difficult to find any Opuntia seeds beneath the plants. However, in August and September when rodents are collecting Opuntia it is easy to find concentrations of the seeds in the fallen fruit.

Creosote bush (Larrea divaricata) is a dominant plant in the Sonoran desert. The pattern of collection of creosote seeds by rodents is interesting because it reflects the production of seeds in both early summer and early fall (Table 2). Collection of creosote by all species of rodents is bimodal with August and September showing a marked reduction in seed collection. Desert zinnia (Zinnia pumila) shows a similar bimodal pattern of collection by rodents that corresponds with seed production. Zinnia seeds are found in cheek pouches in May and June, and again in September. No zinnia was recorded from cheek pouches in July and August.

The seeds of some species of perennial plants are very restricted in their time of occurrence in rodent cheek pouches. Eighty percent of all the records for paper flower (Psilotrophe cooperi) was obtained in June, and 88.9% of the samples of saguaro cactus (Carnegiea gigantea) occurred from June 28 to July 31 (1975-1977, inclusive). These temporal patterns illustrate the ability of heteromyid rodents to respond to current seed production. In addition, the rodents collect fresh plant material such as flowers, stems, and leaves. Eighteen percent of the cheek pouches that I examined contained fresh plant material.

Spatial Patterns of Seed Collection

One of the major sources of variation in seed collection by heteromyid rodents is due to habitat. Because habitats are defined by plant species

composition, they will differ in their production of seed species and the size range of available seeds. In addition, differences among rodent species in foraging and microhabitat selection will affect the collection of seeds. In this section I examine the difference in seed collection between rodent species and assess the importance of microhabitat in determining these differences.

In 1975, I trapped several habitat types including rocky slopes, sandy washes, and saguaro-palo verde and creosote associations. Each rodent species collected a large size range of seeds, and there were significant differences in the size of seeds collected by each species among the different habitats (Table 3). Dipodomys merriami and P. penicillatus occupy several habitats and they show large differences in seed size collection among habitats. Perognathus amplus shows the least variation in seed size collection; however, P. amplus was found in fewer habitats. The question still remained regarding differences in seed collection among rodent species occupying the same habitat. Therefore, in 1976 and 1977, I trapped the study area that revealed the highest diversity of rodent species during the 1975 field work (M'Closkey 1978). This design provided information on microhabitat and seed differences among locally coexisting species.

Apparently, even within the same habitat, rodent species collect seeds of different size ($F = 94.8, p < .001$); however, not all pairs of species show differences in seed size collection (Table 4). Dipodomys merriami and P. amplus collect seeds of the same size, as do P. baileyi and P. pennicillatus. All other pairwise combinations of species show

substantial differences in seed size collection. The difference noted in seed size collection by D. merriami and P. penicillatus (Table 4) departs from earlier reports (Brown and Lieberman 1973; Smigel and Rosenzweig 1974; M'Closkey 1978) on their similarity and emphasizes the role of habitat in determining seed utilization. Cheek pouch contents may also be compared by their seed species composition. Seed species overlap in cheek pouches varies from 0.33 to 0.64 with 0.48 as the mean overlap of the six pairwise comparisons.

In order to examine the relationship between seed collection and habitat selection, microhabitat differences between pairs of rodent species were quantified. The results of the discriminant analysis show significant microhabitat differences among species ($F = 20.1$, $p < .001$). Dipodomys merriami and P. amplus microhabitats are similar as are those of P. penicillatus and P. baileyi. Dipodomys merriami and P. penicillatus are the most different pair of species in their use of microhabitats. The microhabitat differences among the rodents are attributable to two variables measured in the field: the density of large shrubs (4-8 m in mean of shrub height, greatest and least crown diameter; $F = 25.8$, $p < 0.001$), and the volume (m^3 per $100 m^2$) of medium sized shrubs (2-4 m in mean of three linear dimensions; $F = 16.5$, $p < .001$). Perognathus penicillatus prefers microhabitats with more large shrubs, whereas D. merriami uses microhabitats lacking numerous large shrubs. In addition, P. baileyi and P. penicillatus utilize microhabitats with two to three times greater volume of medium sized shrubs than do D. merriami and P. amplus.

It is now possible to examine the relationship between seed differences and microhabitat differences among the six pairs of species. First, there is no correlation between the seed species overlap in cheek pouches and microhabitat differences between pairs of species. If all seeds are used in the computation of overlap, the correlation between seed species overlap and microhabitat separation is not significant ($r = 0.31$). If the presence or absence of seed species is used, in order to reduce the bias caused by very common seed species, the correlation is still not significant ($r = 0.45$). Therefore, it is not possible to predict seed species overlap between pairs of rodent species on the basis of differences in where they forage. Rodents collect the seeds of many plant species, whereas the microhabitats are defined by relatively few shrub species.

Depending on where they forage, rodents may encounter different size ranges of seeds. This could result from either the production of different sized seeds among microhabitats, or from the tendency for certain sized seeds to collect into specific microhabitats. The relationship between seed size differences and microhabitat differences for pairs of species is significant ($r = 0.92$, $p < .01$; Figure 1). It is important to note that it is not possible to predict the seed size that a given rodent species collects. Dipodomys merriami and P. amplus are very similar in seed size collection and microhabitat selection. This is also apparent for P. penicillatus and P. baileyi (Figure 1), but the former pair collects significantly smaller seeds than those collected by P. penicillatus and

P. baileyi. Hence, seed size collection, per se, does not occur. Rather, the differences in seed size collection may be attributed to differences in microhabitat selection by coexisting rodents.

DISCUSSION

This work was designed to observe differences in seed utilization among coexisting rodent species, and the extent to which these differences were due to microhabitat. The temporal pattern of collection of some seed species illustrates the similarity in seed utilization resulting from the production of widespread and abundant seeds. In contrast, the spatial pattern of seed collection suggests that differences in the size of seeds collected are based on microhabitat differences among the rodent species. There may be a component of seed size selection due to body size (Mares and Williams 1977), but it is highly variable (M'Closkey 1978).

Heteromyid rodents are opportunistic and they collect seasonally abundant seeds independent of seed size. The evidence for this is the rapid incorporation of specific seeds into cheek pouches, when seed production occurs. This was documented for several plant species. In April and May cheek pouches contained fresh seeds, flowers, and leaves of annual plants. Bladderpod (Lesquerella gordonii) appeared in cheek pouches as both single seeds and inflated silicles containing several seeds. Perennial plants illustrate similar patterns. In the spring and fall creosote fruits in cheek pouches were villous, indicating recent seed production; however, in the summer the seeds collected were without the hairy coat, suggesting that they had been on the ground for some time. Some seeds

(Opuntia spp.) appear in cheek pouches for longer periods of time, reflecting the prolonged production of seeds by these plants. However, the brief seed production of other perennials (saguaro) appears to be rapidly exhausted.

For the abundant plant species, similarity in seed collection among the rodents is apparent. However, there are two reasons for the observed difference in seed size collection among rodent species. The common seed species are not collected with equal frequency by all rodent species. In addition, there are seed species that are collected primarily by one or two of the rodent species. For example, zinnia and paper flower seeds were scarce in the cheek pouches of P. baileyi and P. penicillatus; Lotus spp. seeds were rare in the cheek pouches of P. baileyi; and saguaro seeds were not frequently collected by P. amplus. Second, differences in seed size collection among rodents reflect microhabitat selection.

These data also suggest that overlap in the seed species content of cheek pouches is probably not indicative of either the intensity of competition or resource scarcity. The ability of the rodents to utilize current seed production suggests that increased productivity may lead to convergence, rather than divergence, of diets. Seasonally abundant seed species are exploited by all rodent species and diet overlap probably increases. When seeds are scarce, diet diversity may increase as less suitable seeds are added to the diet. This may also increase diet overlap, but obviously for a different reason than when seeds are abundant. This point is conjectural, but there are changes in habitat specialization that should accompany changes in diet diversity (MacArthur and Pianka 1966).

There have been other investigations into the simultaneous exploitation of two or more resources (food, habitat, and time) by guilds of species (Brown and Lieberman 1973; Pianka 1973; Brown 1975; Pianka 1975; M'Closkey 1978). The question of interest has been to relate the ecological separation (or overlap) of species on one resource gradient (food size, for example) to the amount of separation between the same species on a second or third resource gradient. If species' exploitation of two or more resources vary independent of one another, the niche space is said to exhibit dimensionality (Schoener 1974) and a greater diversity of coexisting species may be permitted. However, if the exploitation of one resource is constrained by the species' exploitation of a second or third resource, then overall niche space is reduced and fewer species may coexist. Knowledge of species' utilization of major resources, such as habitat and food, has application in developing principles of the assembly of communities (Diamond 1975; M'Closkey 1978).

Earlier research on the exploitation of food, space, and time by similar species has not been a satisfactory test of the concept of niche dimensionality, because the ecological overlap among species was averaged over several different habitats or geographical localities. Differences or similarities in resource use among locally coexisting species were not evaluated. The present study provides evidence that the collection of seeds of different size is determined by differences in the microhabitats used by coexisting rodents. Future work could evaluate these results by experimental manipulation. For example, if rodents passively collect seeds of different size based on where they forage, then one can provide a seed

supply of the same size range among different microhabitats. The prediction is that the size of seeds collected by the different rodent species would be similar. If this were true, then future work could dispense with the size of seeds as an exploitable resource by heteromyid rodents.

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Figure Caption

Figure 1. The significant correlation ($r = 0.92$, $p < .01$) between seed size differences (analysis of variance by the sum of squares, simultaneous test procedure: SS-STP) and microhabitat differences (by discriminant function analysis: F) among four species of heteromyid rodents. Differences are depicted as pairwise contrasts. Key to the pairwise contrasts: M = D. merriami; A = P. amplus; B = P. baileyi; P = P. penicillatus.

HABITAT & SEED-SIZE DIFFERENCES

$r = 0.92$, $p < .01$

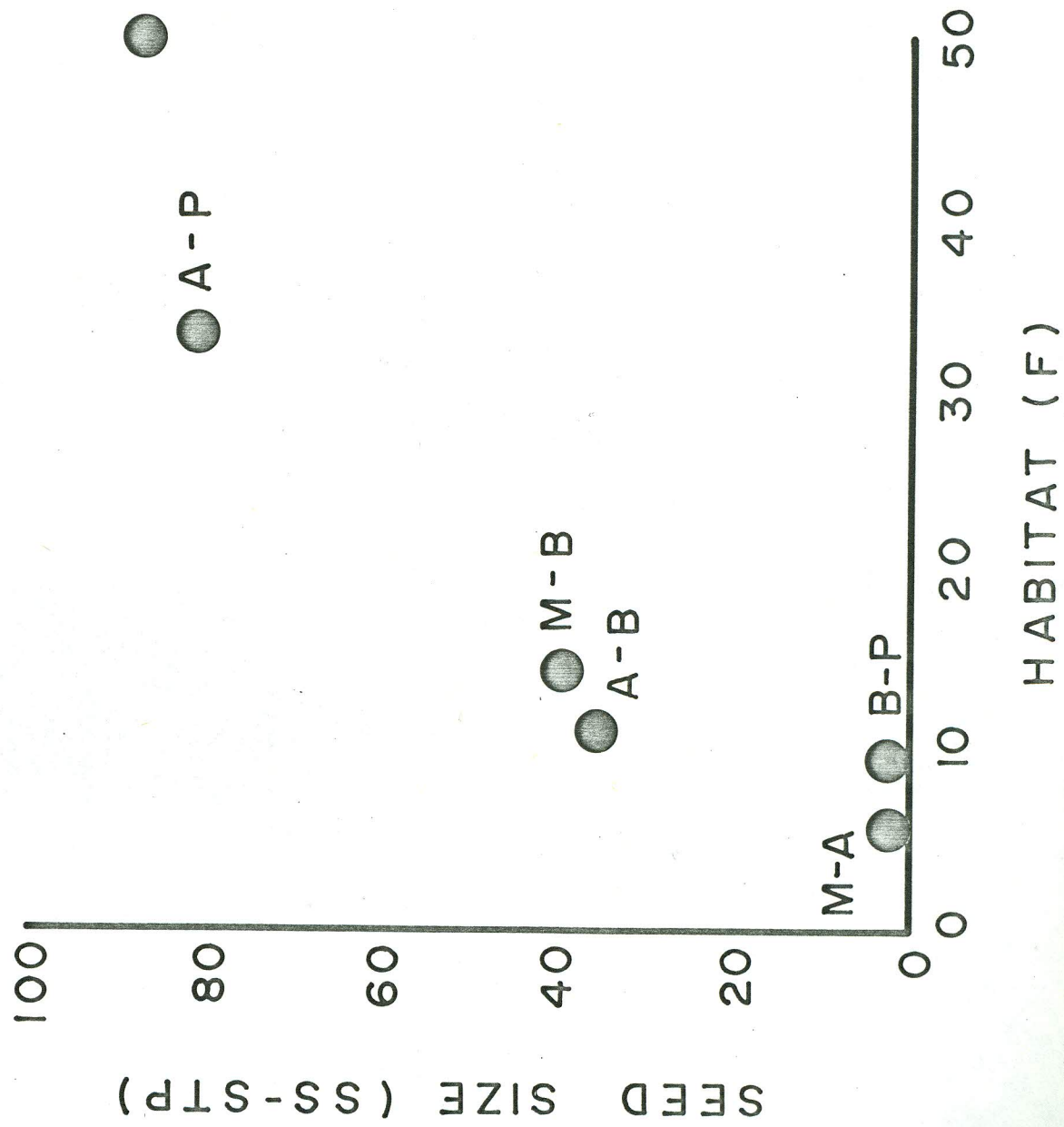


Table 1. The percent of cheek pouches of four species of heteromyid rodents containing seeds of prickly pear (Opuntia spp.).

Month	Rodent Species				All Species
	<u>D. merriami</u>	<u>P. amplus</u>	<u>P. baileyi</u>	<u>P. penicillatus</u>	
June	0	0	20.0	5.9	9.1
July	16.7	40.0	10.7	13.3	16.9
August	66.7	33.3	62.5	90.0	63.9
September	33.3	57.1	100	85.7	70.0
October	100	0	*	20.0	41.7
Number of Cheek Pouches	44	49	45	56	194

*No sample

Table 2. The percent of cheek pouches of four species of heteromyid rodents containing seeds of creosote (Larrea divaricata).

Month	Rodent Species				All Species
	<u>D. merriami</u>	<u>P. amplus</u>	<u>P. baileyi</u>	<u>P. penicillatus</u>	
April	*	0	0	100	16.7
May	22.2	40.0	*	0	26.7
June	80.0	18.2	40.0	23.5	37.2
July	50.0	70.0	46.4	33.3	47.7
August	16.7	44.4	0	10.0	18.2
September	0	14.3	0	42.9	20.0
October	50.0	66.7	*	60.0	58.3
Number of Cheek Pouches	44	49	45	56	194

*No sample

Table 3. Analysis of variance of seed size differences among the habitats used by four species of heteromyid rodents in the summer, 1975.

	Rodent Species			
	<u>D. merriami</u>	<u>P. amplius</u>	<u>P. baileyi</u>	<u>P. penicillatus</u>
Mean Square Among Habitats	27.62	0.22	4.54	10.30
Mean Square Within Habitats	0.39	0.07	0.28	0.31
F	70.70	3.21	16.18	33.20
p	< .001	.05-.10	< .001	< .001
Number of Cheek Pouches	13	9	32	28

Table 4. Mean and standard error of the size of seeds collected by four species of heteromyid rodents during the spring and summer, 1976 - 1977.

	Rodent Species			
	<u>D. merriami</u>	<u>P. amplius</u>	<u>P. baileyi</u>	<u>P. penicillatus</u>
Mean	1.45	1.49	2.18	2.23
Standard Error	.025	.018	.108	.076
Number of Cheek Pouches	31	40	13	28