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PLANT FOOD PREFERENCES OF TWO SYMPATRIC RODENTS
AND THEIR POTENTIAL IMPACT ON A GREAT BASIN
SHRUB COMMUNITY

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Ecology Center, Utah State University, Logan, Utah 84322
ABSTRACT

The plant food preferences and consumption rates of *Peromyscus maniculatus* (deer mice) and *Perognathus parvus* (Great Basin pocket mice) were determined in order to assess the rodents' impact on a 1-km² shrub-bunchgrass community in Curlew Valley, Utah, where plant and rodent densities were known. The rodents preferred seeds of the grass *Sitanion hystrix* which composed nearly 80% by weight of the diet of caged mice presented parts of native plants. The mice ate smaller amounts of *Chrysothamnus viscidiflorus* and *Halogeton glomeratus*. They ate little of the dominant shrubs (*Artemisia tridentata* and *Atriplex confertifolia*). Factors contributing to these results might be size of seeds, ease of husking seeds, ease of locating seeds and absence of secondary plant compounds. In trials in which mice were observed feeding on native plants in outdoor enclosures, 43% of feeding visits by *Peromyscus* and 60% by *Perognathus* were to *Sitanion* seeds. *Sitanion* plants received 22 and 9%, respectively, of the feeding visits of *Peromyscus* and *Perognathus*. The remainder of the visits were distributed among other plants in the enclosures. *Peromyscus* and *Perognathus* ate an average of 7.40 kcal/day and 8.30 kcal/day of plant parts, respectively. These amounts probably represent a majority of the animals' energetic requirements.

*Peromyscus* and *Perognathus* were the most common rodents on the study site (IBP Desert Biome Curlew Valley Validation Site). Their estimated consumption of plant parts probably did not affect plant community composition. Even if the rodents consumed only the least abundant plant food (*Halogeton* seeds), they would remove only 60% of the plant's estimated seed production. However, other activities of the rodents may affect plant distribution and composition.

INTRODUCTION

Biologists have conducted many studies on rodent food habits and plant productivity, but they have done little to relate one to the other. The data available suggest that rodents generally consume less than 2% of net primary productivity (Chew and Chew 1970; Golley 1960; Odum et al. 1962). However, Chew and Chew (1970) and Soholt (1973) have documented that rodent granivores may consume nearly 11% of available primary production in a desert community. Further, since rodents are selective in what they eat, their impact is not uniformly distributed among plant species. Soholt (1973) found that a desert rodent in one community ate 95% of the annual seed production of one plant species. Thus, the influence of rodents on plant communities may vary widely. More information is needed on the relationships between various kinds of rodents and plant communities before reliable generalizations can be made about the impact of rodents on plants. This study attempts to gather this information on two sympatric species, *Peromyscus maniculatus* and *Perognathus parvus*, in an arid lands shrub-bunchgrass community.

OBJECTIVES

1. To identify the major plant foods in the diets of *Perognathus parvus* and *Peromyscus maniculatus* from July to October.
2. To determine the daily rate of ingestion of each item by individual rodents.
3. To determine the rodents' food preferences by relating the composition of their diets to plant food abundance.
4. To estimate the plant food consumption of the two rodent populations.

METHODS

Determination of the rodents' plant food consumption and preferences was approached through two methods; presentation of known quantities of plant parts to individually caged mice, and observation of mice in large outdoor enclosures containing native vegetation. The study was conducted from July 1 to October 1, 1975, at the Green Canyon Ecology Research Station near Logan, Utah.

Every 10 to 15 days two to four mice (one or a pair of each species) were trapped in Sherman small mammal live traps and taken to the research station. Plants and plant parts were collected at the same time for later presentation to the mice. The animals and plants were collected near the US/IBP Desert Biome Curlew Valley southern shrub validation site, approximately 40 km southwest of Snowville, Utah. Vegetation of the trapping area consists of the perennial shrubs, big sagebrush (*Artemisia tridentata*), shadscale (*Atriplex confertifolia*) and low rabbitbrush (*Chrysothamnus viscidiflorus*); the bunchgrass *Sitanion hystrix*; and the annual forbs *Descurainia pinnata* and *Halogeton glomeratus* (Balph et al. 1974).

Entire plants were harvested and transplanted into 4-liter cans; seeds were harvested either directly from the plants or from depressions in the soil surface. Only the major plant species were collected. Plant phenology and the presence of seeds on the soil surface were also noted during trapping. The rodents and plants were transported to the research station immediately after collection.

Each mouse underwent a single two-trial series consisting of one consumption trial and one observation trial. Only those mice which survived an entire trial were included in the analyses of results. The trials' order was alternated with each set of captured mice.

Four *Peromyscus* and 12 *Perognathus* underwent the consumption trials. Single mice were placed in one of four terraria, 76 x 32 x 21 cm. Each terrarium contained approximately 3 liters of desert soil sifted through a 0.71-mm mesh wire screen, one 300-cm² can with paper
nesting material and one 10-ml syringe containing water. Two to four g of the following plant parts were presented every 24 hr between 1600 and 2000 hr: seeds of Sitanion; flower parts of Chrysothamnus; flower parts, stem tips and leaves of Artemisia and Halogeton; and fruits and leaves of Atriplex. Only parts of those plant species which composed more than 1% of total above-ground biomass in the shrub community were given to the mice (Table 1). At the end of each 24-hr period, the majority of the plant material remaining in the terraria was removed and replaced with fresh material. At the end of each three-day trial the plant material remaining in the terraria and nest was weighed; evidence of food caches was noted. The amount of plant material consumed was converted to air-dry weight by incorporating correction factors for evaporative water loss and end of a trial.

Although the manner in which the mice encountered items in the consumption trials differed from that in which they encountered plant items in the field, the method adopted was the only one which allowed accurate quantitative determinations of the rodents' consumption.

Observation trials were designed to provide an independent determination of the rodents' feeding patterns. In these trials single mice were placed in one of two enclosures, 2.5 m in diameter and constructed of 6-mm wire mesh (Fig. 1). A wire mesh floor prevented the mice from digging, and a sheet metal strip 25 cm wide prevented the mice from climbing out of the enclosures. Entire plants transplanted in 20 cm of soil and two nest cans with nesting material were placed in the enclosures; no water was provided. Mature plants (one Artemisia, one Atriplex, one Chrysothamnus, one clump of Sitanion, one group of four Halogeton and one group of five Descurainia) were arranged in a 2-m-diameter circle. The Descurainia was in the enclosures during the first two replications. It was replaced by a clump of Sitanion during replications three through five. Descurainia plants were not included after July 25 because all seeds had been cast and the plants were dry. Approximately 10 g of Sitanion seeds were placed under a wire basket in the enclosures' centers; the basket prevented seeds from blowing around the enclosures, but did not hinder access to the seeds. The plants were in pots to facilitate their replacement; grass seeds were replenished daily.

The location and activity of a mouse were recorded approximately every 10 sec for periods of 10 to 150 min between sunset and midnight; trials were five days long. The data analyzed and presented here include only those observations during which a mouse was engaged in food-related activities; criteria for food-related activities were based on descriptions by Eisenberg (1963) and by McCabe and Blanchard (1950): picking up a food item with the paws or mouth, chewing a food item or caching a food item. Observations were made from a 75-cm-high platform beside the enclosures. The mice were observed through a model 221 Javelin night viewing device with a 75 mm, f 1:1.4 lens. A 25-watt red lamp was required to provide adequate light. After each trial the enclosures were searched for evidence of food caches. Burrows constructed by the mice also were excavated and searched. Four Peromyscus and six Perognathus underwent observation trials.

The observation data were treated as follows. If a mouse fed in less than 50% of the observations taken during the first day of a trial, data for that day for that mouse were deleted. Similarly, if a mouse fed in less than 4% of observations during one period, data for that period were deleted from further analyses. The number of feeding visits by a mouse to each plant station was summed for a single mouse over an entire trial. Dividing the frequencies of feeding visits to a station by the correction factors in Table 2 corrected the frequencies for differences in area of the different stations. The relative frequencies of feeding visits to each plant station were then calculated by dividing the corrected number of visits to each station by the corrected number of visits to all stations.

Importance values and preference indices of the foods tested were calculated following the methods reviewed by Petrides (1975). The importance value of a food is the percentage of that food in the diet. Ivlev's electivity index (1961; in Siefert 1972) was used to determine preference or avoidance of food items: 

\[ EI = \frac{(r_i - p_i) - (r_j + p_j)}{(r_i + p_i) - (r_j + p_j)} \]

where \( r_i \) is the percentage of food item \( i \) in the diet, and \( p_i \) is the quantity of that item expressed as a percentage of the total quantity of food available. \( EI \) has a possible range from -1 to +1, indicating complete neglect of a food to complete selection, respectively. The quantity of plant food available to the rodents during the study period was assumed to equal: 1) the estimated seed reserves in the surface 4.7 cm of the soil; and 2) the estimated production of different plant parts. Although free-living rodents probably ingest plant items which were not presented in this study, the purpose here was to examine the rodents' diets and preferences only in relation to the shrub community's dominant plants. These estimates are based on a study of Atriplex confertifolia in Curlew Valley (Castó 1969) and on unpublished US/IBP Desert Biome data collected in Curlew Valley (Balph et al. 1974; Goodall et al. 1972; Klikoff and Freeman 1974; M. Merritt, pers. comm.; R. Shinn, pers. comm.). The data provided by these sources were collected periodically from 1967 through 1975; the estimates based on the data can thus be regarded only as approximations of available plant food between July and October 1975.

Estimates of energy intake of the mice during consumption trials were calculated from data on the energy content of the plant parts and from the quantities of different plant parts ingested. Figures of caloric content of plants were obtained from the laboratory of J. MacMahon, Utah State University, Logan. Estimates of consumption by populations of Peromyscus and Perognathus in the Curlew Valley shrub vegetation type are based on estimated population densities in Curlew Valley (R. D. Anderson, unpubl. manu.) and on daily ingestion rates of individual mice in the consumption trials.
Table 1. Estimated above-ground biomass of perennial and annual plants, and the percentage which each contributes to total above-ground biomass of the Curlew Valley sagebrush-shadscale-bunchgrass community

<table>
<thead>
<tr>
<th>Plant species and part</th>
<th>Above-ground biomass (kg/ha)</th>
<th>Percentage of total above-ground biomass (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sitanion hystrix</td>
<td>120</td>
<td>3</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td>70</td>
<td>2</td>
</tr>
<tr>
<td>Chrysothamnus viscidiflorus</td>
<td>104</td>
<td>3</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>192</td>
<td>35</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>218</td>
<td>57</td>
</tr>
<tr>
<td>Annuals other than</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>3553</td>
<td>101</td>
</tr>
</tbody>
</table>

Table 2. Correction factors for area occupied by plants and plant parts in outdoor enclosures

<table>
<thead>
<tr>
<th>Plant species and part</th>
<th>Area of plant (cm²)</th>
<th>Correction factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artemisia tridentata</td>
<td>1962</td>
<td>1.10</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>240</td>
<td>1.36</td>
</tr>
<tr>
<td>Chrysothamnus viscidiflorus</td>
<td>314</td>
<td>1.78</td>
</tr>
<tr>
<td>Descurainia pinnata</td>
<td>present only in</td>
<td></td>
</tr>
<tr>
<td>plants</td>
<td>replicates 1-2</td>
<td></td>
</tr>
<tr>
<td>Sitanion hystrix plants</td>
<td>177</td>
<td>1.00 for replicates 1-2</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td>240</td>
<td>1.36</td>
</tr>
<tr>
<td>Sitanion hystrix    seeds</td>
<td>344</td>
<td>2.00 for replicates 3-5</td>
</tr>
<tr>
<td>Total</td>
<td>2000</td>
<td>11.32</td>
</tr>
</tbody>
</table>

RESULTS

Results obtained from consumption trials (DSCODE A3UBL01) and observation trials (A3UBL02) were similar. Both experimental approaches indicated that of the plants presented, Sitanion hystrix seeds comprised the greatest portion of the diets of Perognathus parvus and Peromyscus maniculatus.

The 10 Perognathus which survived consumption trials ingested the different plants in significantly different amounts ($P < 0.01$, $F = 312, 4/45 df$). Tests of least significant difference (LSD) indicated that ingestion of Sitanion seeds was greater than ingestion of Halogeton, which was, in turn, greater than ingestion of Chrysothamnus, Atriplex and Artemisia (LSD, 95, 45 = 39.2 mg). Mean total daily consumption was 2014 mg (Table 3). Although subadult mice ingested a significantly greater amount per g body weight than did adults (175.4 and 118.6 mg/g mean body weight per day, respectively; $P < 0.01, t = 4.06, 8 df$), no significant differences were found in their total ingestion (1960 mg/day for subadults and 2040 mg/day for adults; $0.50 < P < .90, t = 0.51, 8 df$). Selection of food items did not differ between age groups ($0.50 < P < .75, F = 0.160, 1/40 df$), nor between sexes ($0.50 < P < .75, F = 0.225, 1/40 df$).

Peromyscus, like Perognathus, consumed greater amounts of Sitanion seed than of other plant foods (Table 3). Statistical analyses of consumption trial results were not possible for Peromyscus because only two of four individuals survived an entire trial. Mean total daily ingestion of the survivors was 1690 mg.

Dietary importance values calculated for the foods presented in the consumption trials appear in Table 4. Sitanion seeds comprised 77-78% of the rodents' experimental diets. Electivity indices for the plants are also given in Table 4. The indices can be regarded only as rough approximations due to the assumptions involved in estimating food availability. Both mouse species showed a strong preference for Sitanion seeds; whereas they neglected Atriplex and Artemisia, indicating that these three plant species were not consumed in proportion to their abundance in the habitat. Halogeton and Chrysothamnus were taken in approximate proportion to their abundance in Curlew.
Valley; the mice neither strongly preferred nor neglected these plants.

Neither Perognathus nor Peromyscus evidently cached food in the terraria. Although the mice husked Sitanion and Atriplex seeds in the nest cans (seed hulls were in the nests), the mice did not bury any plant parts in the cage soil.

Observation trials yielded results similar to those of the consumption trials. The greatest relative frequency of feeding visits was to Sitanion seeds (43% for Peromyscus and 69% for Perognathus, Table 5). Perognathus visited different plants at significantly different relative frequencies (P < .01, F = 23, 6/35 df). Differences in relative frequencies of visits to different plants by Peromyscus were significant between the .25 and .10 levels (F = 2.06, 6/12 df). The relative frequency of visits to Sitanion seeds was nearly double that of visits to any other plant. Although the level of significance is below that which is generally accepted, the mice did tend to prefer Sitanion seeds. Total feeding on Sitanion (calculated by summing the relative frequencies of visits to Sitanion seeds and plants) was 65 and 78% for Peromyscus and Perognathus, respectively.

The duration of feeding visits was highly variable, from 5 sec to 25 min. Despite this variability, the relative frequencies of visits remain a valid indicator of a mouse’s feeding patterns. That the relative frequency of visits of Perognathus to Sitanion seeds was significantly greater (LSD, .95 = 4.6%) than the frequencies of visits to other plants is thus conclusive evidence of a preference for Sitanion. Peromyscus followed a similar trend, even though the differences in relative frequencies of visits to different plants were significant below the .10 probability level.

During long feeding bouts, Perognathus filled their cheek pouches with Sitanion seeds. They then moved to another area, usually under a plant canopy, where they dug in the soil and deposited the seeds. Evidently, the pocket mice later returned to feed on the buried seeds and left Sitanion seed hulls on the soil surface. Peromyscus also left seed hulls, but no seed caches, in their burrows. Peromyscus did not exhibit caching behavior on the soil surface nor did their shallow burrows contain seed caches.
DISCUSSION

To assess the significance and implications of the experimental diets of *Perognathus parvus* and *Peromyscus maniculatus*, factors affecting dietary selection must first be considered. Second, the validity of applying the experimental results to free-living mice must be examined. Finally, if the application is valid, the significance of the rodents' plant diets in relationship to the community can be discussed.

The relationships of different influences on rodent plant diets are extremely complex. Characteristics of the food, such as its nutrient and physical properties, location, abundance and distribution, must be considered; as well as the characteristics of the feeding animals, such as their learning abilities and foraging patterns.

Some animals are capable of sensing the nutrient properties of foods. Laboratory rats maintained on vitamin-deficient diets preferred foods enriched in the missing vitamins when offered a choice of deficient and enriched foods (Rosin and Rodgers 1967). When presented an array of semipurified nutrients, rats selected a diet which maintained growth (Richter et al. 1938). Burns (1959) found that some kangaroo rats (*Heteromyidae*) sampled various commercial seeds, then changed their diets after several days. Cogshall (1928) reported that *Peromyscus maniculatus* ate some of every food of the 95 presented. Reichman (1975) found that many more items are present in rodents' diets than are abundant in their diets. These consumption patterns presumably form the bases for subsequent food selection.

Freeland and Janzen (1974, p. 128), in reviewing mammalian herbivory with respect to potentially harmful secondary plant compounds, noted that "animals can learn to eat or reject a particular food after a single trial that involves only minute amounts of the new item." However, presence of digestibility-reducing or toxic substances in a food does not automatically preclude inclusion of that food in the diet; an herbivore may possess or develop mechanisms for detoxification which allow consumption of such food.

Water content of food is another factor influencing diet which is especially critical to desert-inhabiting rodents. Heteromyids are capable of obtaining all required water from metabolic breakdown of carbohydrates (Schmidt-Neilsen and Schmidt-Neilsen 1950) and can live indefinitely on a diet of ripe seeds (Kritzman 1974). Free-living *Dipodomys deserti*, when given a choice of commercial seeds with a range of carbohydrate, oil and protein content, generally took those seeds high in carbohydrate and left those high in oil and protein (Lockard and Lockard 1971).

Size of food items and ease of processing food items are physical properties considered important in rodent diet selection. Different sizes of seeds were taken by two sympatric heteromyids of different body size; the larger seeds which formed the major part of the larger rodents' diet were not used by the smaller species (Smith 1942). Although Reynolds (1958, p. 120) noted that *Dipodomys merriami* selected large seeds more frequently than small seeds, he recognized that "factors other than size of seed influenced seed preference." In attempting to determine whether or not sympatric heteromyids should select seeds of differing size according to the rodents' body size, Rosenzweig and Sterner (1970) found that larger body size imparted the ability to husk seeds more rapidly; however, they could not determine whether or not the difference in husking speed influenced the rodents' seed diets. Seeds with thin coats (Lockard and Lockard 1971) and seeds without projections (Pulliam and Brand 1975) were generally preferred over seeds with thick seed hulls and projections.

Food availability is recognized as another major determinant of rodent diets. Blair (1937, p. 190) considered that "availability is the most important factor in the selection of food." French et al. (1974) noted shifts in heteromyids' diets from year to year which were related to favorability of the growing season. They suggested that the animals select preferred foods when plant productivity is high, and that other foods serve as reserves during periods of low plant productivity. Jameson (1952, p. 58) considered both availability and "inherent specific preferences" to be important in affecting the food habits of two omnivorous rodent species. The diets of omnivorous and granivorous rodents are known to change seasonally as different foods become available (Iverson 1967; Johnson 1961; Kritzman 1974).

Availability, as viewed by most authors, is made up of two aspects: food item abundance and food location. Increasing abundance of an existing item obviously increases its availability; likewise, items in the habitat which are unobtainable due to their location are not available to the animals. Seeds located deeper than 15-20 mm below the soil surface generally escaped detection by foraging heteromyids (Burns 1959). Small seeds (<1 mm diameter) covered by 1 cm of soil escaped detection by *Peromyscus maniculatus* and *Perognathus parvus* (Kritzman 1974). However, Lockard and Lockard (1971) found that *Dipodomys deserti* recovered 75-85% of bags containing 1 g of seeds buried 4 cm below the soil surface. The recovery rate dropped as seed depth increased, but evidence suggested that the rodents detected some seeds buried 20 cm deep. The contrasting results of the two studies may have been due to the manner of seed presentation or to differences between the species.

As the abundance of a food item increases, an animal encounters the food item more frequently. If an encounter with a preferred food is a positive reinforcement to a feeding animal, the reinforcement rate increases as the frequency of encounters increases. Within limits the increased reinforcement rate leads to greater effort to recover that item, as has been shown to occur in food-deprived laboratory rats (Perster and Skinner 1957). A rodent feeding on randomly spaced items receives reinforcement at a rate dependent on its search effort. The greater the search effort, the greater the frequency of reward. The reinforcement rate is not
totally dependent on the activities of the feeding rodent; it varies according to environmental factors such as wind, ground cover and plant distribution. Consequently, the food clumps are more conspicuous than single items, and the rodents feeding in field situations might react in a similar manner; their exploitation of a food might drop if the rate of encounter is very low. Clumped foods may modify these patterns. Pulliam (1974) predicts that when food clumps are more conspicuous than single items, animals will specialize on the clumped food.

To determine the validity of applying this study's results to free-living mice, the rodents' natural diets must be considered. Peromyscus maniculatus' diet in dry shrub communities consists of 40-60% seeds and fruits, 21-36% arthropods, 7-20% green plant material and 5-12% miscellaneous material (Jameson 1952; Johnson 1961; Kritzman 1974; Williams 1959). The diet of Perognathus species is made up of 33-80% seeds and fruits, 4-25% arthropods and 25-40% green plant material (French et al. 1974; Iverson 1967; Johnson 1961; Kritzman 1974). The composition of the rodents' diets in this study was assumed to be based on their consumption patterns in the field. The three-day trials were short enough to prevent changes in food preferences from unduly affecting the results.

The major portion of the diets of both species is composed of plant material; and although the lack of arthropods in the experimental diet may have influenced the results, the general pattern obtained should reflect that of free-living mice. The results discussed here are not assumed to hold for seasons or community types other than those covered by this study.

Artemisia tridentata (big sagebrush) flowers and leaves formed a very small part of Peromyscus' and Perognathus' experimental diets (Table 4). No evidence of consumption of Artemisia tridentata was presented for mice in big sagebrush communities in studies by Johnson (1961) and Williams (1959). The reason for such low consumption levels cannot be low availability. Artemisia forms 57% of the above-ground plant biomass in the Curlew Valley study area (Table 1). Its flower parts and stem tips are within reach of Peromyscus and Perognathus; both species were observed climbing in the enclosures. Caloric content (Table 6) and air-dry moisture content (23%) would not appear to deter ingestion. On these bases, one would expect a significant part of the diet to be composed of Artemisia. The presence of digestibility-reducing compounds in the plants is a plausible explanation for the rodents' avoidance of them. Peromyscus and Perognathus, as generalists, would not be expected to possess detoxification mechanisms effective against such compounds (Rhoades and Cates in press).

Table 6. Caloric content of plant and arthropod food items and the estimated caloric intake of those items by Peromyscus maniculatus and Perognathus parvus

<table>
<thead>
<tr>
<th>Plant species and part</th>
<th>Caloric content (kcal/g)</th>
<th>Total caloric content (kcal/rodent intake)</th>
<th>Caloric intake (kcal/day)</th>
<th>Peromyscus</th>
<th>Perognathus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artemisia tridentata</td>
<td>4.079</td>
<td>5.56</td>
<td>6.11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Millegion glomeratus</td>
<td>2.059</td>
<td>3.67</td>
<td>4.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pogonomyrnzus vloizzato</td>
<td>5.101</td>
<td>6.80</td>
<td>7.50</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atriplex confertifolif</td>
<td>5.011</td>
<td>6.00</td>
<td>6.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>5.150</td>
<td>7.28</td>
<td>8.08</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pogonomyrnzus vloizzato</td>
<td>5.101</td>
<td>6.80</td>
<td>7.50</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atriplex confertifolif</td>
<td>5.011</td>
<td>6.00</td>
<td>6.80</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>10.05</td>
<td>13.30</td>
<td>15.30</td>
<td>1.05</td>
<td>1.30</td>
</tr>
</tbody>
</table>

*See text for a description of the method used to estimate the amount of energy provided by arthropods.

Table 6 shows the caloric content of plant and arthropod food items and the estimated caloric intake of those items by Peromyscus maniculatus and Perognathus parvus.
seeds changed. The seeds' physical properties also contributed to their high ingestion levels by rodents. The seeds do not deter rodents from eating the plants.

* Halogeton glomeratus* formed 6 and 11% of *Peromyscus'* and *Perognathus'* diets, respectively. Johnson (1961) found a high incidence of *Halogeton* seeds and leaves in the stomachs of *Peromyscus*. Johnson did not analyze *Perognathus* stomach contents but reported that no *Halogeton* was found in the cheek pouches of pocket mice. *Halogeton* formed only 2% of the above-ground biomass in the Curlew Valley community; its scarcity may have caused a low level of consumption by mice. Its relative succulence (57% moisture content of air-dry weight) renders it a potential source of water. However, the presence of oxalate, a known toxin (Kingsbury 1964), may be the chief cause of the rodents' neglect of it. Although Rhoades and Cates (in press) hypothesized that low-intensity mechanisms for detoxification of compounds affecting internal organs may be prevalent among generalists, oxalate content may be high enough to limit consumption. Additionally, the ability to detoxify oxalates may not be developed in mice that do not often encounter the plant. Johnson (1961) suggested that the ingestion of other foods with *Halogeton* may have reduced the plant's toxicity. Also, the oxalate concentration may have been lower in the area of his study than on the Curlew Valley site. On the above bases, the primary causes of the small contribution by *Halogeton* to the rodents' diets appear to be the plant's relatively low availability, the presence of oxalate in the plant or a combination of these factors.

*Peromyscus'* and *Perognathus'* consumption of grass seed is well documented. The annual grass *Bromus tectorum* and the perennial *Agropyron cristatum* were frequently found in stomachs of both rodent species in southern Idaho (Johnson 1961). *Perognathus* relies heavily on grass seeds during periods when they are ripe (Kritzman 1974). In the present study, seeds of the bunchgrass *Sitanion hystrix* formed 77-78% of the rodents' diets. Although the grass formed only 3% of the community's above-ground biomass, *Sitanion* seeds offered a clumped, easily accessible resource throughout the study period. While seeds remained on the plants, mice in the enclosures were observed harvesting the seeds directly from the plants. They occasionally climbed a stalk and clipped off a seed head, but more frequently they stood on their hind legs and grasped a seed-bearing stalk near the base of the seed head. By mid-July, most *Sitanion* seeds had been cast and were blown into large clumps at shrub bases, thus offering a food resource within easy reach of the mice. Data presented in Table 5 show that the frequency of visits to *Sitanion* plants decreased, and that of visits to the clump of cast seeds increased, as the location of seeds changed. The seeds' physical properties also contributed to their high ingestion levels by rodents. The seeds are relatively large (2.5 mg) and do not require removal of a thick seed coat to determine whether or not a seed is present. Caloric content (Table 6) is comparable to that of other plants, but moisture content is low (1% of air-dry weight); no evidence of toxins is mentioned in the literature. Thus, the factors most probably contributing to the high consumption levels were high seed availability, large seed size, ease of detection and ease of husking.

The factors which appeared to be most important in influencing *Peromyscus'* and *Perognathus'* food selection were the presence or absence of secondary plant compounds, the availability of the food item and ease of processing. Another major factor which must be considered is the general foraging pattern of the mice. Although both species climbed in the enclosures, most of their foraging occurred on the ground. A similar pattern probably held in the field, where the most highly preferred food (*Sitanion* seeds) was on the soil surface or within several centimeters of it. The less preferred items either were difficult to process, were located in plant canopies higher than 40 cm or contained toxins or digestibility-reducers. Rodents whose foraging activities are usually oriented toward the soil surface, except for occasional forays into shrub canopies, should not be expected to select items which require climbing to obtain. These items are unfamiliar and thus may be sampled but not consumed in quantities.

The preference pattern observed in the present study may influence community plant composition. Pressure exerted on preferred species, if strong enough, probably affects the abundance of these species relative to that of nonpreferred plants. In assessing the rodents' potential impact on the major plants in the Curlew Valley shrub community, the following assumptions are made: 1) *Peromyscus'* diet is 60% seed and fruit, 25% arthropods and 15% green vegetation, and *Perognathus'* diet is 60% seed and fruit, 15% arthropods and 25% green vegetation (French et al. 1974; Iverson 1967; Johnson 1961; Kritzman 1974; Williams 1959); 2) the entire plant portion of the diet is composed of only one plant part (e.g., seed, leaf or flower) of a single species; and 3) the rate of consumption of plant material obtained in the present study is similar to that of free-living mice. This latter assumption is justified in that the mice lost weight, indicating that their rate of consumption was inadequate; the arthropod portion of the diet could provide the remainder. Using the caloric equivalents of items in the experimental diets, *Peromyscus'* average daily intake was 7.40 kcal/day (Table 6), generally lower than that cited by others: 8.97 kcal/day averaged over the entire year (Chew and Chew 1970); 11.85-13.05 kcal/day during summer months (Schreiber 1973); 13.77-14.86 kcal/day averaged over the entire year (Schreiber and Johnson 1972); 10.36 kcal/day averaged over the entire year (Turner 1970). *Perognathus'* intake averaged 8.30 kcal/day (Table 6), comparable to estimates by others: 10.8 kcal/day under laboratory conditions (French et al. 1974); 6.35-8.38 kcal/day averaged over the summer months (Schreiber 1973); 6.86-7.80 kcal/day averaged over the entire year (Schreiber and Johnson 1972); 8.47-10.78 kcal/day aver-
Table 7. Estimates of potential consumption by *Peromyscus maniculatus* and *Perognathus parvus* of plant parts in the Curlew Valley sagebrush-shadscale-bunchgrass community

<table>
<thead>
<tr>
<th>Plant species and part</th>
<th>Plant food available to rodents (kg/ha)</th>
<th>Total consumed* (kg/ha)</th>
<th>Percentage of available food</th>
<th>Rodent density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Rodent density</td>
<td></td>
<td>Low</td>
</tr>
<tr>
<td><em>Situation hybrida</em></td>
<td></td>
<td></td>
<td></td>
<td>32</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Fruit production total</td>
<td></td>
<td></td>
<td></td>
<td>70</td>
</tr>
<tr>
<td><em>Chrysothamnus viscidiflorus</em></td>
<td></td>
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<td></td>
<td>12</td>
</tr>
<tr>
<td>Flower production</td>
<td></td>
<td></td>
<td></td>
<td>24</td>
</tr>
<tr>
<td><em>Atriplex confertifolia</em></td>
<td></td>
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<tr>
<td>Soil seed reserves</td>
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<td></td>
<td>376</td>
</tr>
<tr>
<td>Seed production</td>
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<td></td>
<td></td>
<td>12</td>
</tr>
<tr>
<td>Seed + leaf production</td>
<td></td>
<td></td>
<td></td>
<td>246</td>
</tr>
</tbody>
</table>

*The total amount of each item consumed by the rodent populations was calculated as follows:

\[ A_i = \sum_r E_r \times F_i \times t, \]

where \( A_i \) is the total amount consumed of plant item \( i \) (kg/ha); \( D_i \) is the density of rodent species \( r \) (n/ha); \( E_i \) is the energy acquired through ingestion of plant material by species \( r \) (kcal/day); \( K_i \) is the caloric content of plant item \( i \) (kcal/g); and \( t \) is the duration of the study (93 days, from 1 July to 1 October)."

Aged over the entire year (Turner 1970). Ingestion of the normal ration of arthropod material would provide an additional 3.25 kcal/day to *Peromyscus* and 2.03 kcal/day to *Perognathus* to bring the total estimated intake to 10.82 kcal/day and 10.39 kcal/day, respectively. The estimate of arthropod ingestion was obtained as follows. If plant material comprises 75% of *Peromyscus*’ diet, and the mice ingest 1.69 g of plant material per day, their total intake equals 1.69/0.75 = 2.25 g/day. The estimated arthropod intake is 25% of the total intake, or 0.56 g/day. Using 5.8 kcal/g as the energy content of arthropods (Gibb 1957), the mice ingest approximately 3.25 kcal/day of arthropods. For *Perognathus*, whose assumed diet is 85% plant material, ingestion of 2.01 g/day of plant material results in an estimated 0.35 g/day or 2.03 kcal/day consumption of arthropods.

When these assumptions are applied to the Curlew Valley community where *Peromyscus* densities have been found to vary from 0.9-3.8/ha, and *Perognathus* densities from 0.5-9.5/ha (R. D. Anderson, unpubl. manus.), estimates of the potential consumption of available resources during the period of this study can be made (Table 7). It is apparent that of all plant parts available during the summer and early fall, only the seeds of *Atriplex* and *Halogeton* may be removed in significant amounts by *Peromyscus* and *Perognathus* (33% of *Atriplex* and 60% of *Halogeton*). At low densities, the mice could not have any appreciable impact on plant production. Other rodents regularly trapped on the study site -- the least chipmunk (*Eutamias minimus*) and the chisel-toothed kangaroo rat (*Dipodomys microps*) -- have been found to eat shadscale and *Halogeton* leaves and seeds fairly frequently (Johnson 1961; Kenagy 1972). If these rodents, which compose approximately half of the total rodent biomass (R. D. Anderson, unpubl. manus.), consume amounts of plant material equal to those consumed by *Peromyscus* and *Perognathus*, the resultant quantity consumed by all rodents still remains well below 100% of available plant food.

If the assumptions cited above are applied to the entire year, rodents consume more than 100% of the seed production of *Atriplex* and *Halogeton*, but consume less than 100% of other plant parts. The second assumption, which states that only one plant food is in the plant portion of the diet, most certainly does not hold. It was employed only to obtain an estimate of maximum consumption; actual consumption is lower. Insects and annual plants other than *Halogeton* make up greater portions of the diet during the spring and early summer than at other times of the year; thus, total demand for those plant items presented in this study is less than that estimated for the entire year. Consequently, rodent ingestion probably does not approach 100% of seed or leaf production in the sagebrush-shadscale-bunchgrass community during most years.

Chew and Chew (1970, p. 17) considered that the small mammals in a Sonoran Desert community were not food-limited. They suggested that the estimated removal of 85% of the seed crop by the animals may actually “increase the productivity of existing plants by reducing the competition among them.” Soholt (1973) found that 95% of the seed production of one annual plant was consumed by *Dipodomys merriami*. He estimated that a 30% reduction in the plant population would result from the high rate of ingestion, but the rodents probably could not effectively control the plants’ production; rainfall was cited as the major factor limiting annual plant production (Beatley 1969). In another study of *Dipodomys merriami*, Reynolds (1950) found that the kangaroo rats affect perennial grass densities of an Arizona range through their ingestion and caching of seeds; however, the direction of the effect (increased or decreased grass density) was related to the initial range conditions.

Other research has provided evidence that granivorous and omnivorous rodent populations are potentially food-limited (Smith 1971; French et al. 1974), but neither of these considered the effects of rodent consumption on plant composition.

Whether or not the rodents’ levels of consumption as estimated in this study actually produce changes in the plant composition was not determined. Inferences drawn from other research indicate they do not. Wilcott (1973) composed a model describing desert annual seed populations. One component in the model was the rate of seed loss through predation. He demonstrated that high rates of seed loss (80-90%) from the current crop will not result in extinction of the annuals if the loss of older seeds is not too high (generally below 50%). If these loss rates can be
survived by annual plants, then perennials, which do not depend on annual germination of seeds for survival, can probably withstand them.

Although *Peromyscus* and *Perognathus*’ consumption of plant material is, in itself, apparently not capable of limiting the dominant plants, the plant composition and distribution may be affected by activities other than ingestion; e.g., burrowing, caching of seeds (and less than 100% recovery of the caches), surface digging during foraging and removal of portions of plants which are not consumed (reviewed by Chew 1974; Golley 1973; Harper 1969; Janzen 1971). Rodents may slow nutrient turnover rates by binding up nutrients essential to the plants in a community, thus possibly limiting primary productivity. However, the effect of withholding nutrients may be offset by rodents’ burrowing activities which can bring leached nutrients back to the soil surface.

In conclusion, of the dominant plants in the Curlew Valley shrub community, *Sitanion hystrix* seeds composed the greatest proportion by weight of *Peromyscus*’ and *Perognathus*’ experimental diets. Observations of mice feeding in outdoor enclosures yielded results very similar to those obtained in the consumption trials. That the two experimental approaches gave similar results is an indication of their reliability.

The major reasons for the rodents' selection of grass seeds and relative neglect of other plant foods evidently are: 1) the large size of *Sitanion* seeds relative to the size of *Atriplex* seeds; 2) the ease with which *Sitanion* seeds are husked relative to the difficulty of husking *Atriplex* seeds; 3) the location of *Sitanion* seeds in the rodents' habitat; and 4) the apparent lack of toxins and digestion-reducers in *Sitanion* seeds and their presence in *Artemisia, Halogeton* and, possibly, *Chrysothamnius*.

The plant parts ingested by the rodents provided an average of 7.40 kcal/day to *Peromyscus* and 8.30 kcal/day to *Perognathus*. The majority of the rodents’ energy requirements, as estimated by other authors, was thus provided by the plant parts presented. Arthropods would normally contribute the remainder of the rodents’ energy requirements.

*Peromyscus*’ and *Perognathus*’ consumption of plant parts probably does not affect plant community composition. Even if the rodents were to concentrate their feeding efforts on the least abundant plant food (*Halogeton* seeds), only 60% of the estimated production would be removed during the period of this study. Based on inferences drawn from other studies, the rodents' removal of plant parts is not capable of limiting the plant populations. However, other activities of the rodents may affect plant distribution and composition in the community.

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LITERATURE CITED


