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Special Distribution

Interspecific Associations of Rodents
Peromyscus maniculatus, *Perognathus*
parvus, and *Spermophilus townsendi*
on the Arid Land Ecology Reserve
Examined by Diet Overlap and
Related Data

October 1975

Prepared for the U.S. Energy
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M. K. Johnson

October 1975

BATTELLE
Pacific Northwest Laboratories
Richland, Washington 99352

**INTERSPECIFIC ASSOCIATIONS OF PEROMYSCUS MANICULATUS,
PEROGNATHUS PARVUS, AND SPERMOPHILUS TOWNSENDI ON THE
ARID LAND ECOLOGY RESERVE EXAMINED BY DIET OVERLAP
AND RELATED DATA**

ABSTRACT

by

Mark Kenneth Johnson

Vegetational overlap of the diets of three species of rodents (Perognathus parvus, Peromyscus maniculatus, and Spermophilus townsendi) was examined during 1974 on the ALE (Arid Lands Ecology) Reserve in eastern Washington. Diet analysis results were compared with values of aboveground biomass of plant species on the study site in order to indicate food preferences of the animal species.

The S. townsendi diet overlapped minimally with the diets of the other species. Its major food item was determined to be Poa sandbergii which constituted 49% of the relative density of stomach samples. More overlap was observed in the diets of P. parvus and P. maniculatus. Major food items included Bromus tectorum, Descurainia pinnata, and insect materials. Comparison of caloric needs of the species and the caloric supply in the environment suggest that none of the dietary items were limiting during the study period.

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INTRODUCTION

Interspecific competition is one of the most complex of phenomena investigated by the ecologist. It also is one of the most difficult to demonstrate under natural conditions. Grant (1972) states that there is a lack of evidence clearly demonstrating competition between vertebrate species. The evidence is stronger for competition for space than for food.

Space and food requirements of each species should be closely examined. Space, should be examined because there are many biological, psychological, and sociological events that are determined or directed by population densities and, food, because utilizable energy is the fundamental requirement for existence.

The word competition, implies a conflict. Because it is possible to keep social distance without direct confrontation (Esser, 1971), competition based on space availability is considered by myself to have a minimal effect on the study site. This may not be the situation.

There must be, however, something to compete for if competition exists. The primary consideration then, is food. Hairston et al. (1960) believe that herbivores do not directly compete for food. However, this has not been demonstrated.

It is not enough to know that the caloric content of the botanical biomass of an area exceeds the needs of the consumer population. A quantitative measure of the preferred food items of species in a given location is needed in order to answer questions of adaptation which play an intimate role in species competition. Because many of the most intricate adaptations are physiological rather than anatomical and often directly relate to the ability of a species to derive energy from available food, investigations which can indicate digestion efficiencies of botanical food items by species are desirable.

The three most abundant species of small mammals on the Arid Lands Ecology (ALE) Reserve, Benton County, Washington, are Perognathus parvus (granivore), Peromyscus maniculatus (omnivore), and Spermophilus townsendi (herbivore) (O'Farrell et al. 1974). Though the diets of these species are separated into large categories indicating a lack of competition, the diets of these species do overlap as shown by other studies in the area (Kritzman, 1971). Whether the diets truly overlap has not been determined on the study site. Therefore, it is appropriate that this question be answered quantitatively.

It is the purpose of this study to investigate the degree of competition of the three species on the study site with respect to the botanical food items eaten by these species. The importance of any overlap is demonstrated by food preferences as evaluated from item frequencies in the diets

and relative abundance of food items in the environment. Competition by dietary overlap may then be indicated but not unequivocally demonstrated because a complete food-habits analysis has not been made. By the criterion of Voth (1968) a complete food-habits study should include behavioral as well as dietary analysis. The behavior of the species toward the food remains another project for the ethologist.

Finally, these data will be reviewed with respect to other findings on the site, and the effects of the three species upon one another will be discussed.

REVIEW OF SPECIES INVOLVED

Peromyscus

Peromyscus maniculatus is a cricetid rodent with average measurements 121-222 mm (total length), 46-123 mm (tail length), 17-25 mm (right hind foot length), and 12-20 mm (ear length) (Hall and Kelson, 1959). The species ranges over all of North America. The subspecies, gambeli, was described by Baird in 1858; the type locality is Monterey, California; the distribution is extensive, north through eastern Oregon and Washington.

The omnivorous nature of the species has been noted (Williams, 1959) (Whitaker, 1963, 1966) (Flake, 1973). Depending upon the season and locale, deer mouse stomachs have been found to contain as much as 50% animal matter (Jameson, 1952). Flake (1973) reports that the highest concentrations of animal matter occur in spring and early summer with the lowest amounts in mid-winter. Kritzman's (1970) data substantiate these findings. Various seeds were found to comprise a considerable part of the diet in both studies.

Perognathus

Perognathus parvus is a heteromyid rodent with average measurements 148-198 mm (total length), 77-107 mm (tail length), and 19-27 mm (right hind foot length).

The subspecies, yakimensis, was described by Broadbents in 1954; the type locality is Rocky Flat, Yakima County, Washington. It ranges west of the Columbia River from Ellensburg south to Dallesport.

Perognathus has been reported to be essentially granivorous (Von Bloeker, 1931) (Smith, 1942) (Bailey, 1939) (Dice, 1919) (Forbes, 1962). However, many have reported insect materials in stomachs and cheek pouches ranging from small amounts (Arnold, 1942) (Blair, 1937) to considerable amounts (Jameson, 1954) (Gentry and Smith, 1968). Green matter has also been found to be present in considerable amounts (Reynolds and Haskell, 1949) (Von Bloeker, 1932).

Previous observations of the species on the ALE reserve have been performed by Kritzman (1970) and by Schreiber (1973). Kritzman reported seed, insect, and green materials present in the stomachs. Insect material was found in greatest amounts in the spring, with seeds highest in the fall. The relative amount of green material remained stable over the study period. Schreiber examined cheek pouches and found them to contain mostly seeds. Of these, Bromus and Eriogonum were the main constituents.

Spermophilus

Spermophilus townsendi is a sciurid rodent with measurements 167-271 mm (total length), 32-72 mm (tail length), and 29-38 mm (right hind foot length)

(Hall and Kelson, 1959). The type specimen, subspecies townsendi, is from the west side of the Columbia River 300 miles from its mouth. It ranges from Kennewick north to Ellensburg in Washington west of the Columbia River.

The diets of ground squirrels is reported to contain mainly green vegetation. It has been reported that ground squirrels eat meat and actively prey on other species (Cook and Henry, 1940) (Sowls, 1948) (Errington, 1938) (Martin, 1935) (Geist, 1933) (Bailey, 1923). Insects have also been reported to make up a large portion of ground squirrel diets (Bailey, 1931) (Moore, 1930) (Flake, 1973).

In the Sonoran desert region, the diets analyzed consisted of grasses and clover (Schmidt, 1931). Evans and Holdenried (1943) report three species of Bromus, two species of Festuca, and one species of Sisymbrium.

There are few studies of Spermophilus townsendi diets. Alcorn (1938) reported that the species exists mainly on green vegetation. Davis (1949) reported several species of vegetation including wild mustard. Scheffer (1941) related the seasonal activity of the species to the seasonal abundance of green vegetation.

No quantitative studies of the diets of the species have heretofore been carried out, and no qualitative analysis has been made on the species in the study area.

CONCEPTS OF INTERSPECIFIC COMPETITION

"Interspecific competition is any interaction between two or more species populations which adversely affects their growth and survival."

- Odum, 1971

It is of consequence to the understanding of the interspecific associations that the given definition be considered to be only one possible association between two species in a community. The idea stems from Gause's theorem which states that no two species may occupy exactly the same niche at any time or place (Gause, 1965).

Mathematical Models

Lotka (1925) expressed the relationships between populations of two species in mathematical terms. Using simultaneous differential equations, he predicted that one of two species in an isolated environment would be eliminated. These expressions follow Gause's theorem. Brian (1956) approached the problem of analysis by dividing interspecies competition into two components. These were exploitation and interference. Exploitation involved the ability of a species population to obtain vacant resources. Interference involved the ability of a species population to inhibit another species population. In an expansion of mathematical models, Slatkin (1974) has shown that the interaction with a predator may allow both of two competing species to coexist by lowering the populations of one or both species. Cole (1957) states that the amount of association between species should be measured by their frequency of co-occurrence in a series of samples. This is not a measure of competition. It is simply a measure of association. It is doubtful that competition between species can be measured mathematically since the formulae do not differentiate between the specific commodities of the competition. Other investigators have used the approach of Cole. According to Bray (1956):

"if species are indifferent to each other, they will occur together by chance."

Any deviation of the mathematical expressions for random associations determined from areas of overlap indicate that interspecies relations exist. These may, however, be more closely related to community effects rather than direct relations between the species concerned.

Evidence

The real occurrence of interspecies competition in natural situations is yet to be well-demonstrated. Frank (1957) writes:

"Direct proof that a species is, in fact, restricted in its prevalence by the presence of predators is hard to come by."

Of the laboratory demonstrations that have been made, a classical study is that of Park (1962). In his experiments with flour beetles, two species of Tribolium were introduced into an isolated environment which resulted in the eventual elimination of one of the species. Park believed that the result was caused by competition for food. Other examples of competition for food in isolated environments are those presented by Gause (1965) and Frank (1952). Strong evidence that competition for space exists between Chthamalus and Balanus was reported by Connell (1961). It was concluded that the mortality of Chthamalus increased as the population of Balanus increased, and that this was not due to other factors such as the concentration of nutrients or wave shock.

Hence, there is strong evidence that competition for food and space exists in limited environments, but the mechanism of attack of one organism upon another has not yet been elucidated. Griggs (1956) said:

"We have as yet little inkling as to the character of the weapons each species brings to the contest."

When experimentation turns from the simplified associations discussed above to the more complex communities, the argument for effects due to interspecies competition becomes weaker. Excellent reviews of the subject are found in Grant (1972), Orians and Willson (1964) and DeBach (1966).

Cases have been reported involving the introduction of a competitor into an area (Keever, 1955) (Holmgren, 1956) (Franklin, et al. 1972). In these situations invaders are choking out native species. Though these are certainly examples of interspecies competition, they are dramatic events or catastrophes often due to man's intervention in the natural environment which otherwise would not have occurred.

Few field studies have been done in which actual manipulations of the species have been performed. In one of these, (Myton, 1974) the removal by trapping of Peromyscus leucopus did not result in the movements of members of other species into the area. This seems to conflict with theories of competition but perhaps is only evidence for niche separations of the species involved.

It is a waste of energy that a species should actively compete with another species. It is reasonable to suppose that when competitive pressures occur, species diverge through evolutionary mechanisms to wider niche separations such that Gause's theorem is obeyed. Orians and Willson (1964) report that most cases of observable interspecies competition in birds occur in limited environments where the opportunity to diverge is minimal.

A species must naturally be added to a community by encroachment (addition of the species range) which comes about by the expression of genetic potential allowing some individuals of the encroaching population to maintain larger home ranges than the average for the species. This is a very slow process and occurs such that its demonstration requires the monitoring of specific events over years, decades, or centuries.

If Gause's theorem is correct, strenuous interspecific competition does not exist under "natural" conditions without the catastrophe of man's intervention. The more highly evolved communities (vertebrate associations) tend to follow these assumptions.

Other authors have suggested that competition exists as an unstable phenomenon which increases selective pressures causing evolution toward new specializations. This occurs as a consequence of over-reproduction, since, some resource has become limiting (Allee, et al., 1949).

METHOD

The Study Site

The study area is located 15 miles northwest of Richland, Washington on the Arid Land Ecology (ALE) Reserve. The ALE reserve comprises about 120 square miles of the Energy Research Development Administration's (ERDA) Hanford Works Reservation (Fig. 1). It is bound on the east by highway 240 and on the west by the crest of Rattlesnake Hills at 46 degrees 30 minutes north latitude and 119 degrees 40 minutes west longitude. Forty acres of the reserve have been set aside as a coordinating study site of the United States International Biological Program (IBP) Grasslands Biome Project. The specific collection area for this study was chosen to approximate the vegetational structure of the IBP plots at an elevation of 1200 feet in order that comparisons with existing data could be made.

The study site is a portion of the shrub-steppe of Eastern Washington. The average annual rainfall is 6.74 inches, and the average maximum temperature is 91.7 degrees F during July which is one of the warmest months (Franklin, et al. 1972). Most of the precipitation occurs during the winter months.

The soil in the study area is composed of Ritzville silt loams as are the IBP plots (Hajak, 1966) (O'Farrell, et al. 1974).

Vegetation

A survey of relative percent of aboveground biomass of all major plant species harvested in 1972 on the IBP plot is outlined in Table 1.

The dominant vegetational association found on the study site is that of Artemisia tridentata/Agropyron spicatum (Daubenmire, 1970). This association generally occurs at above 1000 foot elevations. Artemisia tridentata (big sage) comprised an average of 43.2% of the aboveground biomass during the 1972 season, and the Agropyron spicatum (Blue-bunch wheatgrass) accounted for an average of 31.1% of the aboveground biomass during the same season.

Mammals

Seven species of small mammals were trapped on the IBP site in 1972. These were: Perognathus parvus (Great Basin pocket mouse), Peromyscus maniculatus (deer mouse), Spermophilus townsendi (Townsend's ground squirrel), Onychomys leucogaster (northern grasshopper mouse), Lagurus curtatus (sagebrush vole), Sylvilagus nuttalli (cottontail rabbit), and Thomomys talpoides (northern pocket gopher) (O'Farrell et al. 1974). Perognathus was the most numerous with 11-18/hectare. Spermophilus, when active, accounted for the highest biomass of any species.

FIGURE 1. The Hanford Reserve and Surrounding Study Areas

TABLE 1. Relative Percent of Botanical Species Aboveground Biomass 1972. Data computed from Rickard *et al.* (1972). Plant nomenclature is after Hitchcock and Cronquist (1973).

Plant Species Scientific Name	Common Name	Harvest Dates				
		3/6	3/27	4/17	5/8	5/30
Perennial grasses						
<u>Agropyron spicatum</u>	Bluebunch wheatgrass	6.8	39.2	26.9	26.9	56.3
<u>Poa cusickii</u>	Cusicki's bluegrass	1.0	10.2	2.4	0.8	2.1
<u>Poa sandbergii</u>	Sandburg's bluegrass	11.7	21.8	7.3	0.1	1.2
<u>Stipa thurberiana</u>	Needle grass	0.1	2.7	---	1.0	0.0
Half-shrubs						
<u>Antennaria dimorpha</u>	Pussytoes	3.3	2.4	3.1	1.2	13.5
<u>Erigeron filifolius</u>	Erigeron	4.2	4.1	2.0	4.4	3.4
<u>Phlox longifolia</u>	Phlox	0.1	3.4	0.1	2.2	0.6
Perennial forbes						
<u>Astragalus purshii</u>	Loco weed	1.6	0.1	0.1	2.6	0.4
<u>Brodiaea douglasii</u>	Wild hyacinth	---	---	---	---	0.5
<u>Calochortus macrocarpus</u>	Sego lily	1.3	0.2	0.0	0.1	0.1
<u>Lomatium macrocarpum</u>	Lomatium	2.0	0.7	---	0.2	0.0
<u>Crepis atrabarba</u>	Hawks beard	---	0.6	0.3	1.4	5.2
<u>Lupinus laxiflorus</u>	Lupine	---	0.4	0.4	0.9	0.1
Winter annuals						
<u>Descurainia pinnata</u>	Tansy mustard	---	---	---	---	---
<u>Draba verna</u>	Draba	---	---	---	---	---
<u>Bromus tectorum</u>	Cheatgrass	---	---	---	---	---
<u>Festuca octoflora</u>	Six weeks Fescue	---	---	2.4	1.1	---
Shrubs						
<u>Artemisia tridentata</u>	Big sage	71.0	16.4	56.0	56.3	16.4
Leaves		4.6	3.4	39.1	11.4	15.7
Wood		66.5	13.0	16.9	44.9	0.1

--- equals trace

Other terrestrial mammals commonly found on the reserve are Lynx rufus (bobcat), Taxidea taxus (badger), Canis latrans (coyote), Odocoileus hemionus (mule deer), Reithrodontomys megalotis (western harvest mouse), Sorex vagrans (vagrant shrew), Lepus californicus (blacktail jackrabbit), and Eutamias minimus (least chipmunk).

Management

Prior to 1943, sheep and cattle grazed in the area, but no grazing has been allowed since that time and the area is now fenced. Activities on the reserve include research by students of several universities and personnel of Battelle Northwest Laboratories. The area is administered for the ERDA (Energy Research Development Administration--formerly Atomic Energy Commission) by Battelle-Northwest.

Trapping

Sherman live traps, Havahart #1 traps, and Victor snap traps were used during the course of the study. The traps were placed on lines or grids and distributed at 10 meter intervals. The trapping schedule and results are given in Table 2.

The traps were baited with Northrup commercial mixed bird seed and oatmeal with a small amount of dacron¹ fibre placed in the rear of each trap. The traps were checked each morning before 8:00 A.M. Havahart traps set for ground squirrels were baited with pieces of carrot and checked several times during the day. Often, they were watched from a distance until an animal was caught.

Upon capture, an animal was shaken into a plastic bag where it could easily be manipulated. It was then returned to the field lab, sacrificed by asphyxiation, and frozen until examined and prepared for study. Later specimens were thawed, study skins made, and gut contents removed. Stomachs were fixed in formaldehyde and preserved in 70% ethanol. Stomach contents of all specimens and caecal contents and feces (taken from the large intestine) of 7 Spermophilus were removed and dried in an oven at 55°C for 48 hours or longer.

Total, tail, right hind foot, right ear lengths and body weights were recorded on all specimens and museum specimens were prepared. On many Perognathus and Peromyscus only the skulls were saved.

Diet Analysis

Methods commonly used in the study of mammalian food habits include scat, stomach, and cheek pouch analysis. Also, direct observations, inspections of feeding areas, and examinations of food items may be used.

¹Dacron is a registered Dupont trade name.

TABLE 2. Trapping Schedule and Results

Date	No. of Traps	Type of Trap	No. Animals Caught Species	Percent Success
2/8/74	50	Sherman	0	0
2/9/74	50	Sherman	0	0
3/1/74	125	Sherman	5 <u>Peromyscus</u> 4 <u>Perognathus</u>	7.2
	25	Victor	0	0
3/2/74	225	Sherman	9 <u>Peromyscus</u> 7 <u>Perognathus</u>	7.1
	25	Victor	0	0
3/15/74	100	Sherman	5 <u>Peromyscus</u> 7 <u>Perognathus</u>	12.0
3/16/74	150	Sherman	6 <u>Peromyscus</u> 10 <u>Perognathus</u>	10.6
	15	Havahart	1 <u>Spermophilus</u>	6.6
3/29/74	100	Sherman	6 <u>Peromyscus</u> 2 <u>Perognathus</u>	8
	50	Sherman (no dacron)	0	0
	10	Victor	0	0
	8	Havahart	0	0
3/30/74	100	Sherman	12 <u>Peromyscus</u> 1 <u>Perognathus</u>	13
	50	Sherman (no dacron)	0	0
	10	Victor	0	0
	8	Havahart	3 <u>Peromyscus</u>	37.5
4/12/74	10	Havahart	0	0
	12	Victor	0	0
4/26/74	100	Sherman	3 <u>Peromyscus</u> 2 <u>Perognathus</u>	5
	20	Havahart	1 <u>Spermophilus</u>	5
	12	Victor	0	0
4/27/74	100	Sherman	3 <u>Peromyscus</u> 2 <u>Perognathus</u>	5
	20	Havahart	4 <u>Spermophilus</u>	20
	12	Victor	0	0
5/10/74	75	Sherman	7 <u>Peromyscus</u> 3 <u>Perognathus</u>	13.3
	15	Havahart	1 <u>Spermophilus</u>	6.6
5/11/74	75	Sherman	4 <u>Peromyscus</u> 3 <u>Perognathus</u>	9.7
	15	Havahart	2 <u>Spermophilus</u>	13.2
6/21/74	25	Sherman	0	0
6/22/74	100	Sherman	1 <u>Perognathus</u>	1
7/29/74	100	Sherman	0	0
7/30/74	200	Sherman	1 <u>Peromyscus</u> 1 <u>Perognathus</u>	1
7/31/74	200	Sherman	0	0
8/1/74	200	Sherman	0	0
8/2/74	55	Sherman	1 <u>Peromyscus</u> 2 <u>Perognathus</u>	5.5
8/3/74	105	Sherman	0	0
8/4/74	105	Sherman	1 <u>Perognathus</u>	1.0
8/5/74	105	Sherman	0	0

The first formal essay on scatology was written by Seton (1925). He pointed out that scats could be used for species identification. Since then, collections of scats of many species have been made, and scatology has become a science in itself. The potential of scat analysis as a method of food-habit study has been most often employed in the study of carnivore food habits. Since the food has already passed through the digestive tract, the data may be unreliable. This was discussed by Murie (1946) when he fed 48 mice to coyotes and only accounted for 25 mice in the scats.

Stomach analysis remains the best method for the diet analysis of most species. This opinion was strongly expressed by Hamilton (1951) when he said:

"Stomach analyses give a far better clue to the dietary of a species than do fecal remnants, since the food remains are less digested and more readily determined."

The granivorous species present a special problem since their diets consist almost exclusively of seeds. These are husked before eating leaving only the endosperm to be found in the stomach. The endosperm forms a soft mass in the stomach which contains few recognizable fragments. Therefore, food-habits analysis of granivorous species have relied upon cheek-pouch analysis (Dice, 1919) (Von Bloeker, 1932) (Arnold, 1942) (Reynolds and Haskell, 1949) (Kritzman, 1970), burrow analysis (Bailey, 1939) (Blair, 1937), and laboratory studies.

Dalke and Sime (1941) used observation of feeding and inspection of feeding areas along with stomach analysis in their examination of cottontail food-habits. An attempt was made to quantify the diet analysis of muskrats by inspection of food platforms and analysis of scraps (Takos, 1947).

The results of most studies are qualitative determinations. This is due to the difficulties of species identification when a wide variety of foods are eaten. One of the most rigorous attempts at precision was done by Whitaker (1966). Seeds were identified to species and arthropods were identified to genus. In most studies green vegetation has been listed only as such, and only rarely segregated into plant organ or plant type categories (Vaughan, 1967).

The method chosen for my research was that of stomach analysis with species identification by plant histological methods. Using the same micro-technique, feces of S. townsendi were also analyzed. This method was chosen because animals of the species studied are readily acquired by trapping and because the food items of most interest were botanical species.

In addition, 12 stomachs of P. parvus donated by Virginia Uresk were examined by the same procedure to determine the percent composition of food that was green vegetation.

The histological method of diet analysis has been well-defined since Baumgartner and Martin (1939) reported that plant cell "ghosts" or larger fragments of plant tissue epidermis found in stomachs could be used to identify botanical food items to species. Their method involved 1) permanent reference slides of plant epidermis, and 2) temporary mounts of items from the food material. The technique was later reviewed and refined by Dusi (1949), by Sparks and Malechek (1968), and most recently by Cavender and Hansen (1970).

The basic technique used in this work has been proposed by Hansen and Flinders (1969) and Cavender and Hansen (1970).

The ability to recognize epidermal fragments of all plant species was acquired before analysis of the slides was performed. Test slides were made of reference species mixtures. The ability to recognize each test species was determined using Kulczynski's expression for similarity (Oosting, 1956):

$$SI = \frac{2w}{a+b} (100)$$

where, SI = similarity index, w = the lowest value of a or b, a = the estimated frequency of occurrence (from slide analysis) of species a, and b = the actual frequency of occurrence of species a. A value of 90 was the minimum accepted SI value for confidence of ability, and this value was exceeded with practice.

Characterization of the various species was made from recognizable differences in size, shape, trichomes, and stomates. Figures 2-9 illustrate these characters. For example, trichomes of both D. pinnata and D. verna are branched while those of E. filifolius are jointed. Epidermal cells of C. atrabarba exhibit a jig saw pattern while those of A. lanulosa have a linear arrangement. L. macrocarpum and C. atrabarba have very similar cells and stomates, but the stomates of C. atrabarba are darker in appearance. It must be pointed out that the species recognition of a fragment was not enough for a recording of the result. The fragment was only recorded when it was recognized as being an epidermal fragment. Recording of fragments of deeper tissues yield biased results due to differential amounts and digestibilities of these parts.

Reference Collection

Tissues of plant species found on the study site were collected and prepared for use in a reference collection of slides. The tissues were air-dried for a week or air-dried in an oven at 55°C for 48 hours. They were then ground in a Waring blender in a small amount of tap water, and washed through a 0.104 mm sieve. It was previously found that grinding in a Waring blender resulted in reference material that most closely assumes the character of tissues found in dietary samples. Reference slides were made directly from this using exactly the same procedures as for dietary samples.

FIGURE 2. Long, Flowing Trichomes
of Artemisia tridentata (100 X)

FIGURE 3. Short, Branched Trichomes
of Draba verna (100 X)

FIGURE 4. Jointed Trichomes
of Erigeron filifolius (100 X)

FIGURE 5. Short Trichomes
of Salsola kali (100 X)

FIGURE 6. Branched Trichomes on Stem
of Descurainia pinnata (100 X)

FIGURE 7. Leaf Epidermis of Crepis atrabarba
with Stomates and Guard Cells (100 X)

FIGURE 8. Leaf Epidermis
of Achillea lanulosa (100 X)

FIGURE 9. Leaf Epidermis of Lomatium macrocarpum
Showing Stomates and Guard Cells. (100 X)

Diet Samples

Dried sample materials were ground in a Wiley laboratory mill over a 1 mm mesh screen. The particles collected were washed through a 0.104 mm mesh sieve. This caused uniform mixing of the sample and reduced all particles to a uniform size. A small amount of washed material was removed from the sieve with a spatula and placed at one end of a microscope slide. A few drops of Hertwig's solution was added to the wet material, and most of the Hertwig's was evaporated over an alcohol burner. The Hertwig's is a decolorizing solution that clears the plant tissue of pigments. Its use is necessary as it is difficult to make accurate identifications when the tissue is saturated with pigments.

The next step was the addition of enough Hoyer's solution to cover the area under a cover slip. A teasing needle was used to mix and spread the material over the area under the cover slip. This is best done such that the finished slide yields about 3 large plant fragments per field (Cavender and Hansen, 1970).

Hertwig's solution - clearing agent

270 g chloral hydrate crystals

19 cc 1 N HCl

60 cc glycerine

Combine glycerine and HCl, add chloral hydrate crystals, stir until crystals dissolve. Warming accelerates the dissolving of the crystals.

Hoyer's solution - mounting medium

200 g chloral hydrate crystals

50 cc water

20 cc glycerin

30 g photo purified gum arabic

Combine glycerin and water, stir in chloral hydrate crystals until they dissolve. Warm the solution and stir in gum arabic. Let stand until the solution clears.

A cover slip was then placed over the mixture and air bubbles were drawn out by passing the bottom of the slide over a cool damp sponge.

Analysis

On each slide 20 randomly chosen microscopic fields were observed at 100 X magnification. Any compound microscope will suffice, but the optics

must be in excellent condition. A phase contrast microscope makes the plant cell structures much more distinctive, thus increasing the reliability of the analysis. The species occurring in each field were recorded and that data expressed as percent frequency of each species (number of fields that a species occurred in out of 100 locations). That is to say, if 5 slides were examined and species X occurred in 20 of 100 fields examined, the frequency would be 20 percent. Then the values were converted to mean density using the Formula $F = 100 (1 - e^{-d})$ derived by Fracker and Brischle (1944) (Appendix I). Finally, the values were converted to relative densities.

RESULTS

Trapping

Trapping results are shown in Table 2. In addition to regular trapping, two Spermophilus were taken when they ran into a dead end drain pipe on March 2, and one was taken when it was hit by a truck on May 18. Trapping of ground squirrels was most successful in the early morning hours. Trap success of Perognathus and Peromyscus ranged from 0% to 13.3%.

Diet Analysis

Summaries of the diet analysis of all three species are given in Tables 3 and 4. Of food items other than seeds found in the diet of Perognathus, D. pinnata (tansy mustard) and insect materials are the most important. When the data is separated by monthly intervals a different emphasis is reflected. Insects decline in importance in May when seeds are becoming abundant. Emphasis on green parts of tansy mustard declines when the seeds become available. The seed of this plant species was the only seed found in the analysis, but others have been reported from cheek pouches of specimens taken from Hanford (Schreiber, 1973). Analysis of the 12 donated stomachs show that green vegetation composed an average of 1.4% of the dry weight of Perognathus stomach contents in June and July.

Results of the analysis of Peromyscus stomachs show that major food items include Bromus tectorum, Descurainia pinnata, Descurainia pinnata seeds, and insect materials. As was found in the analysis of Perognathus stomachs, seeds of D. pinnata increase in dietary importance when they are abundant. The importance of insect materials tends to increase in April. This result may be biased due to the small number of stomachs examined for this period. Peromyscus probably consumes considerable amounts of insect material in dryer seasons.

TABLE 3. Summary of Diet Analysis Results From Stomachs

Food Item	Perognathus Rel.Den. N=25	Number of Stomachs Containing Food	Peromyscus Rel.Den. N=25	Number of Stomachs Containing Food	Spermophilus Rel.Den. N=12	Number of Stomachs Containing Food
Perennial grasses						
<u>Agropyron</u>						
<u>spicatum</u>	--	--	1.8	2	--	--
<u>Poa cusicki</u>	4.4	3	--	--	--	--
<u>Poa</u>						
<u>sandbergii</u>	5.3	4	2.6	4	49.0	12
Half-shrubs						
<u>Antennaria</u>						
<u>dimorpha</u>	--	--	--	--	1.8	3
<u>Erigeron</u>						
<u>filifolius</u>	0.9	1	<1	1	3.0	1
Perennial forbes						
<u>Astragalus</u>						
<u>purshii</u>	--	--	--	--	10.9	3
<u>Crepis</u>						
<u>atrabarba</u>	2.7	2	0.5	1	--	--
<u>Lupinus</u>						
<u>laxiflorus</u>	0.9	1	0.5	1	10.0	7
Winter annuals						
<u>Descurainia</u>						
<u>pinnata</u>	35.4	15	8.5	9	--	--
Seed	9.7	8	41.0	10	8.5	2
<u>Draba verna</u>	2.7	3	0.5	1	--	--
<u>Festuca</u>						
<u>octoflora</u>	--	--	5.5	3	--	--
<u>Bromus</u>						
<u>tectorum</u>	7.1	6	13.0	8	--	--
<u>Achillea</u>						
<u>lanulosa</u>	4.4	6	1.8	4	11.3	5
<u>Salsola</u>						
<u>kali</u>	0.9	2	3.4	3	2.1	2
<u>Sisymbrium</u>						
<u>altissimum</u>	--	--	1.9	5	1.7	3
<u>Lactuca</u>						
<u>serriola</u>	--	--	--	--	0.5	2
<u>Balsamorhiza</u>						
<u>careyana</u>	--	--	--	--	0.3	6
Other Shrubs						
<u>Artemisia</u>						
<u>tridentata</u>	0.9	1	1.8	2	1.5	3
Other						
Lichen	--	--	1.0	3	0.5	1
Chitin	14.2	13	10.1	10	<1	1
Hair	--	--	0.9	1	--	--
Unknown	10.6	9	6.5	7	2.8	6

TABLE 4. Relative Density of Species in Diets Through Sample Periods; Spermophilus (St), Perognathus (P_p), Peromyscus (Pm)

Food Items	March			April			May		
	St N=3	P _p N=15	Pm N=13	St N=5	P _p N=4	Pm N=5	St N=4	P _p N=7	Pm N=7
Perennial grasses									
<u>Agropyron</u>									
<u>spicatum</u>	--	--	2.6	--	--	--	--	--	2.4
<u>Poa cusicki</u>	--	12.1	--	--	--	--	--	--	--
<u>Poa sandbergii</u>	98.2	--	2.6	36.1	3.3	4.2	89.9	19.2	1.8
Half-shrubs									
<u>Antennaria</u>									
<u>dimorpha</u>	--	--	--	3.3	--	--	--	--	--
<u>Erigeron</u>									
<u>filifolius</u>	--	0.9	--	5.7	--	--	--	--	1.0
Perennial forbes									
<u>Astragalus</u>									
<u>purshii</u>	--	--	--	18.0	--	--	8.1	--	--
<u>Crepis</u>									
<u>atrabarba</u>	--	--	0.9	--	5.8	--	--	--	--
<u>Lupinus</u>									
<u>laxiflorus</u>	1.0	1.7	0.9	3.3	--	--	27.4	--	--
Winter annuals									
<u>Descurainia</u>									
<u>pinnata</u> seed	--	28.7	11.2	1.0	57.5	13.3	4.0	--	--
	--	--	13.8	3.3	1.7	50.0	--	73.8	79.9
<u>Draba verna</u>	--	6.0	0.9	--	--	--	--	--	--
<u>Festuca</u>									
<u>octoflora</u>	--	--	8.6	--	--	--	--	--	4.9
<u>Bromus</u>									
<u>tectorum</u>	--	7.8	25.0	--	8.3	--	--	--	--
<u>Achillea</u>									
<u>lanulosa</u>	--	10.4	3.4	17.2	--	--	11.3	--	--
<u>Salsola kali</u>	--	1.7	6.0	0.8	--	--	6.5	--	1.2
<u>Sysymbrium</u>									
<u>altissimum</u>	--	--	3.4	1.6	--	--	2.4	--	1.0
<u>Lactuca serriola</u>	--	--	--	1.0	--	--	--	--	--
<u>Balsamorhiza</u>									
<u>careyana</u>	0.3	--	--	4.9	--	--	--	--	--
Shrubs									
<u>Artemisia</u>									
<u>tridentata</u>	0.9	--	1.7	--	1.7	--	1.0	--	--
Other									
Lichen	--	--	1.7	1.0	--	--	1.6	--	1.0
Chitin	--	18.3	7.8	--	12.5	24.2	--	2.3	6.1
Hair	--	--	1.7	--	--	--	--	--	--
Unknown	0.1	12.1	7.8	--	9.2	8.3	3.2	4.7	3.7

The major food item found in Spermophilus stomachs was Poa sandbergii. It appears to be strongly selected. Other important plant species are Lupinus laxiflorus, Achillea lanulosa, and Astragalus purshii. Insect materials do not appear to be important as a dietary component.

Results of fecal analysis reflect a more varied diet than is shown by stomach analysis. This was expected since stomach samples contain food of only one or two feeding periods. Because of the nature of the sciurid digestive system (monogastric with functional caecum), food of several meals is mixed in the caecum and the food of any given meal will not completely pass through the digestive system for a period of 5 days under normal conditions (Voth, 1968). Results of stomach and fecal analysis are combined in Table 5. Each fecal sample was taken to represent 30 stomach samples. Feces analysis, according to Voth, is the preferred method of analysis on herbivores with this type of digestive system because a comprehensive SCA (stomach content analysis) requires a very large number of samples (Hansen and Graybill, 1956). Voth reports that valuable information can be acquired from relatively few samples. Food preferences of Spermophilus, Perognathus, and Peromyscus are shown in Table 6.

TABLE 5. Relative Density of Plant Species in Spermophilus townsendi.
Stomachs and Feces Combined Through Sample Periods

Items	March N=3	April N=125	May N=63	June N=1
<u>Poa sandbergii</u>	98.2	77.7	85.6	5.3
<u>Antennaria dimorpha</u>	--	0.1	--	--
<u>Erigeron filifolius</u>	--	0.2	0.9	--
<u>Astragalus purshii</u>	--	6.8	0.4	--
<u>Lupinus laxiflorus</u>	0.6	0.6	5.1	0.5
<u>Achillea lanulosa</u>	--	0.7	0.5	--
<u>Balsamorhiza careyana</u>	0.3	12.3	0.4	--
<u>Lactuca serriola</u>	--	>0.1	--	4.8
<u>Salsola kali</u>	--	0.6	0.3	--
<u>Sisymbrium altissimum</u>	--	0.1	0.2	--
<u>Descurainia pinnata</u>	--	3.3	2.7	1.0
<u>D. pinnata</u> seed	--	0.1	--	85.5
<u>Artemisia tridentata</u>	0.9	--	>0.1	--
Lichen	--	0.6	0.1	--
Chitin	--	--	--	0.5
Unknown	0.1	2.1	1.4	0.5

TABLE 6. Food Preferences of Spermophilus (St),
Perognathus (P_p), and Peromyscus (Pm)

Food Item	March			April			May		
	St	P _p	Pm	St	P _p	Pm	St	P _p	Pm
Perennial grasses									
<u>Agropyron spicatum</u>	-	-	0	-	-	-8	-	-	-8
<u>Poa cusickii</u>	-	0	-	-	0	-	-	0	-
<u>Poa sandbergii</u>	+17	-3	-3	+3	0	0	+17	-3	0
Half shrubs									
<u>Antennaria dimorpha</u>	0	-	-	0	-	-	-1	-	-
<u>Erigeron filifolius</u>	0	0	0	0	0	0	0	0	0
Perennial forbs									
<u>Astragalus purshii</u>	0	-	-	+3	-	-	+1	-	-
<u>Crepis atrabara</u>	-	0	0	-	+1	0	-	-1	0
<u>Lupinus laxiflorus</u>	0	0	0	0	0	0	+2	0	0
Winter annuals									
<u>Descurainia pinnata</u>	0	+5	+2	0	+11	+2	0	0	0
seed	*	*	*	*	*	*	*	*	*
<u>Draba verna</u>	-	+1	0	-	0	0	-	0	0
<u>Festuca octoflora</u>	-	-	+1	-	-	0	-	-	0
<u>Bromus tectorum</u>	-	+1	+5	-	+1	0	-	0	0
<u>Achillea lanulosa</u>	0	+2	0	+3	0	0	+2	0	0
<u>Salsola kali</u>	*	*	*	*	*	*	*	*	*
<u>Sisymbrium altissimum</u>	0	-	0	0	-	0	0	-	0
<u>Lactuca serriola</u>	*	*	*	*	*	*	*	*	*
<u>Balsamorhiza careyana</u>	*	*	*	*	*	*	*	*	*
Shrubs									
<u>Artemisia tridentata</u>	-7	-7	-7	-11	-11	-11	-7	-7	-7
Others									
Lichen	*	*	*	*	*	*	*	*	*
Chitin	*	*	*	*	*	*	*	*	*
Hair	*	*	*	*	*	*	*	*	*
Unknown	*	*	*	*	*	*	*	*	-*

+ or - indicates values of mean percent diet composition above or below values for aboveground biomass for the item.

0 indicates values are within 5 numerical units of each other. Each numerical unit is a step of 5 units.

* indicates that there is no existing data for comparison of values.

If there was differential digestion of diet species, the data taken by this method would be unreliable. Free et al. (1970) and Hansen et al. (1973) have shown that there are no statistically significant differences in diet analysis results as obtained from analysis of stomach and fecal samples of ruminant systems.

Because it was the major constituent of the diet, the harvested above-ground biomass values for *Poa sandbergii* in 1972 (Rickard et al., 1972) were compared with values of estimated biomass of *Spermophilus townsendi* in 1972 (O'Farrell et al., 1974). The results are in Figure 10. It appears that the seasonal activity of *S. townsendi* is closely associated with the growing season of *Poa sandbergii*. Observations taken during the 1974 season indicate that the same pattern existed. Therefore, this phenomenon should be studied more thoroughly.

FIGURE 10. Estimated Biomass of *Spermophilus townsendi* (g wet weight) During 1972 on IBP Plot Versus Harvested Biomass (g/m²) of *Poa sandbergii* During 1972 on IBP Plot. Data Taken From Rickard et al. (1972) and O'Farrell et al. (1974)

DISCUSSION

Statistical Tests

According to Hansen and Graybill (1956), stomachs must be collected at random and the number needed to determine the proportion of animals eating one food is calculated from a preliminary sample by the formula:

$$N = \frac{4p(100-p)}{d^2}$$

where N = the number of stomachs needed, p = the percent of sample stomachs having one food, and d = the percent permissible deviation from the true value (d = 3 for 95% confidence).

When applied to the total diet, the formula is used for the major food items and p is chosen to be the percentage occurrence of the major food item that is found in nearest to 50 percent of the sample stomachs. Therefore, if all of the major foods are found in all of the stomachs, only one stomach is necessary or no more stomachs are necessary for that sampling period as shown by the following:

$$N = \frac{4(100)(100-100)}{9} = 0$$

If p = 50 percent 1,111 stomachs are required as shown:

$$N = \frac{4(50)(100-50)}{9} = 1,111$$

It is obvious that the value of the equation is dependent upon the species studied. It is impractical to collect 1,111 stomachs in most situations. This points out one advantage of using fecal pellet analysis over stomach content analysis since each pellet sample may represent the equivalent of many stomach samples.

In his discussion of the above formula, Voth (1968, p. 100) argued that he could use 5 pellet samples per collection date as this represented 150 stomach samples. However, he chose a large allowable error and strict application of the formula would have forced him to examine equivalent material from 219 fecal samples (6570 stomachs) per collection period. Since this would have involved an excessive amount of analysis time, he chose an allowable error to reduce his sample size. He supported the statistical validity of his results (p. 102-103) with an analysis of variance performed on results of 5 samples which yielded an "among pellet" variance quotient within 95 percent confidence limits. This showed that the samples were from a randomly distributed population.

Application of Statistical Test

The results of test application to diet analysis results are shown in Table 7. Food items were termed "major" food items if they accounted for 10% or more of the diet.

The results indicate that statistical validity can only be claimed for Perognathus in May and for Peromyscus in April. The Spermophilus analysis is valid for all periods even though $N = 12$ if one allows 10% error and the use of arguments concerning feces analysis. Then the needed N is 100 and the N claimed is 192.

With respect to the test, the Spermophilus diet analysis results are qualitative while the results of the other analyses remain qualitative. However, the claim of quantitation of Spermophilus diet analysis remains questionable since the sample number was small and no one has yet determined strict values for the preliminary sample size from which the N values were computed.

Diet Analysis

A summary of diet overlap of the three species is outlined in Table 8. The results show that 21 different items are used. Perognathus uses 13 items, and Peromyscus and Spermophilus use 16 and 15 different items, respectively. Of these, only a few were positively selected. The diets of all species overlap by 8 items. No items preferred by Spermophilus were selected by either of the other two species. Peromyscus and Perognathus both selected B. tectorum in March and D. pinnata in March and April. Chitin was also found to represent large percentages of both diets in March and April. Preference for the item is indicated without comparable biomass data since it accounted for 18.3% of Perognathus diets in March and up to 24.2% of Peromyscus diets in April. D. pinnata seed was also used in considerable amounts by both species. It is interesting that A. tridentata, the most noticeable species in the environment, was not used by any of the species.

Bioenergetics

Schreiber (1973) computed the maintenance energy for Spermophilus townsendi to be 196/cal/gm/day in the lab. He also estimated the annual ingestion rates for Perognathus parvus and Peromyscus maniculatus to be 2419 kcal and 5848 kcal, respectively. On a per gram basis, these figures work out to be 150,254.6 cal/gm/yr and 326,592.2 cal/gm/yr.

O'Farrell, et al. (1974) estimated the biomass of mammals on the site during 1972 to be 0.10-0.16 g/m². The maximum occurred in May. The May 1972 value for aboveground harvested biomass of vegetation/m² was 65.503g (Rickard, et al. 1972). This value is taken with the omission of the value of Artemisia tridentata as it was not found to be a significant food species.

TABLE 7. Numbers of Stomachs Needed for Quantitative Analysis

Sample Period	Perognathus			Peromyscus			Spermophilus		
	Indicator Item	Allowable Error		Indicator Item	Allowable Error		Indicator Item	Allowable Error	
		3%	10%		3%	10%		3%	10%
Total	<u>Descurainia</u>			<u>D. pinnata</u>			<u>Poa sandbergii</u>	0	0
	<u>pinnata*</u>	N=915.11	82.36	<u>seed*</u>	1,111	100	<u>Achillea</u>		
	<u>Chitin*</u>	N=915.11	82.36	<u>Chitin</u>	1,100	99	<u>lanulosa*</u>	1,111	100
				<u>Bromus tectorum</u>	502	45			
March	<u>Descurainia</u>			<u>Descurainia</u>					
	<u>pinnata*</u>	N=968	87	<u>pinnata*</u>	1,022	99	<u>Poa sandbergii</u>	0	0
	<u>Poa cusickii</u>	N=968	87	<u>D. pinnata</u> seed	951	86			
	<u>Achillea</u>			<u>Bromus</u>					
	<u>lanulosa*</u>	N=0	0	<u>tectorum</u>	787	71			
	<u>Chitin</u>	N=0	0						
April	<u>Chitin*</u>	N=968	87	<u>Descurainia</u>			<u>Poa sandbergii</u>	0	0
	<u>Descurainia</u>			<u>pinnata*</u>	0	0	<u>Balsamorhiza</u>		
	<u>pinnata*</u>	N=0	0	<u>Chitin*</u>	0	0	<u>careyana</u>	0	0
				<u>D. pinnata</u> seed*	0	0			
May	<u>Poa</u>								
	<u>sandbergii</u>	N=0	0	<u>D. pinnata</u> seed*	711	64	<u>Poa sandbergii</u>	0	0
	<u>D. pinnata</u>								
	<u>seed*</u>	N=0	0						

* Indicated major food item found in closest to 50% of stomachs.

TABLE 8. Summary of Food Item Use by Species

<u>Item</u>	<u>Perognathus</u>	<u>Peromyscus</u>	<u>Spermophilus</u>
Lichen	No	Yes	Yes
<u>Poa sandbergii</u>	Yes	Yes	Yes*MAMy
<u>Antennaria dimorpha</u>	No	No	Yes
<u>Poa cusickii</u>	Yes	No	No
<u>Balsamorhiza careyana</u>	No	No	Yes
<u>Bromus tectorum</u>	Yes*MA	Yes*M	No
<u>Lactuca serriola</u>	No	No	Yes
<u>Descurainia pinnata</u>	Yes*MA	Yes*MA	Yes
<u>D. pinnata seed</u>	Yes	Yes	Yes
<u>Achilles lanulosa</u>	Yes	Yes	Yes*AMy
<u>Draba verna</u>	Yes*M	Yes	No
<u>Erigeron filifolius</u>	Yes	Yes	Yes
<u>Lupinus laxiflorus</u>	Yes	Yes	Yes*My
<u>Salsola kali</u>	Yes	Yes	Yes
<u>Crepis atrabarba</u>	Yes*A	Yes	No
<u>Artemisia tridentata</u>	Yes	Yes	Yes
<u>Chitin</u>	Yes	Yes	Yes
<u>Astragalus purshii</u>	No	No	Yes*AMy
<u>Agropyron spicatum</u>	No	Yes	No
<u>Festuca octoflora</u>	No	Yes*M	No
<u>Sisymbrium altissimum</u>	No	Yes	Yes

*Indicates positive selection for the item.

M indicates March

A indicates April

My indicates May

Underlined answers indicate that no harvest data is available for the species.

Of the 0.16g/m² of mammals in May, Spermophilus townsendi, Peromyscus maniculatus, and Perognathus parvus accounted for 77%, 1.3%, and 21.7%, respectively. Therefore, their concentrations were 0.1232, 0.00208, and 0.03472g/m².

From the above data, the yearly energy budgets of mammals/m² can be estimated as follows:

<u>P. parvus</u>	0.03472g/m ² x 150,254.6 = 5216.8 cal/m ² /yr
<u>P. maniculatus</u>	0.00208g/m ² x 326,592.2 = 679.3 cal/m ² /yr
<u>S. townsendi</u>	365 days x 196 cal/g/day x 0.1232 = 8813.7 cal/m ² /yr

It should be noted that the computed value for S. townsendi is only a maintenance value, but is certainly exceedingly high since energy savings of hibernation have not been taken into account.

The mammals use approximately 14,709.8 cal/m²/yr. With 65.503 g/m² of plant materials on the site, the available energy at May harvesting is computed taking an average value of 4000 cal/gm as the energy content of dried plant materials (Cline, 1974).² The available energy in May was:

$$65.503 \times 4000 = 262,012 \text{ cal/m}^2$$

Schreiber also calculated assimilation efficiencies for the species he studied. None of his values fell below 78%. Therefore, using 75% as a low value of assimilation efficiency for the species in my work, the estimated available energy is:

$$0.75 \times 262,012 = 196,509 \text{ cal/m}^2$$

The computed value far exceeds the theoretical needs of mammals on the site. Also, the true amount of energy available is far greater than this value as it represents only one sample period and does not consider that energy already used or that to come in later seasons. Furthermore, Schreiber's energy analysis of stomach contents yielded values far in excess of the 4000 cal/g dry weight used in this discussion.

By comparing available and needed energies of each plant species in the diets (Table 9), a more definitive look at dietary overlap is made. There does not appear to be enough of six species. However, the harvest data was taken from a single day, and the energy needs of the animals is computed for the whole year. When energy needs are corrected to a daily basis (Table 10), it does appear that the environment provides sufficient energy.

Separation of Species by Biorhythmic Phenomena

The breeding of Spermophilus occurs early in the season, that of Perognathus occurs in June after Spermophilus goes into aestivation, and Peromyscus breeds from October to February (O'Farrell, et al. 1974). It appears that the species are widely separated by reproductive schedules. They are also separated in their activity patterns. Spermophilus is diurnal while the other species are nocturnal. Kritzman (1970) reports that Peromyscus seems active earliest in the evening and the activity of Perognathus does not occur until later. Hence, it appears that any social interaction between the three species is minimal.

²Cline, J., 1974. Personal communication, Ecosystems Dept., Battelle-Northwest, Richland, Washington.

TABLE 9. Comparison of Available and Needed Energy from Plant Species by Spermophilus, Perognathus, and Peromyscus on ALE

Plant Species	Available Digestible Energy (cal/m ²) May 8, 1972	Energy Needed (cal/m ²)/yr		
		St.	P _p	P _m
<u>Agropyron spicatum</u>	34,500	0	0	12.2
<u>Poa cusickii</u>	9,000	0	229.5	0
<u>Poa sandbergii</u>	19,200	6839.4	276.5	17.7
<u>Antennaria dimorpha</u>	2,100	11.45	0	0
<u>Erigeron filifolius</u>	3,600	19.4	47.0	0.7
<u>Astragalus purshii</u>	42	599.3	0	0
<u>Crepis atrabarba</u>	510	0	140.8	3.4
<u>Lupinus laxiflorus</u>	330	54.6	47.0	3.4
<u>Descurania pinnata</u>	6	290.5	1846.7	57.7
<u>Descurania pinnata</u> seed	?	11.5	506.0	278.5
<u>Draba verna</u>	180	0	138.2	3.4
<u>Festuca octoflora</u>	12	0	0	37.4
<u>Bromus tectorum</u>	6	0	370.4	88.3
<u>Achillea lanulosa</u>	9	63.5	230.6	12.2
<u>Salsola kali</u>	?	53.8	47.0	24.1
<u>Sisymbrium altissimum</u>	3	5.2	0	12.9
<u>Lactuca serriola</u>	?	2.6	0	0
<u>Balsamorhiza careyana</u>	?	1084.1	0	0

Trapping Data and Sympatric Populations

Trapping results may often mislead one into thinking that a case for interspecific competition exists. Kritzman reported that the ratio between trapped Perognathus and Peromyscus was depressed when trap concentration was low. She believes that this happened because of the time difference in activity periods of the two species. Peromyscus arrives at the traps first and enters leaving mostly closed traps for Perognathus to find.

In another instance observations were made on the IBP mammal trapping plots. It was observed that when Spermophilus was active (March-June) trapped Perognathus were fewer than after Spermophilus went into aestivation (Hedlund, 1974).³ Perognathus was probably not absent when Spermophilus was aboveground. Rather, Spermophilus found the traps before Perognathus had an opportunity to. This probably was the case since populations of Perognathus did not change peripheral to the area of sympatry.

³Hedlund, John, 1974. Personal communication, Ecosystems Dept., Battelle-Northwest, Richland, Washington.

TABLE 10. Comparison of Available and Needed Energy from Plant Species by Spermophilus, Perognathus, and Peromyscus on ALE

Plant Species	Available Digestible Energy (cal/m ²) May 8, 1972	Energy Needed (cal/m ² /day)		
		St	Pp	Pm
<u>Agropyron spicatum</u>	34,500	0	0	0.068
<u>Poa cusickii</u>	9,000	0	0.011	0
<u>Poa sandbergii</u>	19,200	57.0	0.013	0.098
<u>Antennaria dimorpha</u>	2,100	0.095	0	0
<u>Erigeron filifolius</u>	3,600	0.160	0.002	0.004
<u>Astragalus purshii</u>	42	6.0	0	0
<u>Crepis atrabarba</u>	510	0	0.006	0.019
<u>Lupinus laxiflorus</u>	330	0.46	0.002	0.019
<u>Descurania pinnata</u>	6	2.42	0.090	0.320
<u>Draba verna</u>	180	0	0.006	0.019
<u>Festuca octoflora</u>	12	0	0	0.108
<u>Bromus tectorum</u>	6	0	0.017	0.470
<u>Achillea lanulosa</u>	9	0.530	0.011	0.068
<u>Salsola kali</u>	?	0.450	0.002	0.137
<u>Sisymbrium altissimum</u>	3	0.043	0	0.072
<u>Lactuca serriola</u>	?	0.022	0	0
<u>Balsamorhiza careyana</u>	?	9.0	0	0

Estimated annual activity of species:

1. S. townsendi 120 days
2. P. parvus 300 days
3. P. maniculatus 180 days

SUMMARY AND CONCLUSIONS

Three species of small mammals were studied on the ALE (Arid Land Ecology) reserve near Richland in Eastern Washington. The study site was located at an elevation of 1200 feet.

Dietary analysis was performed on 74 animals (12 Spermophilus townsendi, 37 Perognathus parvus, and 25 Peromyscus maniculatus). The data indicate that dietary overlap occurs, but the species are widely separated in food habits (herbivore, granivore, omnivore). One plant species (B. tectorum) preferred by both Peromyscus and Perognathus is not native to the area. In the natural situation, overlap would not have been demonstrated for this plant species. Another food, (D. pinnata seed), is probably not limited during the period of greatest overlap which occurs in midsummer. Observations indicate that there is a great abundance of these seeds during this period. It is possible that the seeds serve as an important food source for animals other than the species studied.

It is concluded that, in the relations between the three rodent species studied, selective pressures caused by competition have been minimized by the evolutionary process. This conclusion is based on the following:

1. The species are widely separated in general food habits (herbivore, granivore, omnivore).
2. Dietary overlap is minimal.
3. The species activity periods are temporally separated.
4. Food does not appear to be limiting.

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APPENDIX

THE COMPUTATION OF RELATIVE DENSITY

Fracker and Brischle (1944) developed a table (Table 11) from the expression $F = 100 (1 - e^{-d})$; where F = frequency, and d = density. The relationship is used (Hansen and Flinders, 1969) (Cavender and Hansen, 1970) to convert percent frequency to mean density. An example follows, i.e.,

$$\text{if } F = 20$$

$$20 = 100 (1 - e^{-d})$$

$$0.2 = 1 - e^{-d}$$

$$0.2 - 1 = -e^{-d}$$

$$0.8 = e^{-d}$$

To find the value of d look up the value of x of $e^{-x} = 0.8$ in a standard mathematical table of exponential functions. The answer is 0.22 (refer to Table 11).

From the mean densities of each species in a given stomach relative densities are easily computed. An example follows, i.e.,

$$\text{species } x \text{ mean density is } 0.22$$

$$\text{species } y \text{ mean density is } 0.22$$

$$0.22 + 0.22 = 0.44$$

$$\frac{0.22}{0.44} = 0.50$$

Hence, 50 percent of the stomach material is species x where only species x and y are found in the stomach.

TABLE 11. Relations of Frequency to Density and Abundance (for strictly random distributions) from Cavender and Hansen, 1970.

Freq. %	Den. Q	Abun. Q	Freq. %	Den. Q	Abun. Q	Freq. %	Den. Q	Abun. Q	Freq. %	Den. Q	Abun. Q
1	0.01	1.01	26	0.30	1.16	51	0.71	1.40	76	1.43	1.88
2	0.02	1.01	27	0.31	1.17	52	0.73	1.41	77	1.47	1.91
3	0.03	1.02	28	0.33	1.17	53	0.75	1.42	78	1.51	1.94
4	0.04	1.02	29	0.34	1.18	54	0.77	1.44	79	1.56	1.98
5	0.05	1.03	30	0.35	1.19	55	0.80	1.45	80	1.61	2.01
6	0.06	1.03	31	0.37	1.20	56	0.82	1.47	81	1.66	2.05
7	0.07	1.04	32	0.38	1.20	57	0.84	1.48	82	1.71	2.09
8	0.08	1.04	33	0.40	1.21	58	0.86	1.49	83	1.77	2.14
9	0.09	1.05	34	0.41	1.22	59	0.89	1.51	84	1.83	2.18
10	0.10	1.05	35	0.43	1.23	60	0.91	1.53	85	1.89	2.23
11	0.11	1.06	36	0.44	1.24	61	0.94	1.54	86	1.96	2.28
12	0.12	1.06	37	0.46	1.25	62	0.96	1.56	87	2.04	2.34
13	0.14	1.07	38	0.48	1.26	63	0.99	1.58	88	2.12	2.41
14	0.15	1.08	39	0.49	1.27	64	1.02	1.60	89	2.20	2.48
15	0.16	1.08	40	0.51	1.28	65	1.05	1.61	90	2.30	2.56
16	0.17	1.09	41	0.52	1.29	66	1.08	1.63	91	2.40	2.64
17	0.18	1.10	42	0.54	1.30	67	1.11	1.65	92	2.52	2.75
18	0.20	1.10	43	0.56	1.31	68	1.14	1.67	93	2.66	2.86
19	0.21	1.11	44	0.58	1.32	69	1.17	1.70	94	2.81	2.99
20	0.22	1.12	45	0.60	1.33	70	1.20	1.72	95	2.99	3.15
21	0.23	1.12	46	0.62	1.34	71	1.23	1.74	96	3.22	3.35
22	0.25	1.13	47	0.63	1.35	72	1.27	1.77	97	3.51	3.62
23	0.26	1.14	48	0.65	1.36	73	1.31	1.80	98	3.91	3.99
24	0.27	1.14	49	0.67	1.37	74	1.35	1.82	99	4.60	4.65
25	0.29	1.15	50	0.69	1.38	75	1.39	1.85	99.6	5.30	5.32
									99.9	6.91	6.91
									100	----	----

DERIVATION OF THE RELATIONSHIP $F = 100(1-e^{-d})$

If there is an area made up of k quadrants. The probability of a point arriving in the area and landing in a given quadrant is:

$$1 - \frac{1}{k}$$

For n trails this becomes:

$$(1 - \frac{1}{k})^N$$

The probability of a point arriving in an already occupied quadrant is:

$$1 - (1 - \frac{1}{k})^n$$

For k quadrants this becomes:

$$k [1 - (1 - \frac{1}{k})^n]$$

or:

$$i = k[1 - (1 - \frac{1}{k})^n]$$

which is the probable distribution of n points which arrive in the area at random.

Multiplying by $\frac{k}{k}$ we have:

$$i = k[1 - ((1 - \frac{1}{k})^k)^{\frac{n}{k}}]$$

By definition:

$$e^x = \lim_{\alpha \rightarrow \infty} (1 + \frac{x}{\alpha})^\alpha$$

Since our special case is where:

$$x = -1 \text{ and } \alpha = k$$

Then:

$$\lim_{k \rightarrow \infty} (1 - \frac{1}{k})^k = e^{-1}$$

Which means that:

$$i = k[1 - (e^{-1})^{\frac{n}{k}}]$$

$$i = k[1 - e^{-\frac{n}{k}}]$$

$\frac{n}{k}$ is the density of points per quadrant = d.

Hence:

$$i = k[1 - e^{-d}]$$

or:

$$F = 100(1 - e^{-d})$$

where $k = 100$

and $i = F$

As we see, the application of the formulae to food habits analysis, is the use of the expression in the reverse of its derivation.

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