The University of Manitoba

The effect of the occurrence of certain plant species on the local distribution of *Microtus pennsylvanicus pennsylvanicus* (Ord.) in southeastern Manitoba

by

Judith J. Yaremchuk

A thesis

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Zoology Department

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Table 8. List of preference values derived by subtracting the percentage of the total vegetation represented by each plant species from the percentage of stomachs in which each species was found.

Abstract

The food habits of Microtus pennsylvanicus in southeastern Manitoba were studied in conjunction with an analysis of the plant community existing on the study plot. Snap-trapping, laboratory food preference tests, and examination of the stomach contents were employed to determine local distribution of the animals and their food preferences.

Both the preference tests and stomach analysis showed that certain plant species were highly preferred. Species which were preferred both in the laboratory and in the wild included Bromus inermis, Taraxacum officinale, species of Carex and Melilotus, and Trifolium repens. Underground stems, roots, underground fungi, and mosses were also eaten frequently.

Multiple regression analysis indicated an association between Microtus and species of Poa, which were not, however, a preferred food. The degree to which Poa was associated with some preferred plant species suggested that the association of voles with Poa may reflect the ability of these preferred foods to coexist with Poa. The animals may choose this habitat because it affords both cover and preferred foods. Vole numbers were not correlated with good cover as provided by a species (such as Calamagrostis inexpansa) which was not readily eaten and did not occur in association with more palatable plants.

The evidence of selective feeding and the indication that voles tend to be associated with certain plant associations suggested that food preferences, and, to some extent, cover, affect local distribution and perhaps migration and population levels.

Introduction

The purpose of this study was to elucidate some of the factors controlling the distribution of Microtus pennsylvanicus pennsylvanicus (Crd.), the meadow vole, in southeastern Manitoba. The problem of distribution was suggested by reports in the literature (Buckner,1957; Aumann, 1965; Ashby,1967; Fuller,1967; Getz,1969,1970,1971; Batzli and Pitelka,1971; and Grant,1971) and by the results of a preliminary small mammal census conducted in the Sandilands Forest Reserve of southeastern Manitoba in 1969. This census indicated that the distribution of Microtus was unusually discontinuous, the animals being present as small aggregations separated by a distance of some miles from neighbouring concentrations. No obvious reason for this discontinuity was discernible in terms of cover, soil type, presence of predators, or effects of weather.

Appraisal of the sites trapped during the census suggested that, although all sites seemed to provide sufficient cover to sustain a vole population, the plant associations providing these resources were exremely diverse. Therefore, since other workers have shown that the type of food eaten can affect the physiology of voles (Negus and Pinter, 1966; Schevchenko,1969; Hansen and Ueckert, 1970; and Watts, 1970), it was decided that a study of the relationships between a given plant society and its resident vole population would be an informative contribution to the present body of knowledge concerning population dynamics.

The thesis was designed to study the feeding habits of *M. pennsylvanicus* in a localized region to determine whether or not certain plant species were preferred food species and whether or not the existence of such preferences affected distribution.

Litereature review

The question of the extent to which the environment influences the activities of small mammals has been pondered by numerous researchers for many years. The appearance of marked fluctuations in numbers of small mammals, especially voles, has caused many people to look for the controlling factors behind these population peaks and "crashes" which appear to have a cyclic periodicity of between three and four years. Among the first analyses of these cycles were those of Elton(1924, 1925, and 1942), Bailey (1924), Hamilton (1937) and Hatt (1930).

Weather was one of the first factors suggested to control animal populations. Elton (1924) commented on the apparent correlation between periodic fluctuations in the numbers of animals and the occurrence of sunspots and volcanic irruptions which, he presumed, affect the climate. Some authors, notably Andrewartha and Birch (1954) feel that weather plays an important role in regulating population densities while other workers are less willing to recognize weather as a major controlling factor, although they may concede that it is significant at certain times and under certain circumstances. Many feel that cold weather, particularly if combined with dampness, may increase mortality. Barnett and Manly (1959) showed that cold delays maturity in female Mus and that the oestrus cycle was longer and less regular. This would lower the number of pregnancies per summer and greatly affect the population density.

Bateman (1957) found that less milk was produced by female Mus under cold stress and concluded that more of the food ingested was used for heat production and less for milk production.

While cold may be disadvantageous at times, it is not necessarily true that winter is the season of highest stress if a sufficient snow cover protacts small mammals from the worst effects of wind, radiant heat loss, and predation. Formozov (1946), Pruitt (1957,1960), Gentry and Odum (1957), Fuller (1967) and Vose and Dunlap (1968) have all reported that deep snow cover provided good protection for voles.

The presence or absence of sufficient vegetative cover would seem to be an important component of a vole's environment since it provides shelter from heat, cold, and predators as well as giving the structural materials for organizing the population into a system of runways, nests, home ranges and feeding areas. Warnock (1965) found that the presence of cover greatly reduced mortality associated with crowding. Cover furnished the means of dividing the population into functional units and effectively reduced intraspecific strife by giving the community a pattern of organization.

The availability of water may have some effect on the distribution and number of microtines. Voles (Clethrionomys) are known to require up to ten times as much water as deer mice (Peromyscus) (Odum,1944) and Getz (1963,1967) found that not only did M. pennsylvanicus drink more than M. ochrogaster, the prarie vole, but also water consumption was

higher at lower relative humidities. However, a study by Getz in 1965 failed to prove that humidity in vole runways was responsible for voles' choosing marsh over upland habitat.

Another factor which may affect Microtus distribution is the availability of certain minerals in the soil. Aumann (1965) and Aumann and Emlen (1965) published results indicating that microtine populations reached their highest peaks in regions with a high sodium level. Laboratory studies showed that groups of animals with sodium available "ad libitum" maintained a higher net population level over the test periods and that crowding yielded more selection for sodium.

Interspecific competition may affect vole distribution as demonstrated by the studies of DeCoursey (1957), Getz (1961,1962), Koplin (1962), Clough (1964), Koplin and Hoffmann (1968) and Murie (1971).

Predation also may affect vole numbers and distribution, especially in areas where cover is scarce. Craighead and Craighead (1950) stated that predation can be the chief limiting factor on determining prey populatio n levels. Pearson (1942) and Eadie (1952) have both found that predation by shrews, especially of the genus Blarina, may influence vole numbers from year to year. Metzgar (1967) made an interesting contribution to understanding predation effects when he reported that transient mice were more subject to predation than residents, perhaps because residents, being more familiar with the terrain, spend less time exploring and are able to hide more quickly if danger threatens. This

factor may have far-reaching effects on migration and hence distribution in the wild.

Intraspecific interactions may affect populations of small mammals. Much space has been devoted to this aspect of population dynamics in recent years. One of the first people to study so-called density dependent regulation was Christian who published a series of papers (1950, 1963, 1964, and 1965) which attempted to prove that increased adrenal weight in times of high population reflects an adrenopituitary adaptation to stresses. This theory, that increased demands on the pituitary to secrete gonadotropic hormones in the spring caused exhaustion of the adreno-pituitary adaptation with consequent late winter and early spring mortality, was advanced on the basis of Selye's general adaptation principle (Selye,1950) which states that the resistance to stress diminishes in a population in proportion to increase in adrenal function as indicated by adrenal hypertrophy and thymus involution. Christian and Davis (1966) found that adrenal weight increased in female Microtus at sexual maturity and that the weights seemed to reflect density ofthe population. There seemed to be no correlation with pregnancy and lactation. These data agreed with McKeever (1959) and Chitty (1961) but disagreed with Chitty and Clarke (1963). Clough (1965) found that survival of M. pennsylvanicus showed no correlation with population density and that adrenal, thymus and spleen weights were contrary to what the general adaptation principle predicted.

Another possible explanation of fluctuations in microtine numbers is the idea that genetic changes over a period of several years can result in reduced viability and increased susceptibility to environmental stress. This theory was first proposed by Chitty in 1960.

Chitty's theory, if taken in conjunction with those advanced by Nicholson (1933) and Andrewartha and Birch (1954), explains population cycles as being chiefly the result of physical factors with this action being governed by some population attribute. Other publications by Chitty (1952, 1955, 1958, and 1961) have not proved the existence of factors which could lower viability in a cyclic fashion. This was also the case for Newson and Chitty (1962). More recently, Chitty (1966) has sug ested that behaviour of animals toward one another may change at high densities. The relationship of parents and offspring was suggested as the critical interaction.

The foregoing literature has been briefly cited to indicate the current state of knowledge regarding the effects of the environment on Microtus populations. Obviously the environmental factors are many and the possible physiological effects complex. However, one of the most basic and least understood factors affecting any animal community has yet to be discussed. This is the problem of food supply which forms the basis of the topic of this thesis.

Materials and Methods

A. Collection of animals

a. Collection of animals for stomach analysis

Animals to be used in the analysis of stomach contents were collected on the study site at the Whiteshell Nuclear Research Establishment at Pinawa, Manitoba. Trapping was conducted on a sixty-four station grid with eight rows of eight trapping stations one hundred feet apart. This plot has been trapped annually since 1968 using Museum Special snap-back traps. The program is carried out under the supervision of Dr. S. L. Iverson. Trapping was done for a period of thirty consecutive days beginning sometime in July of each year. Three traps, baited with a mixture of peanut butter, oatmeal, and castor oil, were set at each station and checked daily. The animals were kept frozen until needed for stomach analysis.

b. Collection of animals for preference tests

Microtus used in the preference tests were collected using both Sherman box traps and Longworth traps. Most of these animals were caught in a grass-willow scrub association close to the snap-trapped grid but separated from it by a wide gravel road.

Unfortunately, a low population in the summer of 1971

necessitated collection of voles at some distance from Pinawa. For this reason, six animals were caught in a tamarack bog in the Whiteshell Provincial Park about thirty miles east of Pinawa. Of the twelve animals required for food preference tests, three were from the Whiteshell and nine from Pinawa.

Sherman traps were baited with a mixture of shortening and wild bird seed. This combination was readily eaten by voles and did not attract insects to the the same degree as a mixture of seed and peanut butter. The absence of peanut butter and the use of only a little shortening to keep the seeds together also prevented the animals from getting their hair glued together and generally kept them in better condition. Longworth traps were baited with a handful of oats and a piece of carrot supplied moisture. Both types of traps were provided with a small handful of green grass. This was placed over the metal bar behind the door in Sherman traps and never interfered with closure of the door when so placed. The grass was placed in the nest box of Longworth traps. Bedding and additional bait were thus provided for voles. Traps were checked each morning at Pinawa and in the early morning and late evening in the bog.

B. Plant community analysis

Analysis of the plant community was carried out on the trapping grid at Pinawa in July 1971, just before the yearly snap-trapping was done.

A fifty centimeter square quadrat was marked off to the northwest of each trapping station. That is, a line was marked, fifty centimeters long, to the west of the stake marking the trapping station and a quadrat laid out to the north of this line. Analysis of the vegetation within this quadrat was then begun by cutting all the plants within the square to ground level. The loose debris fraction was gathered separately, any mosses present being included in this fraction, and the samples placed in plastic bags and taken to the laboratory where the plants of each species were separated and weighed. The debris composing the litter layer was also weighed and, for the first twenty-four quadrats, the sod was cut out to a depth of about ten centimeters and the roots shaken free of soil and weighed. This last procedure was discontinued as it seemed to offer little return for the amount of work involved due to the doubtful accuracy of the results. This clip-sampling technique is similar to that employed by Golley (1960) except that he washed the roots, used dry weights instead of wet weights and did not measure the litter fraction.

The method of vegetation sampling used in this study, therefore, gave a measurement of the aboveground weight of

each plant species present on the plot, as well as the total weight of the green vegetation and the litter layer.

Separation of the species present was not difficult except for a few graminoid species. Nonetheless, these seemed to be successfully sorted on the basis of the colour, texture, turgor, and dimensions of the blade as well as the presence of hairs on the blade or ligule, and the form of the stem and roots. The accuracy of the separation of the grass species was judged by basing the decisions solely on characteristics of the stem and leaf and ignoring inflorescences or seed heads, if present. Each resulting pile of plants was then examined to see if all the inflorescences were of the desired species. If this was so, it was assumed that the characters used to differentiate the given species from the other species on the plot were sufficient and reliable. Little difficulty was encountered in separating the grasses satisfactorily except in the case of Poa pratensis and P. nemoralis. These were totally indistinguishable from one another unless heads had developed and, to avoid errors in attempting to separate the blades, the two species were weighed together and recorded as Poa spp. The number of heads of each species was recorded as an approximation of the proportion of each species present but these estimates were not used in any calculations. Similar methods were employed with some other plants such as Aster and Solidago which were both present as a number of very similar species which could not be distinguished in their early growth stages.

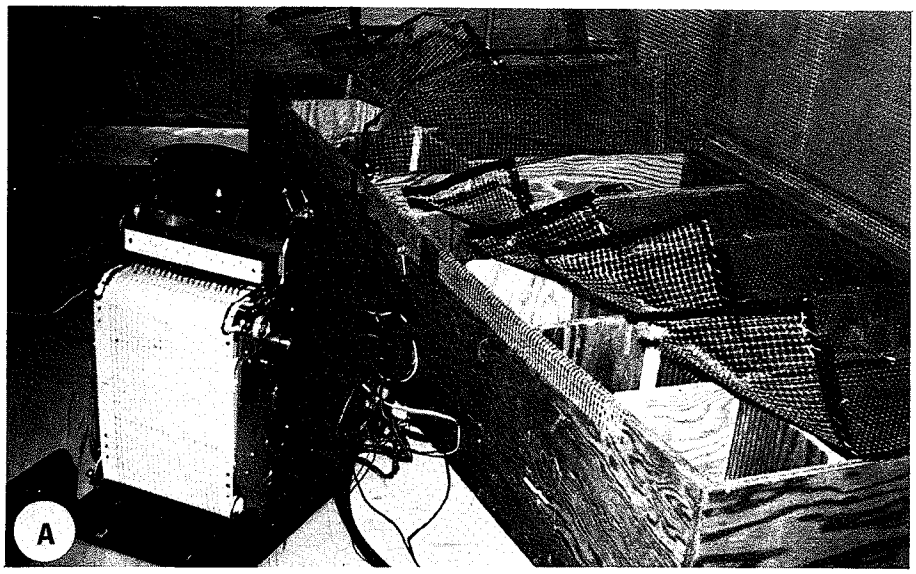
C. Food habit studies

a. Feeding trials

Laboratory studies of the food preferences of voles have, in the past, been largely restricted to stomach analysis methods or cafeteria tests. Attempts to gather prefe ence data via observations of food cuttings in the field, cafeteria tests involving a choice of a number of foods, or recorded responses to two different choices through electrical systems, have been made by Hatt (1930), Hatfield (1940), Jameson (1947), Holling (1955), Martin (1956), Marsh (1962), Gorecki and Gebczynska (1962), Buckner (1964), Thompson (1965), Batzli and Pitelka (1970, 1971), Menhusen (1963), Riewe (1971), and Bergeron (1972).

It was felt that an attempt should be made to give at least a broad estimate of the preference of M. pennsylvanicus toward plant species found on the study plot. Ideally, it would be possible to give each plant species a value, or at least a rank, according to the order of preference of various foods. Therefore, the apparatus illustrated in Figures 1 and 2 was devised to test the reaction of a captive vole to a given plant species. Each plant species was tested with twelve mice, except for Mentha arvensis where only enough plant material was available for seven mice.

In each trial, the hardware cloth basket at the front of each individual chamber was packed full of the plant



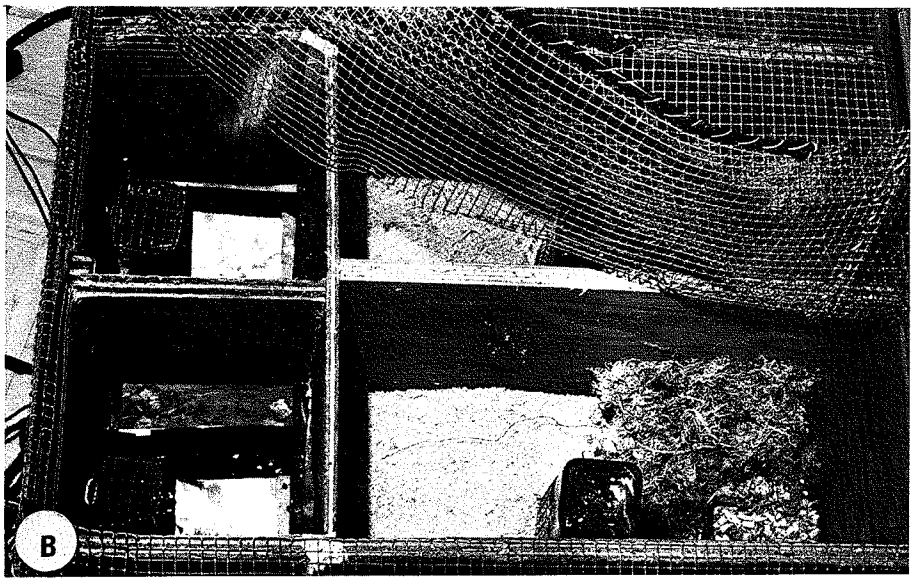


Fig. 1. Apparatus used in preference tests. A-large cage, containing eight separate compartments, plus recording apparatus. B-interior of one compartment, showing nesting area and treadle section.

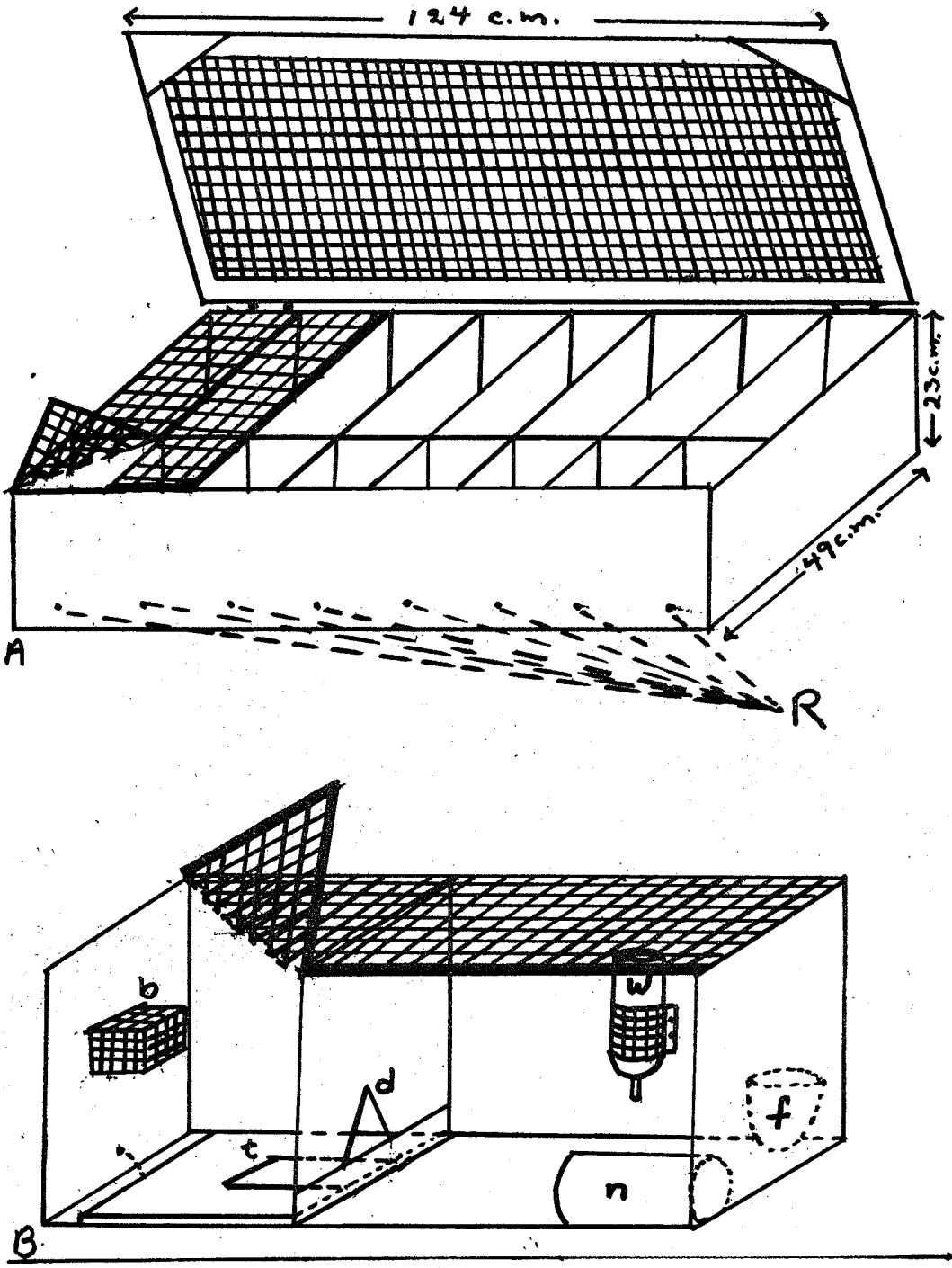


Fig. 2. A-preference test cage, divided into eight units, each with two compartments. In the interests of clarity, individual covers are shown on only two units. Wires lead from cage to recorder (R). B-detail of one unit showing basket (b) to hold plant sample and treadle (t) to record visits. Opening (d) leads to section with nesting tube (n), water bottle (w).

material to be tested. The entire plant, including roots, stem, leavss, and flowers or seeds, if present, was cut into approximately one inch sections and the resulting chopped plant material was mixed well to distribute the various parts as evenly as possible. This material was pressed into one and one-half inch cubical baskets suspended in the front of each chamber.

Visits to the basket were recorded on a twenty-pen Esterline Angus recorder via a treadle (Ray,1969) between the door of the food chamber and the food. The opening to the food compartment was just large enough to admit a vole and the treadle was placed immediately behind the door. These conditions, plus the fact that the animal had to cross a raised partition in passing through the door, made it impossible for the vole to enter the food chamber without stepping on part of the recording switch. The raised partition also kept sawdust from being kicked under the treadle.

The rest of the animal's chamber consisted of a nesting compartment supplied with sawdust, tissue paper for nests, a nesting tube, a water bottle, and food "ad libitum." This food was a standard ration of wild bird seed, pig starter pellets, and small animal food pellets in a ratio of about three parts seed to on part of each of the pellets. The ration was consumed readily and seemed to keep the captives in excellent physical condition .

The trial for each plant species was run for twenty-two hours. The remaining two hours of the twenty-four, between 2100 and 2300 hours, were used for cleaning

the food chamber of the remains of the previously tested plants, testing and, if necessary, repairing the treadles and replenishing food and water supplies. The food compartment was cleaned with a vacuum cleaner to ensure that every scrap of the preceding plant species was removed. This was done at the same time every day in order that all trials would cover the same phase of the vole's activity cycle.

The animals were given an accustomization period of four days prior to the first trial. During this time, the treadles were covered with a piece of plywood to keep them from being chewed in the voles' initial search for a way out. After the accustomization period, the treadles were rarely chewed and had to be replaced occasionally due only to the gradual effects of normal use.

The traces on the recorder charts were used to determine the preferences. The number of visits of each animal to each food sample were counted and the totals for all twelve animals summed for each plant species. These averages were compared to the number of visits made to empty baskets on so-called standard runs. These standard runs were made to separate visits to the food chamber in the course of normal exploratory and exercise activities from visits made in search of the food itself. Because vole activity patterns may change depending on the season, time of month, weather, etc. standard runs were made approximately every seven days. Therefore, seven standard trials were made during the course of this experiment. The results of these trials were summed

and an average number of standard visits per vole was calculated on the basis of all seven runs combined.

The comparison of the test runs to the standard activity score was reduced to an index of preference. This index is the positive or negative number of visits of the test score above or below the standard score. That is:

$$\text{test score} = \frac{\text{sum of visits of all animals to food}}{\text{no. of animals}}$$

$$\text{standard score} = \frac{\text{sum of visits of all animals to empty baskets}}{(\text{no. of animals}) \times (\text{no. of runs})}$$

Therefore, for each plant species, the degree of preference is expressed by:

$$\text{degree of pref.} = \text{test score} - \text{standard score}$$

To arrive at the final preference index, the degree of preference of each plant was expressed as a decimal fraction of highest degree of preference value. Hence, the plant species with the highest degree of preference is ranked as one and the other species as progressively smaller decimal values.

Hence:

$$\text{Pref. Index for species } i = \frac{\text{Degree of pref. of species } i}{\text{Highest degree of pref. value}}$$

b. Analysis of stomach contents

Stomach analysis has been attempted in relatively few studies of the food habits of voles. This is because voles chew their food so thoroughly that the dissecting microscope is of little value in separating the components. Also, the diet consists mainly of green plants which are unidentifiable without using a compound microscope.

However, Baumgartne and Martin (1939) developed techniques for preparing reference slides which were examined with a compound microscope and compared to samples of the stomach contents of squirrels. The tissues studied were fixed and cleared but unstained. Dusi (1949) modified this technique for use in cottontail rabbit food studies by staining the samples and using only the epidermal plant tissues for reference. Williams (1962) again modified the process for use on microtines by changing the staining procedures. These methods all had the great disadvantage, however, of requiring that the tissues of reference slides be fixed, cleared, stained, warmed, dried, warmed, dried,etc. These operations, as well as the preparation of special reagents required, demand a great expenditure of time. Using these methods to prepare a collection of

reference slides of all the anatomical features of all the plants on several study plots, or even on one such plot in some cases, might take several years. The diverse nature of the different types of plant epidermis and the varying thicknesses of fragments in the stomachs leads to a problem of overstaining or understaining, in many cases. This also leads to a great expenditure of time and materials if the reference collection is to be clear and easy to use.

For these reasons, therefore, a method was devised for studying stomach contents which is both rapid and functional. No fixing or staining were involved since a phase microscope was employed for examining the tissues. Phase microscopy greatly increases the contrast in unstained plant material and has the great advantage of not requiring tedious preparation techniques.

The plant species for the reference slides were collected and frozen in plastic bags. Reference slides were then prepared by stripping epidermal tissues from various parts of the plant using a pair of fine forceps. In most cases the epidermis came off easily, but in some cases the mesophyll tissue adhered and had to be scraped off with a fine needle.

The epidermal sheet was then quickly transferred to a drop of lactophenol (a mounting medium) on a slide. The thin tissue floated on the surface and could be straightened easily if it had become twisted in pulling it off the plant. A cover slip was then applied , pressed down, and sealed around the edges with clear nail,polish.

Slides were prepared in this manner for the root, stem, both leaf surfaces, and seeds and flowers of all plant species encountered on the plot. However, most roots and many seed coats were so much alike that such material could not be identified even to genus.

Stomach sample slides were prepared in much the same way as reference slides. The frozen stomachs were thawed, a small sample removed from the oesophageal sac, and the material mixed with a drop of lactophenol on a slide. A cover slip was applied and the edges sealed.

The oesophageal sac has been found (Golley,1960; Dearden,1969) to be essentially a storage sac for food which has passed down the oesophagus but has not entered the more muscular stomach where much of digestion takes place. The oesophageal sac was chosen as the sampling site because the plant fragments were little changed by digestion and because no strong digestive secretions had been added. Therefore, the identifying features of the plants remained intact; for example, hairs remained attached to sheets of epidermis. Also, the sample mixed more readily with lactophenol if no digestive juices were present. Watts (1966) used samples from the caecum for stomach analysis, stating that by this time digestion had proceeded far enough that the epidermis had separated from the fragments making identification easier.In this study, however, it was found that most fragments showed some epidermis and the attachment of hairs and spines to the fragments was very advantageous.

Samples were examined at approximately four hundred times magnification. This magnification was necessary to see gland hairs, secondary cell wall characteristics, granules, and other tiny structures typical of certain plant species. The sample was examined by traversing (moving the microscope stage) the length of the cover slip (forty millimeters) and back four times and identifying as many fragments as possible. Mesophyll pieces could not be identified but isolated hairs and spines often could be. No attempt was made to identify roots; these were placed in a separate category. Hynes (1950) considered the use of point counts to be meaningless and inaccurate when dealing with plants in stomach analysis. Any estimate of the volume of foods ingested would likely be highly inaccurate based on one minute sample of the stomach contents. Therefore, the presence of a plant species was noted and an estimate made of the percentage of each species in the sample. Preference conclusions were based on the percentage of stomachs in which each species was found.

To speed identification of the plant fragments, a catalogue was prepared using photographs of the reference slides as seen through the phase microscope. Figures 3 and 4 show photomicrographs of fragments from the reference collection and from the samples. Figure 5 shows some of the spines, hairs, and gland hairs which were useful in identification.

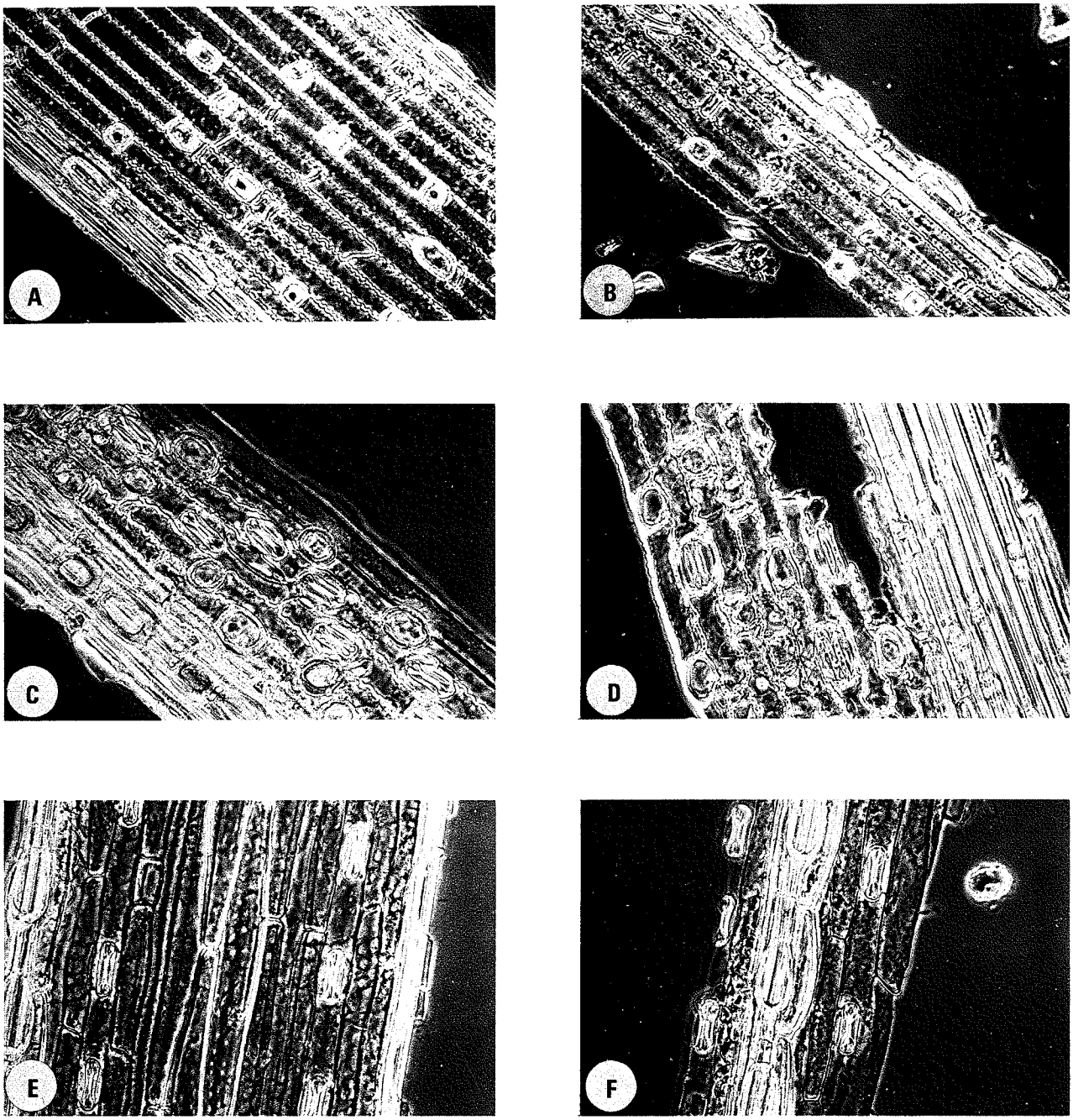


Fig. 3. Examples of monocotyledonous species in stomach contents. Calamagrostis inexpansa Gray var. brevior (Vasey) Stebbins, A-leaf blade epidermis, photomicrograph from reference slide; B-photomicrograph from stomach sample. Beckmannia syzigachne (Steud.) Fern., C-stem epidermis from reference slide; D-from stomach sample. E-leaf blade epidermis, from reference slide; F-from stomach sample. All magnified about 320x.

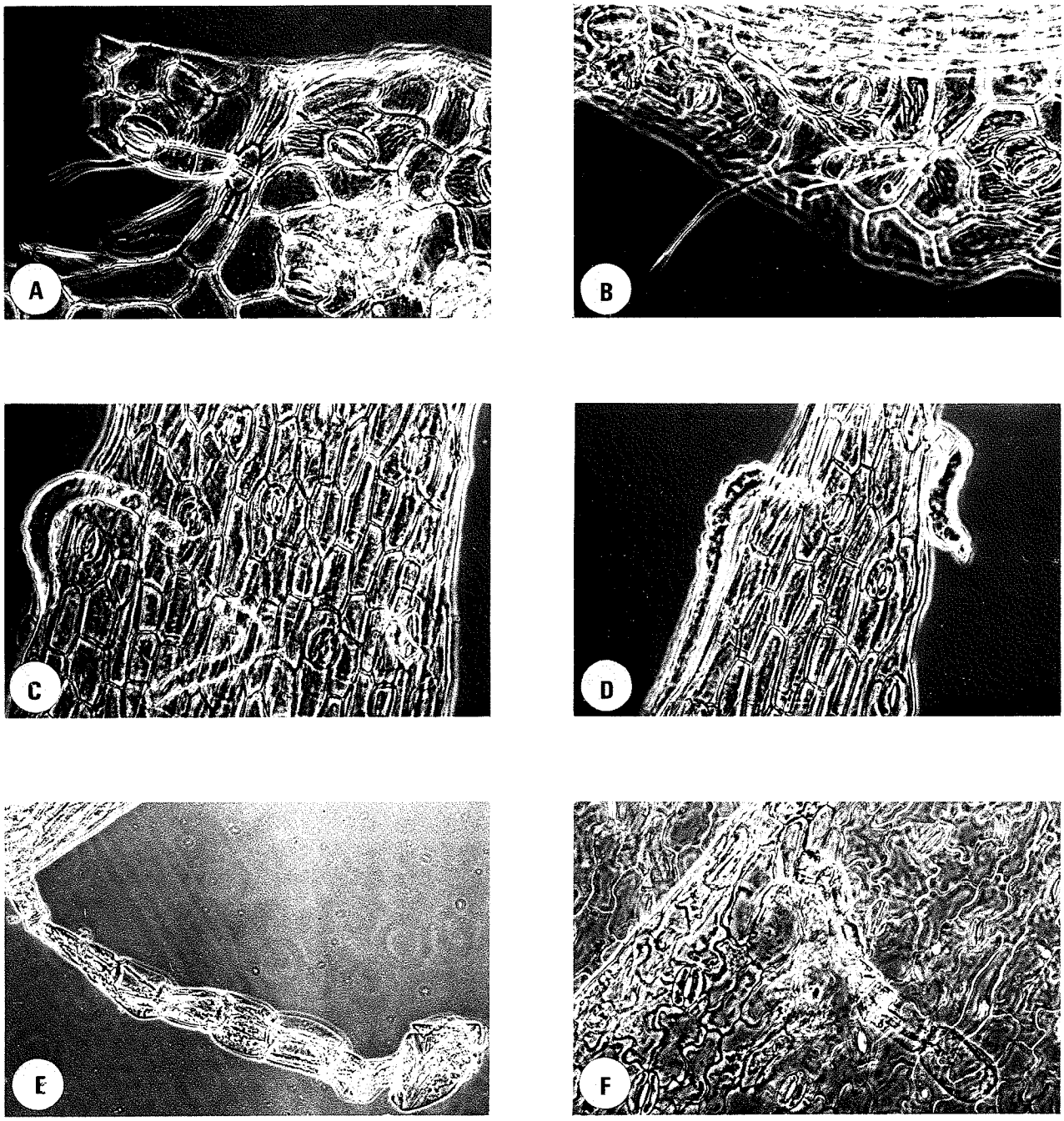


Fig. 4. Examples of dicotyledonous species found in stomach contents. Solidago gigantea Ait. var. leiophylla Fern., A-photomicrograph from reference slide; B-photomicrograph from stomach sample. Melilotus officinalis (L.) Lam., C-from reference slide; D-from stomach sample. Taraxacum officinale Weber, D-from reference slide; E-from stomach sample. All magnified about 320x.

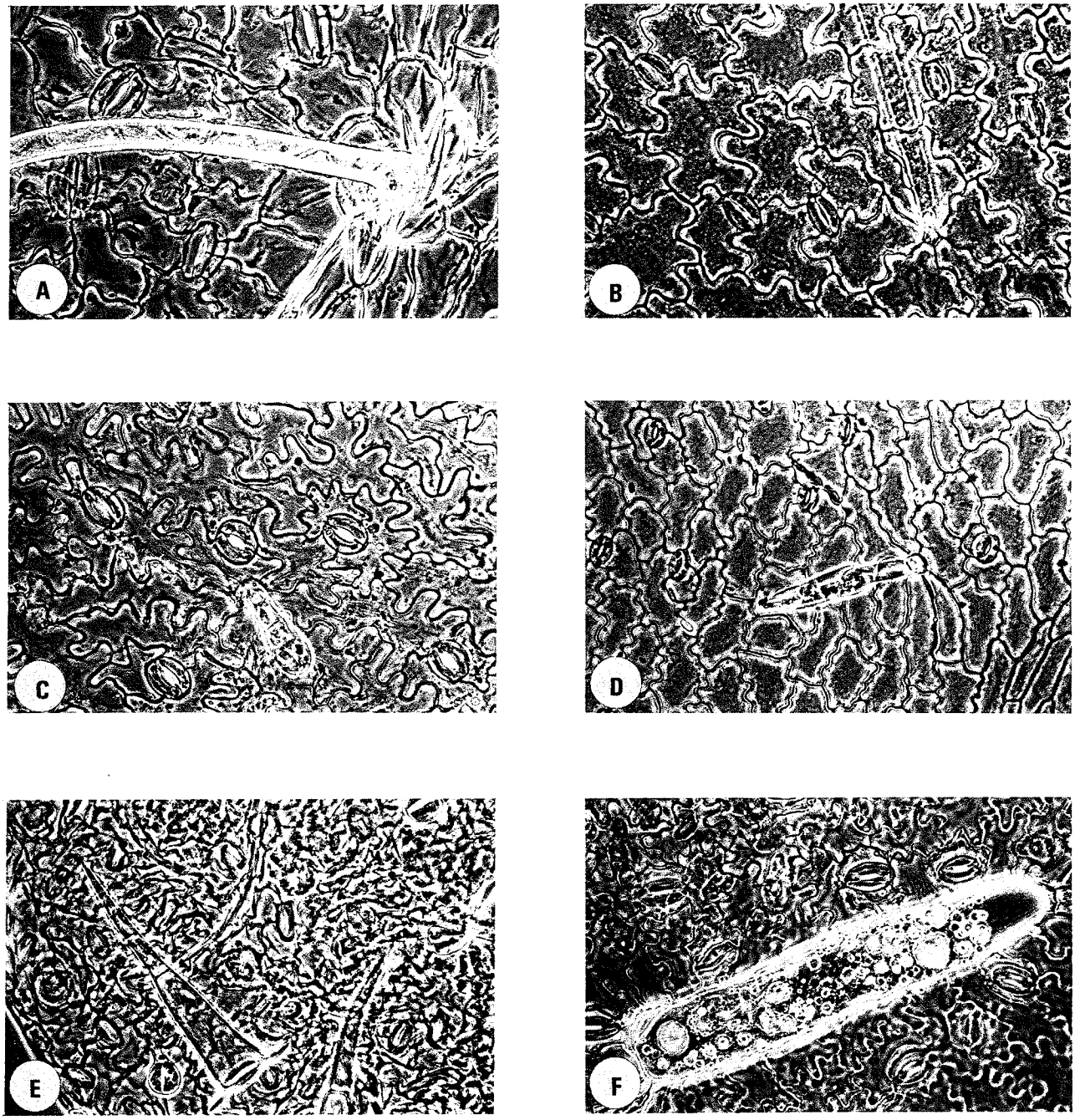


Fig. 5. Examples of epidermal features used in identification of stomach contents. A-Ranunculus abortivus L., epidermal hair. B-Trifolium repens L., epidermal hair. C-Vicia americana Muhl., gland hair. D-Trifolium repens L., gland hair. E-Mitella nuda L., epidermal spines.. F-Galium septentrionale R. & S., spine. All magnified about 320x.

Results and Discussion

A. Distribution of voles

Results of the trapping program conducted on the study grid during the years 1968 through 1971 are shown in Table 1. This shows the total number of *M. pennsylvanicus* caught at each of the sixty-four trapping stations for all four years combined.

B. Distribution of plant species

Table 2 lists the plant species found to be eaten by *Microtus* in this study. The sum of the weights of each species at all sixty-four quadrats is given plus the percentage of the green vegetation represented by each species. The exact weight of each species at each quadrat may be found in Table 1 of the Appendices.

The dominant herb species, by weight, was *Calamagrostis inexpansa*; *Poa* was second in total weight and *Sonchus* third. It is interesting to note that *Trifolium repens* ranked fifth in dominance according to weight although it appeared, from a purely visual assessment of the area, to have been a relatively insignificant member of the plant community.

Statistical analysis was employed to attempt to outline the relationships, if any, between the distribution of voles and the distribution of six plant species on the

Table 1. Combined trapping records for the years 1968-1971.

Station number	Number of captures	Station number	Number of captures
1	1	33	5
2	2	34	5
3	3	35	5
4	3	36	10
5	2	37	2
6	5	38	6
7	5	39	11
8	11	40	7
9	12	41	11
10	4	42	7
11	6	43	7
12	3	44	6
13	1	45	3
14	9	46	3
15	3	47	0
16	5	48	5
17	4	49	2
18	12	50	10
19	7	51	5
20	6	52	11
21	7	53	6
22	4	54	4
23	12	55	5
24	12	56	15
25	8	57	17
26	5	58	10
27	4	59	10
28	9	60	7
29	4	61	13
30	7	62	4
31	3	63	10
32	7	64	3

Table 2. Frequencies of some plant species on the study plot, expressed as total of all weights from all quadrats and percentages of total weight vegetation sampled.

Plant species	Total weight of species (grams)	% of total weight* of quadrats (g.)
Calamagrostis inexpansa Gray var. brevior (Vasey) Stebbins	5611.1	26.36
Poa pratensis L. + Poa nemoralis L.	3928.8	18.46
Sonchus arvensis L.	3091.5	13.58
Carex spp.	1670.2	7.84
Trifolium repens L.	1014.9	4.76
Aster spp.	638.9	3.00
Petasites saggitatus (Pursh.)A. Gray	612.9	2.87
Solidago spp.	560.1	2.63
Bromus inermis Leyss	541.7	2.05
Taraxacum officinale Weber	217.6	1.02
Phleum pratense L.	134.4	0.63
Agropyron repens (L.)Beauv.	129.4	0.60
Fragaria virginiana Duchesne	94.3	0.44
Bromus ciliatus L.	92.8	0.43
Galium septentrionale R.&S.	63.0	0.29
Achillea spp.	41.0	0.19
Melilotus spp. (M. alba Desr. + M. officinalis (L.)Lam.	29.3	0.14
Vicia americana Muhl.	29.0	0.13
Beckmannia syzigachne (Steud.)Fern.	11.8	0.06
Lathyrus ochroleucus Hook.	3.5	0.02
Mitella nuda L.	2.7	0.01

*Total weight of vegetation sampled was 21,283 grams.

Table 3. Correlation coefficient matrix of multiple regression analysis.

	Microtus	*Sonchus*	*Poa*	*Trifolium*	*Taraxacum*	*Carex*	*Calamagrostis*
Microtus	1.00000						
Sonchus arvensis	-.02463	1.00000					
Poa pratensis	.25990	.23000	1.00000				
Trifolium repens	.08355	.48748	.20362	1.00000			
Taraxacum officinale	.07812	.32029	.27050	.36718	1.00000		
Carex spp.	.02724	-.08891	-.34995	-.23618	-.23251	1.00000	
Calamagrostis inexpansa	-.13936	-.33303	-.56354	-.38926	-.38552	.17028	1.00000

study plot.

A step-wise multiple regression analysis using Microtus numbers as the dependent variable and the weights of the six plant species as independent variables, showed that the only species that was significant as a predictor of Microtus numbers at the 95% level was Poa. The simple correlation cefficients among all seven variables are given in Table 3. Degrees of freedom = n-1 = 63 in all cases. Log-transformation of the variables did not change these results.

C. Food habit studies

a. Feeding trials

The results of the food habits tests are shown in Tables 4, 5, and 6. Table 4 gives a list of all plant species tested as well as the total number of visits to each plant by all twelve animals. The third column shows the average number of visits per animal to each plant species and the fourth column gives the standard error for each test. The foregoing data for the seven standard runs are

Table 1. Continued.

Station number	Plant species	Weight (grams)
2	Total	385.3
3	*Poa* spp.	130.7
	Trifolium pratense L.	64.7
	Sonchus arvensis L.	31.5
	Bromus inermis Leyss.	24.0
	Fragaria virginiana Duchesne	13.5
	Cirsium arvense(L.) Scop.	12.1
	Phleum pratense L.	12.1
	Achillea spp.	6.6
	Trifolium repens L.	4.1
	Vicia americana Muhl.	2.9
	Solidago spp.	0.7
	Agropyron repens L.	0.5
	Taraxacum officinale Weber	0.2
	Lathyrus ochroleucus Hook.	0.1
	Lathyrus palustris L.	0.1
	Total	303.8
4	*Poa* spp.	94.7
	Bromus inermis Leyss.	55.0
	Solidago spp.	42.9
	Phleum pratense L.	20.6

Table 1. Continued.

Station number	Plant species	Weight (grams)
4	Sonchus arvensis L.	9.5
	Cirsium arvense (L.) Scop.	6.2
	Achillea spp.	5.1
	Melilotus spp.	2.3
	Vicia americana Muhl.	1.2
	Trifolium repens L.	0.1
	Fragaria virginiana Duchesne	0.1
	Total	237.2
5	Solidago spp.	94.2
	Poa spp.	92.8
	Bromus inermis Leyss.	33.3
	Cirsium arvense(L.) Scop.	18.5
	Sonchus arvensis L.	4.9
	Achillea spp.	3.4
	Galium septentrionale R.&S.	2.7
	Lathyrus ochroleucus Hook.	2.7
	Trifolium repens L.	0.7
	Lathyrus palustris L.	0.3
	Total	253.5
6	Poa spp.	79.8

Table 1. Continued.

Station number	Plant species	Weight (grams)
6	Bromus inermis Leyss.	24.8
	Phleum pratense L.	20.3
	Melilotus spp.	3.1
	Cirsium arvense (L.) Scop.	2.0
	Vicia americana Duchesne	1.1
	Solidago spp.	1.0
	Sonchus arvensis L.	1.0
	Achillea spp.	0.6
	Lathyrus ochroleucus Hook.	0.6
	Total	133.2
7	Sonchus arvensis L.	104.8
	Poa spp.	103.9
	Solidago spp.	63.3
	Bromus inermis Leyss.	23.9
	Cirsium arvense (L.) Scop.	15.8
	Taraxacum officinale Weber	5.5
	Fragaria virginiana Duchesne	4.1
	Melilotus spp.	0.9
	Vicia americana Muhl.	0.2
	Achillea spp.	0.1
	Phleum pratense L.	0.1
	Total	322.5

Table 1. Continued.

Station number	Plant species	Weight (grams)
8	*Poa* spp.	104.0
	Sonchus arvensis L.	47.2
	Bromus inermis Leyss.	40.2
	Phleum pratense L.	23.3
	Cirsium arvense (L.) Scop.	16.2
	Solidago spp.	9.5
	Taraxacum officinale Weber	7.1
	Aster spp.	3.9
	Achillea spp.	2.5
	Trifolium repens L.	2.3
	Vicia americana Muhl.	0.8
	Total	257.5
9	*Poa* spp.	233.3
	Sonchus arvensis L.	102.7
	Calamagrostis inexpansa Gray	45.4
	Solidago spp.	33.9
	Trifolium repens L.	20.1
	Achillea spp.	7.7
	Taraxacum oficinale Weber	7.6
	Ribes hirtellum Michx.	1.0
	Ranunculus macounii Britt.	0.3
	Aster spp.	0.1
	Total	452.1

Table 1. Continued.

Station number	Plant species	Weight (grams)
10	*Calamagrostis inexpansa* Gray	103.3
	Scirpus spp.	67.5
	Poa spp.	32.0
	Carex cristatella Britt.	21.9
	Lycopus americanus Muhl.	11.0
	Equisetum arvense L.	4.0
	Solidago spp.	2.0
	Aster spp.	1.8
	Sonchus arvensis L.	1.2
	Stachys palustris L.	1.0
	Galium labradoricum Wieg.	0.1
	Heuchera richardsonii R. Br.	0.1
	Total	247.5
11	*Calamagrostis inexpansa* Gray	335.0
	Carex cristatella Britt.	10.1
	Scirpus spp.	9.9
	Solidago spp.	9.0
	Poa spp.	3.7
	Sonchus arvensis L.	2.9
	Total	370.6
12	*Poa* spp.	193.8

Table 1. Continued.

Station number	Plant species	Weight (grams)
12	*Solidago* spp.	152.3
	Sonchus arvensis L.	41.3
	Calamagrostis inexpansa Gray	19.6
	Fragaria virginiana Duchesne	16.3
	Trifolium repens L.	9.9
	Bromus ciliatus L.	6.9
	Cirsium arvense (L.) Scop.	2.8
	Phleum pratense L.	1.4
	Agropyron repens L.	0.8
	Vicia americana Muhl.	0.1
	Total	445.2
13	*Solidago* spp.	102.6
	Sonchus arvensis L.	96.1
	Cirsium arvense (L.) Scop.	83.3
	Fragaria virginiana Duchesne	32.7
	Bromus ciliatus L.	21.0
	Poa spp.	17.3
	Taraxacum officinale Weber	10.5
	Agropyron repens L.	7.8
	Trifolium repens L.	7.8
	Calamagrostis inexpansa Gray	5.0
	Mentha arvensis L.	4.8

Table 1. Continued.

Station number	Plant species	Weight (grams)
13	Galium septentrionale R.&S.	2.6
	Achillea spp.	0.1
	Aster spp.	0.1
	Total	391.7
14	Poa spp.	211.7
	Trifolium repens L.	85.7
	Cirsium arvense (L.) Scop.	64.6
	Sonchus arvensis L.	61.6
	Solidago spp.	33.0
	Taraxacum officinale Weber	5.2
	Geum aleppicum Jacq.	0.1
	Vicia americana Muhl.	0.1
	Total	462.0
15	Calamagrostis inexpansa Gray	172.1
	Solidago spp.	113.7
	Sonchus arvensis L.	97.9
	Trifolium repens L.	34.1
	Poa spp.	26.2
	Taraxacum officinale Weber	8.9
	Cirsium arvense (L.) Scop.	7.8
	Vicia americana Muhl.	1.3

Table 1. Continued.

Station number	Plant species	Weight (grams)
15	Achillea spp.	1.0
	Equisetum arvense L.	0.1
	Total	463.1
16	Calamagrostis inexpansa Gray	106.2
	Sonchus arvensis L.	57.7
	Poa spp.	41.5
	Bromus inermis Leyss.	25.7
	Solidago spp.	24.1
	Bromus ciliatus L.	4.9
	Aster spp.	0.1
	Equisetum arvense L.	0.1
	Trifolium repens L.	0.1
	Vicia americana Muhl.	0.1
	Total	261.5
17	Calamagrostis inexpansa Gray	210.6
	Poa spp.	18.5
	Sonchus arvensis L.	17.3
	Cerastium arvense L.	1.6
	Total	248.0
18	Calamagrostis inexpansa Gray	145.0

Table 1. Continued.

Station number	Plant species	Weight (grams)
18	*Sonchus arvensis* L.	87.1
	Poa spp.	55.5
	Solidago spp.	46.3
	Trifolium repens L.	21.0
	Lathyrus palustris L.	1.7
	Cirsium arvense (L.) Scop.	0.1
	Heuchera richardsonii R.Br.	0.1
	Vicia americana Muhl.	0.1
	Total	357.9
19	*Solidago* spp.	63.1
	Poa spp.	42.7
	Trifolium repens L.	40.3
	Achillea spp.	26.0
	Calamagrostis inexpansa Gray	22.7
	Sonchus arvensis L.	20.0
	Cirsium arvense (L.) Scop.	15.5
	Taraxacum officinale Weber	9.9
	Bromus ciliatus L.	2.0
	Fragaria virginiana Duchesne	1.9
	Vicia americana Muhl.	0.1
	Total	245.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
20	*Solidago* spp.	111.7
	Poa spp.	77.0
	Sonchus arvensis L.	76.0
	Cirsium arvense (L.) Scop.	52.0
	Calamagrostis inexpansa Gray	26.5
	Trifolium repens L.	17.5
	Taraxacum officinale Weber	6.5
	Bromus ciliatus L.	4.0
	Achillea spp.	1.1
	Equisetum arvense L.	1.0
	Fragaria virginiana Duchesne	1.0
	Vicia americana Muhl.	1.0
	Total	375.8
21	*Sonchus arvensis* L.	121.0
	Calamagrostis inexpansa Gray	75.0
	Trifolium repens L.	42.0
	Bromus ciliatus L.	37.0
	Solidago spp.	24.0
	Poa spp.	22.0
	Aster spp.	5.0
	Cirsium arvense (L.) Scop.	4.0
	Anemone canadensis L.	2.0
	Aster spp.	0.1

Table 1. Continued.

Station number	Plant species	Weight (grams)
21	Achillea spp.	0.1
	Convolvulus arvensis L.	0.1
	Heuchera richardsonii R. Br.	0.1
	Vicia americana Muhl.	0.1
	Total	333.5
22	Calamagrostis inexpansa Gray	126.5
	Poa spp.	123.7
	Scirpus spp.	20.1
	Cirsium arvense (L.) Scop.	0.1
	Lathyrus palustris L.	0.1
	Solidago spp.	0.1
	Total	271.6
23	Calamagrostis inexpansa Gray	204.7
	Scirpus spp.	76.2
	Carex lanuginosa Michx.	5.7
	Poa spp.	1.0
	Glyceria borealis (Nash.) Batch.	0.2
	Total	287.8
24	Calamagrostis inexpansa Gray	146.4
	Poa spp.	30.7
	Carex lanuginosa Michx.	9.0

Table 1. Continued.

Station number	Plant species	Weight (grams)
24	*Aster* spp.	8.8
	Sonchus arvensis L.	5.3
	Glyceria borealis (Nash.) Batch.	1.2
	Bromus ciliatus L.	0.9
	Cerastium arvense L.	0.4
	Heuchera richardsonii R. Br.	0.1
	Total	202.8
25	*Scirpus* spp.	311.5
	Cirsium arvense (L.) Scop.	34.5
	Sonchus arvensis L.	32.0
	Elymus canadensis L.	9.2
	Calamagrostis inexpansa Gray	8.4
	Solidago spp.	5.4
	Poa spp.	5.2
	Mentha arvensis L.	3.2
	Hordeum jubatum L.	0.2
	Aster spp.	0.1
	Heuchera richardsonii R. Br.	0.1
	Total	409.8
26	*Calamagrostis inexpansa* Gray	184.9
	Aster spp.	53.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
26	*Scirpus* spp.	44.2
	Sonchus arvensis L.	23.0
	Trifolium repens L.	16.2
	Potentilla norvegica L.	13.2
	Fragaria virginiana Duchesne	3.9
	Bromus inermis Leyss.	3.0
	Bromus ciliatus L.	2.5
	Panicum sp.	1.9
	Cerastium arvense L.	1.8
	Cirsium arvense (L.) Scop.	1.7
	Solidago spp.	1.5
	Geum aleppicum Jacq.	1.2
	Heuchera richardsonii R. Br.	0.9
	Carex cristatella Britt.	0.8
	Poa spp.	0.7
	Achillea spp.	0.5
	Aster spp.	0.3
	Hordeum jubatum L.	0.3
	Erigeron philadelphicus L.	0.1
	Total	357.8
27	*Calamagrostis inexpansa* Gray	187.4
	Sonchus arvensis L.	105.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
27	Bromus inermis Leyss.	100.2
	Poa spp.	88.0
	Cirsium arvense (L.) Scop.	37.1
	Aster spp.	13.3
	Scirpus spp.	12.1
	Agropyron repens(L.) Beauv.	6.9
	Geum aleppicum Jacq.	0.8
	Total	551.0
28	Calamagrostis inexpansa Gray	239.4
	Scirpus spp.	61.8
	Cirsium arvense (L.) Scop.	16.0
	Mentha arvensis L.	4.5
	Sonchus arvensis L.	2.3
	Poa spp.	1.0
	Lycopus americanus Muhl.	0.6
	Aster spp.	0.5
	Solidago spp.	0.5
	Cerastium arvense L.	0.1
	Heuchera richardsonii R. Br.	0.1
	Total	326.8
29	Calamagrostis inexpansa Gray	127.8
	Aster spp.	23.1

Table 1. Continued.

Station number	Plant species	Weight (grams)
29	Sonchus arvensis L.	25.1
	Trifolium repens L.	19.3
	Solidago spp.	16.8
	Poa spp.	12.8
	Fragaria virginiana Duchesne	11.1
	Bromus ciliatus L.	6.9
	Carex cristatella Britt.	5.4
	Geum aleppicum Jacq.	3.6
	Mentha arvensis L.	3.0
	Equisetum arvense L.	2.7
	Agropyron repens (L.) Beauv.	2.5
	Panicum sp.	1.7
	Achillea spp.	1.3
	Taraxacum officinale Weber	1.2
	Cerastium arvense L.	0.2
	Cirsium arvense (L.) Scop.	0.2
	Total	264.7
30	Calamagrostis inexpansa Gray	95.3
	Sonchus arvensis L.	55.5
	Solidago spp.	53.2
	Trifolium repens L.	28.0
	Galium sepentrionale R.&S.	22.0

Table 1. Continued.

Station number	Plant species	Weight (grams)
30	*Poa* spp.	19.2
	Lathyrus palustris L.	3.8
	Achillea spp.	0.6
	Taraxacum officinale Weber	0.6
	Bromus ciliatus L.	0.3
	Cerastium arvense L.	0.1
	Total	278.6
31	*Calamagrostis inexpansa* Gray	109.3
	Aster spp.	30.9
	Sonchus arvensis L.	8.5
	Solidago spp.	7.3
	Carex projecta Mack.	6.1
	Fragaria virginiana Duchesne	4.0
	Poa spp.	1.9
	Lycopus americanus Muhl.	1.2
	Trifolium repens L.	1.2
	Carex cristatella Britt.	0.3
	Cerastium arvense L.	0.1
	Heuchera richardsonii R. Br.	0.1
	Total	171.7
32	*Calamagrostis inexpansa* Gray	133.8

Table 1. Continued.

Station number	Plant species	Weight (grams)
34	Mentha arvensis L.	5.5
	Epilobium latifolium L.	1.3
	Sonchus arvensis L.	1.3
	Equisetum arvense L.	0.8
	Cerastium arvense L.	0.6
	Cicuta maculata L.	0.6
	Hordeum jubatum L.	0.4
	Bromus ciliatus L.	0.2
	Total	164.2
35	Calamagrostis inexpansa Gray	382.0
	Solidago spp.	60.1
	Carex lanuginosa Michx.	47.3
	Sonchus arvensis L.	9.1
	Bromus ciliatus L.	0.1
	Total	498.6
36	Petasites saggitatus (Pursh.) A. Gray	322.5
	Calamagrostis inexpansa Gray	191.1
	Carex lanuginosa Michx.	68.7
	Cirsium arvense (L.) Scop.	40.4
	Solidago spp.	1.1

Table 1. Continued.

Station number	Plant species	Weight (grams)
36	Heuchera richardsonii R. Br.	0.9
	Cicuta maculata L.	0.4
	Lycopus americanus Muhl.	0.1
	Total	625.2
37	Petasites saggitatus (Pursh.) A. Gray	290.4
	Carex lanaginosa Michx.	43.5
	Calamagrostis inexpansa Gray	39.7
	Sonchus arvensis L.	26.4
	Cirsium arvense (L.) Scop.	17.0
	Poa spp.	5.2
	Bromus inermis Leyss.	1.8
	Aster spp.	1.0
	Geum aleppicum Jacq.	0.6
	Total	425.6
38	Sonchus arvensis L.	83.1
	Calamagrostis inexpansa Gray	74.2
	Cirsium arvense (L.) Scop.	66.8
	Agropyron repens (L.) Beauv.	43.2
	Poa spp.	59.6
	Potentilla norvegica L.	13.6

Table 1. Continued.

Station number	Plant species	Weight (grams)
38	Anemone canadensis L.	6.8
	Carex scoparia Schk.	6.6
	Taraxacum officinale Weber	6.1
	Trifolium repens L.	3.8
	Bromus ciliatus L.	3.2
	Lathyrus palustris L.	3.0
	Erigeron philadelphicus L.	2.4
	Achillea spp.	1.7
	Carex aurea Nutt.	0.3
	Cerastium arvense L.	0.1
	Hordeum jubatum L.	0.1
	Lycopus americanus Muhl.	0.1
	Total	364.8
39	Sonchus arvensis L.	99.6
	Aster spp.	78.8
	Poa spp.	47.1
	Calamagrostis inexpansa Gray	33.7
	Solidago spp.	32.9
	Trifolium repens L.	28.4
	Taraxacum officinale Weber	4.4
	Achillea spp.	2.2
	Hordeum jubatum L.	0.6
	Equisetum arvense L.	0.4

Table 1. Continued.

Station number	Plant species	Weight (grams)
39	Panicum sp.	0.1
	Erigeron philadelphicus L.	0.1
	Total	328.3
40	Sonchus arvensis L.	247.3
	Solidago spp.	132.5
	Carex lanuginosa Michx.	128.3
	Calamagrostis inexpansa Gray	57.9
	Poa spp.	27.7
	Potentilla norvegica L.	15.5
	Cirsium arvense (L.) Scop.	14.2
	Erigeron philadelphicus L.	6.9
	Bromus inermis Leyss.	5.4
	Trifolium repens L.	3.8
	Cerastium arvense L.	3.2
	Panicum sp.	2.7
	Carex projecta Mack.	0.8
	Agropyron repens (L.) Beauv.	0.7
	Hordeum jubatum L.	0.2
	Total	647.1
41	Calamagrostis inexpansa Gray	220.7

Table 1. Continued.

Station number	Plant species	Weight (grams)
41	Poa spp.	64.6
	Solidago spp.	54.9
	Sonchus arvensis L.	6.2
	Cirsium arvense (L.) Scop.	4.9
	Total	351.3
42	Poa spp.	128.6
	Sonchus arvensis L.	65.9
	Aster spp.	26.2
	Cirsium arvense (L.) Scop.	20.4
	Taraxacum officinale Weber	12.2
	Erigeron philadelphicus L.	3.8
	Trifolium repens L.	3.8
	Potentilla norvegica L.	3.0
	Anemone canadensis L.	2.9
	Cerastium arvense L.	2.5
	Salix bebbiana Sarg.	1.7
	Achillea spp.	1.4
	Vicia americana Muhl.	1.3
	Equisetum arvense L.	0.7
	Hordeum jubatum L.	0.3
	Panicum sp.	0.1
	Total	274.8

Table 1. Continued.

Station number	Plant species	Weight (grams)
43	Poa spp.	91.3
	Sonchus arvensis L.	82.7
	Trifolium repens L.	38.9
	Taraxacum officinale Weber	35.1
	Solidago spp.	11.4
	Agropyron repens (L.) Beauv.	10.9
	Carex projecta Mack.	7.1
	Calamagrostis inexpansa Gray	5.7
	Cirsium arvense (L.) Scop.	5.5
	Carex cristatella Britt.	1.9
	Bromus inermis Leyss.	1.7
	Hordeum jubatum L.	1.2
	Achillea spp.	0.9
	Elymus canadensis L.	2.7
	Melilotus spp.	0.7
	Vicia americana Muhl.	0.5
	Total	298.2
44	Solidago spp.	215.1
	Sonchus arvensis L.	70.2
	Trifolium repens L.	49.0
	Poa spp.	22.1
	Taraxacum officinale Weber	16.4
	Vicia americana Muhl.	7.0
	Agropyron repens (L.) Beauv.	5.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
44	*Agropyron repens* (L.) Beauv.	5.2
	Erigeron philadelphicus L.	3.7
	Mentha arvensis L.	1.0
	Achillea spp.	0.1
	Panicum sp.	0.1
	Total	389.9
45	*Carex lanuginosa* Michx.	55.3
	Carex scoparia Schk.	41.5
	Trifolium repens L.	35.2
	Poa spp.	34.2
	Sonchus arvensis L.	28.3
	Cirsium arvense (L.) Scop.	18.7
	Carex cristatella Britt.	3.1
	Achillea spp.	3.0
	Hordeum jubatum L.	2.2
	Calamagrostis inexpansa Gray	1.3
	Agropyron repens (L.) Beauv.	0.7
	Aster spp.	0.6
	Cerastium arvense L.	0.3
	Panicum sp.	0.1
	Total	216.5

Table 1. Continued.

Station number	Plant species	Weight (grams)
46	*Calamagrostis inexpansa* Gray	194.8
	Aster spp.	159.8
	Sonchus arvensis L.	3.8
	Carex lanuginosa Michx.	1.7
	Poa spp.	0.8
	Total	360.9
47	*Calamagrostis inexpansa* Gray	334.7
	Aster spp.	148.3
	Carex lanuginosa Michx.	23.4
	Equisetum arvense L.	1.8
	Sonchus arvensis L.	0.5
	Poa spp.	0.4
	Panicum spp.	0.2
	Total	509.3
48	*Calamagrostis inexpansa* Gray	268.2
	Scirpus spp.	75.3
	Poa spp.	1.5
	Lathyrus palustris L.	0.9
	Cerastium arvense L.	0.7
	Sonchus arvensis L.	0.3
	Aster spp.	0.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
48	Total	347.1
49	Sonchus arvensis L.	104.6
	Poa spp.	86.1
	Trifolium repens L.	39.2
	Achillea spp.	29.3
	Calamagrostis inexpansa Gray	23.8
	Carex lanuginosa Michx.	7.4
	Agropyron repens (L.) Beauv.	4.6
	Erigeron philadelphicus L.	0.9
	Hordeum jubatum L.	0.6
	Carex cristatella Britt.	0.5
	Carex scoparia Schk.	3.0
	Solidago spp.	0.1
	Galium sepentrionale R.&S.	0.1
	Total	309.2
50	Calamagrostis inexpansa Gray	78.4
	Carex lanuginosa Michx.	70.3
	Scirpus spp.	54.1
	Poa spp.	39.6
	Solidago spp.	2.2
	Hordeum jubatum L.	1.1

Table 1. Continued.

Station number	Plant species	Weight (grams)
50	*Sonchus arvensis* L.	0.7
	Trifolium repens L.	0.5
	Total	246.9
51	*Calamagrostis inexpansa* Gray	183.0
	Poa spp.	24.9
	Sonchus arvensis L.	22.8
	Aster spp.	9.2
	Scirpus spp.	6.9
	Lathyrus palustris L.	1.3
	Trifolium repens L.	1.1
	Total	249.2
52	*Poa* spp.	138.3
	Agropyron repens (L.) Beauv.	32.7
	Cirsium arvense (L.) Scop.	24.0
	Trifolium repens L.	18.0
	Solidago spp.	13.6
	Phleum pratense L.	12.0
	Bromus inermis Leyss.	6.5
	Sonchus arvensis L.	2.9
	Taraxacum officinale Weber	2.8
	Vicia americana Muhl.	0.6

Table 1. Continued.

Station number	Plant species	Weight (grams)
52	Bromus ciliatus L.	0.1
	Fragaria virginiana Duchesne	0.1
	Total	251.6
53	Poa spp.	84.1
	Solidago spp.	64.5
	Sonchus arvensis L.	41.8
	Trifolium repens L.	36.7
	Taraxacum officinale Weber	10.7
	Cirsium arvense (L.) Scop.	10.0
	Total	247.8
54	Poa spp.	88.9
	Trifolium repens L.	37.0
	Phleum pratense L.	34.2
	Sonchus arvensis L.	22.0
	Agropyron repens (L.) Beauv.	15.8
	Solidago spp.	14.4
	Taraxacum officinale Weber	14.3
	Cirsium arvense (L.) Scop.	11.4
	Vicia americana Muhl.	3.2
	Fragaria virginiana Duchesne	0.4
	Melilotus spp.	0.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
54	Total	241.8
55	*Sonchus arvensis* L.	252.3
	Poa spp.	143.9
	Taraxacum officinale Weber	20.3
	Trifolium repens L.	20.2
	Melilotus spp.	8.1
	Vicia americana Muhl.	0.9
	Hordeum jubatum L.	0.2
	Achillea spp.	0.1
	Bromus ciliatus L.	0.1
	Total	446.1
56	*Poa* spp.	248.8
	Bromus inermis Leyss.	30.1
	Sonchus arvensis L.	19.2
	Elymus canadensis L.	2.8
	Fragaria virginiana Duchesne	1.9
	Trifolium repens L.	1.4
	Hordeum jubatum L.	1.3
	Achillea spp.	0.2
	Aster spp.	0.2
	Solidago spp.	0.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
56	Equisetum arvense L.	0.1
	Total	306.2
57	Poa spp.	176.1
	Galium septentrionale R.&S.	38.7
	Sonchus arvensis L.	36.8
	Trifolium repens L.	26.6
	Solidago spp.	19.1
	Taraxacum officinale Weber	6.4
	Agropyron repens (L.) Beauv.	2.2
	Hordeum jubatum L.	2.2
	Fragaria virginiana Duchesne	0.4
	Total	308.5
58	Solidago spp.	192.8
	Calamagrostis inexpansa Gray	70.1
	Cirsium arvense (L.) Scop.	34.6
	Sonchus arvensis L.	11.9
	Poa spp.	8.0
	Anemone canadensis L.	5.2
	Hordeum jubatum L.	2.1
	Galium septentrionale R.&S.	1.9
	Trifolium repens L.	0.8
	Lycopus americanus Muhl.	0.6

Table 1. Continued.

Station number	Plant species	Weight (grams)
58	*Melilotus* spp.	0.2
	Total	328.2
59	*Trifolium repens* L.	116.7
	Sonchus arvensis L.	104.3
	Cirsium arvense (L.) Scop.	93.9
	Poa spp.	74.4
	Calamagrostis inexpansa Gray	1.9
	Hordeum jubatum L.	1.5
	Phleum pratense L.	0.9
	Achillea spp.	0.1
	Bromus ciliatus L.	0.1
	Total	396.9
60	*Poa* spp.	109.7
	Sonchus arvensis L.	59.1
	Cirsium arvense (L.) Scop.	56.4
	Trifolium repens L.	44.0
	Taraxacum officinale Weber	25.4
	Melilotus spp.	12.8
	Calamagrostis inexpansa Gray	6.7
	Vicia americana Muhl.	5.6
	Agropyron repens (L.) Beauv.	4.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
60	Bromus ciliatus L.	0.4
	Total	324.3
61	Anemone canadensis L.	91.8
	Poa spp.	74.2
	Galium septentrionale R.&S.	33.8
	Sonchus arvensis L.	6.9
	Phleum pratense L.	5.6
	Taraxacum officinale Weber	5.3
	Cirsium arvense (L.) Scop.	5.1
	Agropyron repens (L.) Beauv.	3.5
	Fragaria virginiana Duchesne	3.4
	Achillea spp.	2.9
	Hordeum jubatum L.	2.2
	Trifolium repens L.	1.8
	Bromus ciliatus L.	1.5
	Lathyrus palustris L.	0.4
	Viola nephrophylla Greene	0.1
	Total	238.5
62	Calamagrostis inexpansa Gray	90.1
	Poa spp.	12.1
	Beckmannia syzigachne (Steud.) Fern.	11.8

Table 1. Continued.

Station number	Plant species	Weight (grams)
62	Agropyron repens (L.) Beauv.	9.9
	Solidago spp.	3.0
	Hordeum jubatum L.	1.8
	Saggitaria cuneata Sheld.	0.6
	Aster spp.	0.2
	Trifolium repens L.	0.1
	Total	129.6
63	Calamagrostis inexpansa Gray	151.1
	Carex projecta Mack.	67.0
	Poa spp.	33.8
	Carex cristatella Britt.	6.8
	Equisetum arvense L.	2.7
	Hordeum jubatum L.	1.4
	Trifolium repens L.	1.4
	Aster spp.	0.2
	Total	264.4
64	Sonchus arvensis L.	194.3
	Poa spp.	54.3
	Trifolium repens L.	50.9
	Calamagrostis inexpansa Gray	47.3
	Cirsium arvense (L.) Scop.	28.2

Table 1. Continued.

Station number	Plant species	Weight (grams)
64	Agropyron repens (L.) Beauv.	8.9
	Vicia americana Muhl.	6.6
	Bromus ciliatus L.	0.2
	Achillea spp.	0.1
	Total	380.8

Table 4. Results of preference tests showing plant species tested, total visits to each plant species, and average number of visits to each species per animal with the standard error of this average.

Species tested	Total visits of 12 animals	Average per animal	Standard error
Mentha arvensis L.*	1531	218.7	20
Bromus inermis	2455	204.6	11
Phleum pratense	2447	203.9	13
Taraxacum officinale	2320	193.3	5
Galium septentrionale	2294	191.0	10
Carex lanuginosa Michx.	2144	178.6	10
Melilotus spp.	2138	178.1	10
Trifolium repens	2117	176.4	6
Agropyron repens	2089	174.0	13
Fragaria virginiana	2061	171.8	11
Lathyrus ochroleucus	2069	172.4	7
Vicia americana	1991	165.9	12
Trifolium pratense L.	1926	160.5	11
Lycopus sp.	1922	160.1	11
Hordeum jubatum L.	1879	156.6	12
Solidago spp.	1854	154.5	7
Cirsium arvense	1836	153.0	10
Achillea spp.	1833	152.8	7
Elymus canadensis L.	1797	149.8	5
Poa pratensis	1724	143.7	10
Aster spp.	1679	139.9	8
Lathyrus palustris	1621	135.0	8
Calamagrostis inexpansa	1616	134.7	9
Petasites sagittatus	1331	110.9	8
Sonchus arvensis	1268	105.7	9
Astragalus canadensis L.	1240	103.3	8

*In this trial, only 7 animals were used.

Table 5. Results of preference test standard runs showing the total number of visits to the empty baskets for each trial and the average number of visits per animal with the standard error.

Number of Trial	Total visits of 12 animals	Average per animal	Standard error
1	1315	109.6	7
2	860	71.7	6
3	1131	94.2	10
4	1233	108.2	6
5	1064	88.7	6
6	1407	117.2	8
7	1445	120.4	8

Table 6. Results of preference tests showing degree of preference and preference index number for each species

Species tested	Degree of preference	Preference index
Mentha arvensis	122	1.00
Bromus inermis	104	0.85
Phleum pratense	103	0.84
Taraxacum officinale	92	0.75
Galium septentrionale	90	0.73
Carex lanuginosa	78	0.64
Melilotus spp.	77	0.63
Trifolium repens	75	0.61
Bromus ciliatus	74	0.60
Agropyron repens	73	0.59
Fragaria virginiana	72	0.58
Lathyrus ochroleucus	71	0.58
Vicia americana	66	0.54
Trifolium pratense	60	0.49
Lycopus sp.	59	0.48
Hordeum jubatum	56	0.46
Solidago spp.	54	0.44
Achillea spp.	53	0.43
Elymus canadensis	49	0.40
Poa pratensis	43	0.35
Aster spp.	39	0.32
Lathyrus palustris	34	0.28
Calamagrostis inexpansa	34	0.28
Petasites sagittatus	10	0.08
Sonchus arvensis	4	0.03
Astragalus canadensis	2	0.01

given in Table 5 along with the overall average number of visits to the empty baskets per animal for all seven runs combined. This is the estimate of activity in the food chambers not related to the presence of the plant species. Table 6 gives the degree of preference and the preference index for each species as described in the methods section.

The standard error of the preference test runs averaged just under ten percent. The highest error, twenty percent was with Mentha arvensis. Probably this was because only seven animals were used for this test. The relatively high degree of error associated with all the tests may be due to the differing activity patterns among the voles. While some ventured out of their nests only once or twice a night, others were continually active, taking short rest periods once or twice a night. Individuals were quite consistent in their type of activity pattern, however.

The responses of the voles to the various plant species were markedly different. In some cases the chopped plants were pulled from the baskets immediately and, by the next evening, were consumed almost entirely. This was the case with highest scoring plants, such as Mentha, Bromus inermis, Taraxacum and even Lathyrus ochroleucus and Vicia. Other plants were not removed from the baskets completely, and what was pulled out was only partly eaten. Sometimes the baskets were

hardly touched. This happened with Lathyrus palustris and Astragalus.

Only one plant seemed to score higher than it should have done in the preference test as compared to the quantity of food actually eaten from the baskets. This was Hordeum jubatum. It was pulled out of the baskets readily, but it seemed that the animals wanted it for nesting material rather than for food. The soft "squirrel tail" heads were collected and carried into the nesting chamber to add to the nests which were already of considerable size. This phenomenom also occurred with Poa in several cases. However, the bluegrass was eaten more than Hordeum. Therefore, on the basis of palatability alone, it is likely that Hordeum should have scored lower than Poa in the preference index.

The presence of many leguminous species in the upper half of the preference list agrees with the results of Thompson (1965) who found that M. ochrogaster preferred introduced grasses and legumes in grazing trials. The presence of one legume, Astragalus, at the bottom of the list may be due to the fact that it is a very erect, tough, bush-like species. It also may be poisonous to sheep and cattle if it grows on high selenium soils. The preferred legumes, Trifolium, Melilotus, Lathyrus ochroleucus, and Vicia are more succulent plants that bear at least some green shoots at ground level. The fact that legumes have a notably high protein level (Morrison, 1949) may account in part for the utilization of these species. Golley (1960) felt that voles

may augment their diets with such high-protein foods as legumes and insects. Although further results of this thesis indicated that insects were not frequently eaten, the presence of fairly large quantities of legumes on the plot may have provided a soure of protein. It would be interesting to study whether or not a dearth of legumes may result in increased insect consumption.

b. Analysis of stomach contents

The results of the stomach analysis are shown in Table 7. This gives the species of plants represented in the stomachs and the actual number of stomachs in which each plant was found as well as the percentage of stomachs in which each was found. The second column shows the percentage of the total vegetation weight sampled from the quadrats represented by each plant species.

If a preferred food is defined, not as the food most frequently consumed,but as the food most frequently consumed in relation to its availability, one can create a second preference list by subtracting from the the percentage of animals eating a particular species the frequency of that species as expressed by weight percentage. Table 8 presents the order of preference which results from such computations. Comparison of this list with the one derived from the preference tests shows some agreement between them. The majority of the high positive values in Table 8 are also concentrated in the upper

Table 7. Results of stomach analysis showing the number of stomachs in which each plant species was found as well as the percentage of stomachs in which it was found and the percentage by weight of each species of the total vegetation sampled.

Species	% of total weight	No. of stomachs in which found	% of stomachs
Sphagnum		51	34
Carex spp.	7.84	39	26
Roots		34	23
Melilotus spp.	1.33	31	21
Trifolium repens	4.76	29	19
Endogone sp.		27	18
Poa spp.	18.46	27	18
Vicia americana	0.13	24	16
Taraxacum officinale	1.02	22	15
Agropyron repens	0.60	21	14
Solidago spp.	2.63	19	13
Bromus inermis	2.05	17	12
Seeds		15	10
Bromus ciliatus	0.43	14	9
Beckmannia syzigachne	0.06	13	9
Calamagrostis inexpansa	26.36	12	8
Phleum pratense	0.63	11	7
Lathyrus ochroleucus	0.02	7	5
Unidentified fungi		7	5
Mitella nuda	0.01	6	4
Achillea spp.	0.19	5	3
Sonchus arvensis	13.58	5	3
Insects		4	3
Galium septentrionale	0.29	4	3
Fragaria virginiana	4.41	3	2
Petasites sagittatus	2.87	2	1

Table 8. List of preference values derived by subtracting the percentage of the total vegetation represented by each plant species from the percentage of stomachs in which each species was found.

Species	Preference value
Melilotus spp.	19.0
Carex spp.	18.0
Vicia americana	16.0
Trifolium repens	14.5
Taraxacum officinale	13.5
Agropyron repens	13.3
Bromus inermis	10.0
Solidago spp.	10.0
Phleum pratense	6.6
Lathyrus ochroleucus	4.6
Achillea spp.	3.1
Galium septentrionale	2.3
Poa pratensis	0.0
Petasites saggitatus	- 1.5
Fragaria virginiana	-22.4
Sonchus arvensis	-10.6
Calamagrostis inexpansa	-18.4

half of Table 6 while the lower half of the preference test list shows few species which occurred regularly in the stomachs. The two greatest exceptions to this general pattern were Mentha which was not found in any stomachs but scored highest in the feeding trials, and Solidago which was quite common in the stomachs but scored low on the feeding trial list.

The absence of Mentha in the stomachs is possibly explained by its extreme scarcity on the study plot. It was found in only one quadrat of the sixty-four. However, when this plant was provided for the voles, they ate it readily. The significance of this preference for such a rare component of the plant community is difficult to assess on the strength of such little evidence. Whether or not Mentha is actually sought out and forms a regular, albeit small, fraction of the diet is completely unanswerable from this study.

The low preference index of Solidago in comparison to its frequency in the stomachs may be easier to explain. When the feeding trial was performed, the plant material used in the Solidago test was composed of both mature and immature specimens. However, mature plants predominated and, as these are rather woody, they may not have been palatable to the voles. Zimmerman (1965) found that Solidago was not eaten but suggested that it might be used more often in the spring when it was young and tender. Therefore, the low preference index probably resulted from the voles' eating

the young Solidago and discarding the older pieces which were certainly not eaten by the end of the test. In the field, the animals would feed selectively on the young plants which would account for the Solidago in the stomachs. Perhaps a food preference list would change from season to season depending on the stage of growth of the various plants, but it is likely that such a list gives an indication of the real food preferences existing at the time of the experiment.

The concurrence between the results of the two examinations of food preferences seems to indicate that certain food species were indeed preferred. Such items as Melilotus, Carex, Triflium repens, Agropyron, Taraxacum and Bromus inermis seemed to be preferred over such items as Calamagrostis, Poa, Elymus, and Hordeum. The preference for a number of non-graminoid species suggests that they play a more important role in vole diets than is generally supposed. Possibly food cutting examinations may tend to underestimate the number of such species consumed since they may be eaten almost completely, unlike grasses from which pieces of older leaves and stems may be discarded. Also, leftover bits of such plants would quickly shrivel so as to become very difficult to identify in a food midden. Stomach analysis methods may also tend to overestimate the importance of grasses unless the composition of the plant community is known. It may become apparent that less energy is expended consuming available grasses than in searching for other plants.

The most interesting item on the food preference lists

is, perhaps, Poa. While showing a significant degree of association with the numbers of Microtus, it scored low on the preference tests and showed no degree of preference when the frequency in the stomachs was compared to the frequency on the plot. Feeding studies by Golley (1960) suggested that M. pennsylvanicus could not live on Poa alone, although Dice (1922) was able to maintain them on this diet. Morrison (1949) found that the protein content of Poa was low compared to the content of alfalfa, but a comparison of the nutritional qualities of other vole food species would be necessary to determine whether or not this factor influences the selection of Poa.

Zimmerman (1965) found that Poa and Muhlenbergia were most frequent in vole stomachs and most prevalent on the study area. Getz (1971) found no positive correlation with bluegrass but cover seemed to be important. Since Poa provides good cover, it may be argued that this is the reason why Microtus seems to be associated with the occurrence of Poa, without the necessity of Poa being a preferred food. The correlation coefficients of Table 3, on the other hand, indicates that food preferences may still influence Microtus to live in stands of Poa since this species often grows in association with preferred plant species such as Trifolium and Taraxacum. If cover were the most important consideration, voles should have been correlated with Calamagrostis since this grass probably provided the best cover on the plot. The greatest difference between stands of Poa and Calamagrostis

is that hte former allows the growth of other herb species in conjunction with the grass while the latter forms a tall, dense canopy which prohibits the growth of all but the hardiest herbs such as Solidago and Aster. Therefore, a grassy area dominated by Poa but supporting a good admixture of other herbs may provide the best opportunity for voles to obtain a varied (and, perhaps, therefore balanced) diet. This problem of food preferences as a reflection of dietary requirements is currently unsolvable as little is known of the nutritional qualities of wild plants or the dietary requirements of wild animals.

In short, the relationship between Poa and Microtus is probably influenced by a number of factors, the least of which would seem to be palatability of bluegrass itself. The provision of cover, the availability of other varieties of plants, and possibly the provision of a soft, easily manipulated nesting material may all be important to the relationship. It has been mentioned that Poa was woven into the nests during the feeding trials while coarser grasses like Calamagrostis never were.

Certain items in the stomachs could not be analyzed in terms of preference. Sphagnum, for example, was not weighed as a separate fraction of the samples because its strands were often mixed with the litter and soil. It seems that it might have been worthwhileto have attempted to separate this moss in view of its high frequency in the stomachs. However, when the quadrats were being cut, Sphagnum did not seem to comprise

a large fraction of the groundcover. The fact that underground stems and roots were often found with Carex stems and leaves in the gut suggests that the underground parts were of Carex origin. If this was so, moss may have been ingested with the roots since Sphagnum often exists with Carex. Koshkina (1961) found, with the Norwegian lemming, Lemmus lemmus, that the underground parts of sedges were often preferred to the aboveground parts and that mosses were widely eaten, although Sphagnum was not eaten as much as leafy mosses such as Polytrichum.

The consumption of underground plant parts may account, in part, for the large quantities of Endogone in the stomachs. This polyphagous fungus is parasitic on plant roots and other fungi and may have been ingested with roots or particles of soil. On the other hand, Endogone has been reported in small mammals by a number of workers including Diehl (1939), Dowding (1955 and 1959), Bakerspiegal (1956 and 1968), Whittaker (1962) and Williams and Finney (1964). Both Bakerspiegal (1958) and Williams and Finney stated that it is difficult to isolate Endogone from the soil and, therefore, it is possible that the fungus is only eaten coincidentally with other foods. However, Endogone may be more obvious to voles than it is to people. Tevis (1952) observed chipmunks purposefully digging up and eating underground fungi and the forest floor was pitted as a result of these excavations. Bakerspiegal (1958) stated that the variety of Endogone which appears most often in western Canada, Endogone fasciculata Thaxter, has extremely small fruiting bodies which may not occur frequently enough to be eaten by rodents. Obviously

the question of preference regarding this food is a thorny one. In this study, Endogone appeared as the only item in four stomachs. This would seem to indicate that the fungus was eaten alone and in some quantity and that the voles must have searched for it. In other cases, the fungus may have been ingested with the roots, but also the roots may have been ingested with the Endogone and it is impossible to even speculate on the preference.

Seeds appeared in ten percent of the stomach samples. In one case, leguminous seeds, probably Vicia, were the sole contents of a stomach. Small seeds were often found in conjunction with Melilotus and Trifolium and were thought to be seeds of these species. Grain seed coats were evident in a number of stomachs but never constituted the entire contents or even a large proportion of the sample. Whether or not seeds were actively sought out cannot be determined from these data and, although the presence or absence of seeds may affect the degree of preference toward a species, this could not be tested here.

Insects were present in only four percent of the stomachs and in each case only one or two small fragments of insect remains were found. In one case the insect was believed to be a flea ingested during grooming but positive identification could not be made on the basis of the small amount of insect material found. Certainly, insects did not comprise a large part of the trapped voles' intake. This agrees with the results of Golley (1960), Zimmerman (1965) and Batzli and Pitelka (1971).

D. Significance of food preferences

The significance of food preferences in small mammal population dynamics is difficult to quantify,but a body of work on this topic is rapidly growing and patterns are beginning to form.

While the environment seems to affect the distribution of Microtus to the point of generalized habitat preferences (Buckner,1957; DeCoursey,1957; Morris,1955; Getz, 1960,1961,1970,1971; Warnock,1965; and Zimmerman,1965), it is also recognized that Microtus affects its environment. Summerhayes (1941), Formozov and Kodachova (1961), Koshkina (1961) and Smirnov and Tokmakova (1971) have all shown that the activities of voles affect the plant community. Summerhayes found a decrease in the prevalence of angiosperms other than the dominant species and an almost total lack of mosses when voles were excluded from the study area. It was felt that this effect was due to increased vigour of the dominant species following the removal of vole attack. Also, underground stems were found to be clipped off when voles were feeding on the plots. Smirnov and Tokmakova (1971) found that tundra plants bore more vegetative shoots but fewer inflorescences when vole numbers were high and Koshkina (1961) noted that flowering shoots and green mosses were greatly depleted in years of high vole abundance.

What do voles require of a habitat besides cover? Getz (1969) found that removal of cover did not cause M.

pennsylvanicus to leave home ranges although many animals were taken by crows due to lack of shelter. These animals were survivors during a population low and had chosen a marshy site although nearby fields seemed to offer plenty of food and cover. The fact that the animals remained even without cover indicates that the site offered more than protection. Evidence from this thesis study and from other studies previously cited possibly offers part of the explanation on the basis of food preferences. If underground plant parts, particularly those of sedges, are much preferred food items, as they seem to be, this may be one factor in the choice of marshy sites.

Some authors persist in disregarding food shortage as being limiting to populations because there seems to be no obvious damage to the standing vegetation. Such opinions have been voiced by Chitty (1952), Barbehenn (1955), Godfrey (1955), Krebs and DeLong (1965), Murray (1965), ans Krebs et al (1969). Godfrey pointed out that the field was full of grass and that the voles were known to eat all the species of grass available. However, while this is doubtless strictly true, the palatability and nutritional qualities of the grasses were totally unknown. The fact that a plant may be eaten occasionally does not prove that the creature can subsist on large quantities of that species alone. In short, the effect of the plant on the animal must be considered as well as the effect of the animal on the plant.

The factor of food quality and its effect on pop-

ulations is just beginning to be investigated. Certainly outright starvation can affect the reproductive rates of the population, especially if it occurs at a critical period such as just before conception (McLure,1958). Food chemistry is much more difficult to study but some work is proceeding in this line. Bickoff et al (1959) extracted estrogens from forages and Negus and Pinter (1966) proved that such hormones in fresh plants and extracts can certainly affect reproduction in Microtus. The relationship between levels of estrogens in the diet and population densities of small mammals has yet to be explored fully. Stodart and Myers (1966) found that green food produced greater fecundity in rabbits plus less disease among the young, as compared to the effects of dry food. The relationship of such results to food preferences may be inferred from a study by Hansen and Ueckert (1970) in which they found that forcing animals to feed on non-preferred foods generally decreased survival, longevity, fecundity, body size and proportions, and rate of development. They also stressed the variation in the nutritive value of plants from season to season and among species.

When it is known that food causes such effects and that animals feed selectively, it is plain that no generalization about the adequacy of a population's diet can be made from a cursory glance at the standing crop of the dominant species.

The literature review cited in the first part of this thesis quoted Nicholson (1933) and Chitty (1960) to

the effect that an environmental factor such as food or weather must operate with a density dependent factor if the population is to be controlled. Numerous possible interactions with respect to food have been postulated. Scheffer (1958) felt that increasing populations resulted in decreasing food supply with a resultant increase in strife. Smaller animals would then be killed in the resulting battles leaving a smaller population of larger animals. Jameson (1955) also felt that stress due to food shortage was the cause of population declines but could not define the expression of this stress. Southwick (1955) offered data from a confined house mouse population in which dominant mice prevented subordinates from feeding freely at high population levels even if food was abundant. The result was declining fecundity. Bendell (1959) felt that while food was an important factor, it acted more to intensify the effect of another factor such as weather. For example, the young might suffer as a result of a nutritional deficiency of the mother and adverse weather might result in a high death rate among nestlings.

Habitat may play an important role in animal movements as well as population fluctuations. Grant (1971) suggested that intraspecific interactions increased as the density of cotton rats increased, forcing some animals into less desirable habitat such as woodland. Goertz (1964) also suggested that cotton rats survived in "reservoir" areas during population lows and colonized surrounding

marginal habitat until some environmental factor, such as a severe winter, depleted the population by decimating the colonies in marginal habitat. Fuller (1967)and Anderson (1969) also felt that favourable microhabitats were necessary for survival of "reservoir" populations.

Again we come to the problem of what animals require of their habitat. What is marginal habitat for Microtus pennsylvanicus? Particularly, what is marginal in terms of food supply? Perhaps the frequency of preferred foods is one parameter of marginality. A population may increase in marginal habitat until certain foods are depleted below the marginal limit and this may result in stress expressed as behavioural change, reproductive or mortality changes, or changes in migration rates which reduce the population allowing the plant community to recover.

Probably the situation is more complex than the one outlined above, but equally probably food habits play a role in population dynamics.

Conclusions

The evidence of this thesis outlined some basic interactions between *Microtus pennsylvanicus* and plant species within the area studied. Conclusions drawn from the data were as follows:

1. Food preference tests showed that certain plant species were preferred over others as food items and nesting materials.

2. Stomach analysis showed that certain plants and plant parts were eaten more often than could be accounted for on the basis of availability alone. The methods used proved that phase microscopy can be a valuable technique in analysis of vole stomach contents.

3. Correlation coefficients suggested that both *Microtus* and foods preferred by *Microtus* may be associated with the distribution of *Poa* species. Step-wise multiple regression analysis showed a significant correlation between *Microtus* and *Poa*. It was felt that the correlation with *Poa* reflected both the presence of adequate cover and species of preferred food plants.

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Table 1. The aboveground weights of each plant species found at each quadrat.

Station number	Plant species	Weight (grams)
1	Solidago spp.	138.8
	Poa spp.	76.5
	Sonchus arvensis L.	62.8
	Bromus inermis Leyss.	24.8
	Achillea spp.	18.1
	Cirsium arvense (L.) Scop.	5.1
	Phleum pratense L.	3.9
	Equisetum arvense L.	3.6
	Trifolium repens L.	2.0
	Total	335.6
2	Poa spp.	129.0
	Sonchus arvensis L.	62.2
	Trifolium repens L.	52.4
	Bromus inermis Leyss.	38.1
	Cirsium arvense(L.)Scop.	24.6
	Solidago spp.	15.0
	Aster spp.	10.0
	Agropyron repens L.	1.8
	Lathyrus palustris L.	1.6
	Vicia americana Muhl.	0.4
	Achillea spp.	0.2