A C T A T H E R I O L O G I C A

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Food Habits and Food Supply of Rodents in the Beech Forest [1])

[With 5 Figs. & 7 Tables]

Food habits of voles *Clethrionomys glareolus* (S c h r e b e r, 1780) and mice *Apodemus flavicollis* (M e l c h i o r, 1834) were studied in the beech forest in Ojców National Park near Cracow. The food preference was studied using choice test; stomach contents were microscopically analysed. In the laboratory the animals were prefering similar food to that consumed in the forest. The voles can consume variable kinds of bulky and concentrated food, while mice are eating mainly concentrated food. In the natural food of voles greens and seeds are prevailing (the average of 44 and 40% of stomach contents, respectively) the remainder being composed of invertebrates and fungi (9 and 7%). Mice in the natural habitat are consuming mostly seeds (74% of volume) and invertebrates (15%); much less greens and fungi (10 and 1%, respectively). In the beech forest potential food of voles is composed of herb vegetation, tree seeds and, to much smaller extent, fungi, insects, leaves, buds and tree twigs. Seeds and insects are the main food of mice. In addition some fungi and herbs are eaten. For these rodent species the food supply in beech forest was estimated to be 1,949,000 kcal/ha/year for the vole and 1,085,000 kcal/ha/year for the mouse. The food available to these rodents amounts only to 4.4% and 2.4% of the yearly primary net production of the studied forest.

I. INTRODUCTION

In the studies of energy flow through the populations of small rodents, the food consumed by these animals is usually compared with the total primary net production of ecosystem. However, the majority of ecologists studying this problem takes into consideration that food available to rodent is only a part of plant production. The energy available for rodents was defined by G r o d z i ń s k i (*in litt.*) as "the food which is easy to find and is being chosen and eaten by these animals". Consequently, it is difficult to estimate plant production "from the point of view" of a mouse or a vole; food habits of these small mammals have to be known in some detail.

Such estimation is troublesome and was usually quite arbitrary. In the old-fields community all live parts of plants above the ground were considered as a food available to *Microtus pennsylvanicus* (O r d, 1815), (G o l l e y, 1960). In

[1]) This study was carried out under the Rodent Project of the International Biological Programme in Poland.

another community of old-fields Odum, *et al.* (1962) considered as food available to *Peromyscus polionotus* (Wagner, 1843) only the seeds i.e. 7% of above-ground plant production. Similarly, Pearson (1964) assumed that in rich production of herbs and grasses in the meadow ecosystem seeds are prevailing potential food for small rodent species: *Microtus californicus* Peale, 1848, *Reithrodontomys megalotis* Baird, 1858 and *Mus musculus* Linnaeus, 1758. In the forest community it is even more difficult to estimate the amount of food available to rodents. Forests have very high total production but it consists mostly of impalatable for rodents trunks and branches (Grodziński, 1961, 1963; Górecki & Gębczyńska, 1962).

The purpose of this investigation was to estimate the resources of food available to rodents in the beech forest (*Fagetum carpaticum*). Forests of this type are prevailing in the lower mountain forest of Carpathians and other European mountains. The food habits of bank vole, *Clethrionomys glareolus* (Schreber, 1780) and yellow necked field mouse, *Apodemus flavicollis* (Melchior, 1834) were studied in the Ojców National Park near Cracow. It is a considerable area of beech forest located in the valleys Jamki and Sąspowska (50°13′ north lat. 19°40′ east long). Voles and mice are definitely prevailing in this forest making up over 98% of all rodents (Grodziński, *et al.*, *in litt.*).

The net primary production of herb layer and tree layer in this forest was studied by the botanists from the Nature Conservation Research Center of the Polish Academy of Sciences (Rajchel, 1965; Kaźmierczakowa, 1967; Myczkowski, 1967). The influence of herbivores on the plants of herb layer was also studied (Łomnicki, *et al.*, 1965).

II. MATERIALS AND METHODS

All voles and mice used in this work were taken in the Ojców beech forest. Two methods were used; feeding experiments and the analysis of stomach contents. The former indicates which kinds of natural food can be eaten by rodents, the latter — which are actually consumed in the nature.

In feeding experiments planned to study the food preference so called "cafeteria test" was employed. This method named by Elton was subsequently used, often with some modifications, by many ecologists working with rodents (Naumov, 1948; Chitty, 1954; Miller, 1954; Górecki & Gębczyńska, 1962; Petrov, 1963). Cafeteria test means offering animals the choice of several kinds of food and estimating the degree of their consumption. Feeding experiments were carried out in the laboratory in three seasons: spring, summer-autumn and winter. Most of food components available in the forest during given season were tested in each series. Every animal was offered the group of 3 to 5 kinds of food during three consecutive days. In subsequent three day periods different groups of food were offered. Besides, food unwillingly eaten in previous tests was sometimes offered again at the and of experimental period. The degree of consumption of separate components of the diet was estimated using scale 0 through 3 (Naumov, 1948; Sviridenko, 1961; Górecki & Gębczyńska, 1962; Petrov, 1964). The numbers in this scale correspond roughly to the following percentages: 0—0% (food was not touched), 1—0% to 30%, 2—30% to 60%, 3—60% to 90% of consumption. During the experiment animals were placed in the metal cages 40×25×15 cm or in 10 liters glass jars. In the addition to tested food the animals had water and pellets of standard food available at all times (for composition

of standard food see Drożdż, 1964). Small amount of standard food was meant as a reserve in case of tested diet being inedible for the animal. The rodents caught in nature are not familiar with pelleted food and try to eat it only when remaining food is inacceptable. The total of 85 specimens of both species was used to study the food preference. The series in each season consisted of 10 to 15 animals.

The analysis of stomach contents was carried out microscopically following the method of Williams (1955, 1959, 1962), Holišova (1959, 1960, 1965) and Holišova, *et al.* (1962). For the green parts of plants diagnostic features are: shape of epidermis cells, tracheal tissue and trichomes, for seeds — general structure and shape of starch granules. Animal materials can be recognized from striated muscles and chitin fragments, but they are difficult to classify. This method allows identification of majority of plant species consumed by rodents. For comparison, permanent histological slides and drawings of epidermis were prepared from most of plant species occuring in the studied forest [2]). These drawings were used as a key for identification of sample components. The stomachs to be studied were dissected from fresh voles and mice caught in snap-traps. Stomachs were dried (Holišova, 1960) or fixed in 80% alcohol. The contents of dried stomachs were studied after being soaked in water for 24 hours. In every stomach the approximate volume of seeds, green parts of plants and animal food was estimated. This was done by sorting out different kinds of food from the stomach contents with binocular. Then the frequency i.e. the per cent of stomachs containing given food component was calculated for all animals studied.

Table 1.
Number of stomachs studied in different seasons.

Seasons	C. *glareolus*	A. *flavicollis*	Total
Spring	86	47	133
Summer	54	33	87
Autumn	40	30	70
Winter	29	15	34
Total	209	125	334

The voles and mice for the analysis of stomach contents were captured during two years (1964—1965) in four different seasons in order to detect seasonal changes in food habits. The prevernal season was given special consideration as then the food situation of rodents is probably most critical. The total of 334 stomachs was studied (Table 1).

III. RESULTS

1. Food preference

The mean values of food preference of voles and mice offered green plants, shrubs, twigs, buds and tree seeds are given in tables (cf. Table 3). In these tables the mean values for separate food components are

[2]) The drawings were prepared by Dr. Krystyna Worytkiewicz from the Dept. of Plant Anatomy and Cytology, Jagiellonian University, Cracow.

Table 2.

An example of individual variation of food preference in voles (*Clethrionomys glareolus*) and mice (*Apodemus flavicollis*) in relation to herb layer vegetation in summer.

The degree of consumption as on Table 3; mean values calculated as described in the text (p. 364).

Herb layer vegetation	*Clethrionomys glareolus*												*Apodemus flavicollis*											
	1	2	3	4	5	6	7	8	9	10	$\bar{x}$	%	1	2	3	4	5	6	7	8	9	10	$\bar{x}$	%
Oxalis acetosella	3	3	3	3	3	3	3	3	3	3	3.0	90	0	0	1	0	0	0	1	0	0	0	0,2	0
Mycelis muralis	3	3	3	3	2	3	2	3	3	3	2.8	80	3	2	2	2	3	3	2	2	1	2	2,2	70
Majanthemum bifolium	3	2	3	3	2	3	2	3	2	3	2.6	80	0	0	0	0	0	0	0	0	0	0	0,0	0
Aruncus silvester	3	3	3	3	1	3	2	3	3	1	2.5	70	1	0	0	0	0	0	0	0	1	1	0.3	10
Viola silvestris	3	2	3	3	2	2	3	2	1	3	2.4	70	2	0	0	1	2	2	0	1	0	1	0.9	30
Ranunculus lanuginosus	3	3	3	1	0	3	2	3	3	1	2.2	70	0	1	0	0	0	1	1	0	0	0	0.3	10
Lathyrus vernus	0	3	3	1	1	1	3	3	2	1	1.8	50	0	0	1	0	1	1	1	0	1	1	0.6	20
Lusula pilosa	1	2	0	3	2	1	3	2	1	3	1.8	50	0	0	0	1	1	0	0	0	1	0	0.3	10
Epipactis latifolia	1	2	3	3	3	0	1	2	0	0	1.5	40	0	1	0	1	3	0	2	1	2	0	1.0	30
Galeobdolon luteum	0	3	3	2	1	1	0	2	1	1	1.4	40	1	0	0	1	1	0	0	0	1	0	0.4	10
Asperula odorata	1	1	1	1	0	3	2	0	1	0	1.0	30	0	0	0	0	0	0	0	0	0	0	0.0	0
Ajuga reptans	0	2	1	2	3	1	0	0	1	0	1.0	30	0	2	0	1	0	0	1	0	2	0	0.6	20
Mercurialis perennis	0	2	1	0	1	1	1	0	1	1	0.8	20	2	0	1	2	2	1	1	0	1	1	1.1	30
Hepatica nobilis	0	1	1	0	0	2	1	1	1	1	0.8	20	0	0	1	0	1	0	0	0	1	0	0.3	10
Hieracium murorum	0	3	2	0	0	1	1	0	0	1	0.8	20	0	1	0	0	3	2	0	1	0	0	0.7	20
Actaea spicata	0	2	2	1	1	0	2	0	0	0	0.8	20	0	0	2	1	2	0	0	1	2	0	0.8	20
Carex silvatica	0	1	1	1	0	2	0	0	0	0	0.5	10	0	0	0	0	0	0	0	0	0	0	0.0	0
Pulmonaria obscura	0	0	1	0	0	0	2	0	0	2	0.5	10	0	0	2	1	2	0	0	0	0	0	0.5	10
Athyrium filix femina	0	1	0	1	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0.0	0
Dryopteris filix mas	0	0	0	0	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0	0	0	0	0	0.0	0
Asarum europaeum	0	0	0	0	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0	0	0	0	0	0.0	0

expressed both in four-grade scale and in corresponding per cent values. The method of calculating these rounded means is given in the Table 2, where the individual variation in consuming the plants of herb layer in summer was given as an example of our raw data. The arithmetic mean of estimations in four-grade scale for 10 individuals was used as the mean degree of consumption. In addition the percent values are given. For these calculations the upper limits of individual grades of scale were used i.e. 1 was considered 30%, 2—60% and 3—90%. Food that was not touched was corresponding to 0%. However, the consumption estimated as 0.1 to 0.2 in our scale was also assumed to be 0. The sums obtained were rounded to the nearest 10 to avoid suggesting higher accuracy than the method allows. This method of calculations appears to represent quite well upper grades in our scale (i.e. 2 and 3) and tends to overestimate the consumption represented by the lowest grade.

The food preference of bank voles was slightly different in the spring, summer and winter. In the spring voles were offered two kinds of food currently available in the forest, twigs of trees and bushes and plants of herb layer. From the twigs of deciduous trees voles were eating buds and some bark. They did not eat at all the twigs of coniferous trees. In the early spring the animals are very willingly eating young plants of the herb layer, especially *Anemone nemorosa*, *Oxalis acetosella*, and *Mycelis muralis* (Table 3). In summer they were prefering *O. acetosella* and *M. muralis* from other green plants. They were also eating well the leaves of *Sorbus aucuparia*. Of the tree seeds they were most willingly consuming fresh seeds of *Fagus silvatica* but they did not eat cones of coniferous trees. The fruit of *Sorbus aucuparia*, *Vaccinium myrtilus* and *Rubus hirtus* was readily eaten by all voles. In the winter voles were fed evergreens i.e. plants which they can find under the snow cover. Of these *Galeobdolon luteum* and *Hepatica nobilis* were most willingly consumed, while *Asarum europaeum* was never eaten. In winter the voles were eating seeds of all trees except fir (Table 3).

Over the period of whole year voles are eating both the seeds of trees and shrubs and the plants of herb layer (low energy food). Of 24 tested herb layer species 15 were eaten well i.e. more than grade 1 of employed scale. Twigs, buds and tree leaves were being chosen less frequently.

The field mice appeared to have more specialized food requirements than the bank voles. In the spring, mice were offered tree twigs and prevernal herbs. Twigs were rarely touched; and if so, only buds were eaten. *Mycelis muralis* was distinctly preferred over other plants of herb layer (Table 3). The diet composed exclusively of green plants proved clearly insufficient for mice; the animals fed this diet were dying during the experiment. In summer mice are eating very well unripe seeds of

Table 3.

Food preference of voles (*Clethrionomys glareolus*) and mice (*Apodemus flavicollis*).

Species of plant	*Clethrionomys glareolus*						*Apodemus flavicollis*					
	Spring		Summer		Winter		Spring		Summer		Winter	
Herb layer vegetation	x̄	%	x̄	%	x̄	%	x̄	%	x̄	%	x̄	%
Anemone nemorosa	3.0	90	—	—	—	—	0.3	10	—	—	—	—
Oxalis acetosella	3.0	90	3.0	90	1.1	30	0.3	10	0.4	10	0.3	10
Dentaria glandulosa	2.5	70	—	—	—	—	0.2	10	—	—	—	—
Mycelis muralis	3.0	90	2.8	80	—	—	2.0	60	2.2	70	—	—
Majanthemum bifolium	2.4	70	2.6	80	—	—	0.2	10	0.1	10	—	—
Aruncus silvester	—	—	2.6	80	—	—	—	—	0.3	10	—	—
Viola silvestris	1.5	40	2.4	70	0.9	30	0.8	20	0.9	20	0.3	10
Ranunculus lanuginosus	—	—	2.2	70	—	—	—	—	0.2	10	—	—
Lathyrus vernus	—	—	1.8	50	—	—	—	—	0.6	20	—	—
Petasites albus	1.0	30	—	—	—	—	0.5	10	—	—	—	—
Lusula pilosa	1.2	40	1.8	50	—	—	—	—	0.3	10	—	—
Epipactis latifolia	—	—	1.5	40	—	—	—	—	1.0	30	—	—
Galeobdolon luteum	2.4	70	1.4	40	2.0	60	0.4	10	0.6	20	0.8	20
Asperula odorata	2.3	70	1.0	30	0.5	10	0.3	10	0.0	0	0.0	0
Ajuga reptans	0.6	20	1.1	30	—	—	—	—	0.6	20	—	—
Mercurialis perennis	1.6	50	0.8	20	—	—	0.8	20	1.1	30	—	—
Hepatica nobilis	2.1	60	0.8	20	2.0	60	0.7	20	0.3	10	0.5	10
Hieracium murorum	0.5	10	0.8	20	—	—	—	—	0.7	20	—	—
Actaea spicata	—	—	0.8	20	—	—	—	—	0.8	20	—	—
Carex silvatica	0.1	0	0.5	10	—	—	0.0	0	0.0	0	0.0	0
Pulmonaria obscura	2.1	60	0.5	10	—	—	0.8	20	0.5	10	—	—
Athyrium flix femina	0.2	0	0.1	0	—	—	0 0	0	0.0	0	0.0	0
Dryopteris filix mas	0.0	0	0.0	0	—	—	0.0	0	0.0	0	0.0	0
Asarum europaeum	0.2	0	0.0	0	0.2	0	0.1	0	0.0	0	0.1	0
Shrubs												
Vaccinium myrtilus	—	—	0.0	0	0.5	10	0.0	0	0.0	0	0.0	0
Rubus hirtus	2.0	60	0.5	10	1.8	50	0.4	10	0.5	10	0.1	0
Lonicera xylosteum	—	—	0.0	0	—	—	0.0	0	0.0	0	0.0	0
Twigs and tree buds												
Fagus silvatica	0.4	10	0.4	10	0.5	10	*	—	0.2	0	*	—
Quercus pedunculata	0.5	10	0.6	20	0.4	10	*	—	0.3	10	*	—
Carpinus betulus	*	—	0.5	10	*	—	*	—	0.3	10	*	—
Corylus avellana	*	—	—	—	*	—	*	—	—	—	*	—
Abies alba	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Picea excelsa	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Pinus silvestris	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
Sorbus aucuparia	0.2	0	2.3	70	0.1	0	0.0	0	0.2	0	0.0	0
Seeds and fruits												
Fagus silvatica	—	—	3.0	90	3.0	90	—	—	3.0	90	3.0	90
Carpinus betulus	—	—	1.5	40	2.1	60	—	—	1.5	40	2.4	70
Pinus silvestris	—	—	0.6	20	3.0	90	—	—	0.4	10	3.0	90
Picea excelsa	—	—	0.7	20	3.0	90	—	—	0.5	10	3.0	90
Tilia cordata	—	—	—	—	3.0	90	—	—	—	—	3.0	90
Quercus pedunculata	—	—	—	—	3.0	90	—	—	—	—	3.0	90
Abies alba	—	—	0.4	10	0.5	10	—	—	0.5	10	0.6	20
Sorbus aucuparia	—	—	2.8	80	—	—	—	—	1.9	60	—	—
Vaccinium myrtilus	—	—	3.0	90	—	—	—	—	1.4	40	—	—
Rubus hirtus	—	—	2.3	70	—	—	—	—	1.7	50	—	—

Herbs, shrubs, twigs and buds of trees, seeds and fruits were offered in different seasons. The average degree of consumption is given in 4 grade scale and in corresponding rounded per cent values (3 — 60% to 90% of food was consumed, 2 — 30% to 60%, 1 — less than 30%, 0 — 0%). * — only buds were eaten. Notice: summer was always given together with the autumn.

Fagus silvatica and, quite willingly, seeds of *Carpinus betulus* and fruits of *Vaccinium myrtilus, Sorbus aucuparia* and *Rubus hirtus*. If there is little other choice, some tree leaves are consumed. Of over 20 herb species tested in the summer mice were eating in considerable degree only three: *Mycelis muralis, Mercurialis perennis* and *Epipactis latifolia* (Table 3). In the winter mice were offered tree seeds, twigs and evergreens. The seeds of all trees except *Abies alba* were willingly eaten. Twigs and green plants were eaten in minimal quantities.

These experiments indicate that of different kinds of plant food only the seeds and fruits are proper for the field mice. Herb layer vegetation, leaves and buds can be only a small supplement in their diet. This is clearly indicated by the observation that of 27 herb species mice were consuming only *Mycelis muralis, Mercurialis perennis* and *Epipactis latifolia*. Moreover, these species were eaten only to the extent corresponding to the grades 1 to 2 of employed scale.

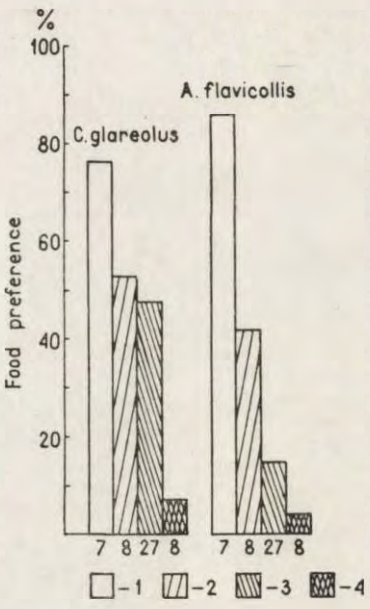

Fig. 1. Food preference of voles (*Clethrionomys glareolus*) and mice (*Apodemus flavicollis*). Different kinds of plant food were offered in "cafeteria test".
Bars — average degree of consumption of all plants in given group (in per cent); numbers in circles — number of species tested in given group. 1 — tree seeds, 2 — unripe tree seeds, 3 — herb layer plants, 4 — twigs and buds of trees.

The results of all experiments on the food preference of both rodent species are summarized on Fig. 1. Mean per cent values of consumption of all tested kinds of food are pooled into four groups: tree seeds, fresh seeds and fruits, herb layer vegetation, twigs and buds. The differences in food preference between the bank vole and the field mouse are readily seen. This difference is most pronounced in consumption of herb layer plants: 50% for voles and 15% for mice. Twigs, buds and tree leaves are also much better eaten by voles. There is no difference in consumption of seeds and fruits; these are willingly chosen by both voles and mice.

2. Stomach Contents

Stomach contents of voles and mice were classified into the following groups: tree bark, tree seeds, fruits of shrubs and herb layer plants, green parts of plants, flowers, underground parts of plants, fungi, animal food (Table 4, 5). Moreover an attempt was made to identify the species composition of plants and seeds present in stomach contents.

In the autumn of 1964 there was a heavy fall of beechmast, so called "seed year". Consequently, beechmast was available in considerable quantity from the late summer 1964 until the spring 1965. During spring 1964 and both summer and autumn 1965 tree seeds were almost completely lacking. It created the opportunity to compare the natural food of rodents in these two extremely different periods. These periods will be referred to as: "seed year" and "no seeds year".

In the bank vole the frequency of occurence of individual food components differed both between seasons and between "seed year" and "no seeds year" (Table 4, Fig. 2). In the stomachs of voles captured during

Table 4.

Frequency of different food components in the stomachs of voles (*Clethrionomys glareolus*) in per cent.

Season	No. of stomachs	Per cent of stomachs containing:							
		Bark	Tree seeds	Fruits	Green parts of plants	Flowers	Roots	Fungi	Invertebrates
Spring 1964	16		50.0		68.7		12.5		43.7
Spring 1965	70		85.7		57.6	18.8			11.5
Summer 1964	39	7.6	61.5	17.9	69.2	7.6	20.0	38.4	35.8
Summer 1965	15		40.0	6.6	93.3			46.6	46.6
Autumn 1964	30		66.6		60.0			23.3	20.0
Autumn 1965	10		20.0		70.0		10.0	90.0	20.0
Winter 64/65	29	7.0	67.4		51.7		7.0	7.0	34.4
Total	209	2.6	66.9	3.8	66.5	6.7	7.2	19.6	25.8

The material from two years is broken into separate seasons. In the summer--autumn 1964 and in the winter and spring 1965 beechmast was plentiful, while in the spring 1964, summer and autumn 1965 it was lacking.

spring 1964 (no seeds year) green parts of plants and seeds were predominant, animal food was frequently found. During the spring 1965 when beechmast was still in rich supply its frequency in stomachs was considerably higher (87.5%), while the frequency of animal food and greens decreased. In summer the stomach contents are most diversified. When unripe beechmast started to fall in summer 1964 the frequency of these seeds in vole stomachs was slowly increasing, while the per cent of stomachs with greens, fungi and invertebrates was still high. On the

opposite, during the "no seeds" summer of 1965 green parts of plants were present in almost all stomachs and seeds only in 40%. The scarcity of seeds was being compensated by consuming more fungi, invertebrates and fruits (Table 4). In the autumn 1964 of all kinds of food the seeds were most frequently found in the vole stomachs. Concurrently, the frequency of green parts of plants, fungi and invertebrates was rapidly decreasing. In the autumn of 1965 the frequency of seeds was three times lower than during the heavy fall of beechmast in autumn 1964. However, the frequency of greens and fungi was much higher. In winter vole stomachs usually contained seeds and invertebrates, most rarely greens. In addition bark and roots were found.

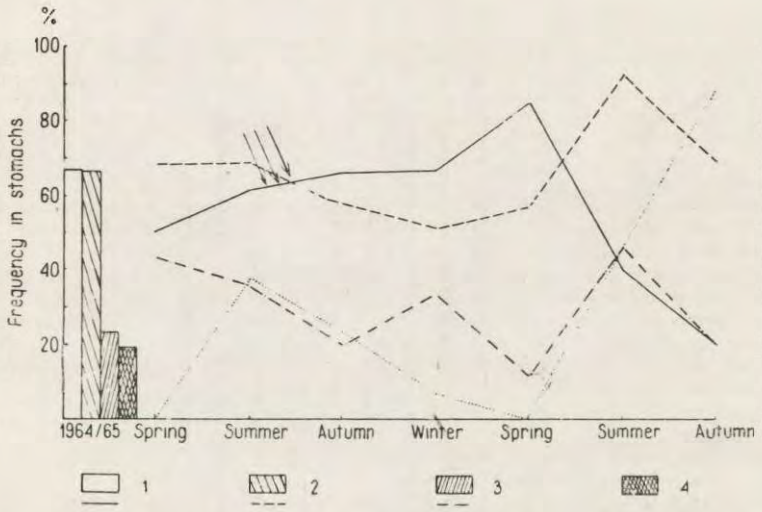

Fig. 2. Seasonal changes of the frequency of main food components in the stomachs of voles (*Clethrionomys glareolus*) during two years cycle (seed years and "no seeds year").

Bars at the left — mean frequency during this period. Arrows — the period of heavy beechmast fall. 1 — seeds, 2 — green parts of plants, 3 — invertebrates, 4 — fungi.

The mean frequency of main food components during two year period indicates that voles as frequently eat seeds (66.9%) as bulky greens (66.5%). The frequency of consuming animal food and fungi is approximately three times lower (Fig. 2, Table 4).

Fifteen species of herb layer plants were identified in the stomach contents of voles (Table 5). Occurence of different plants in the stomachs depends on both food preference of the animal and the phenology of plant species. Considering the results from whole year it can be concluded that plants most readily eaten by voles are: *Oxalis acetosella, Galeobdo-*

lon luteum, Hepatica nobilis as well as *Viola silvestris* and *Hieracium murorum.*

The spores of different fungi were also found in the vole stomach contents. The folowing genera were identified: *Russula, Hydnotria, Tuber, Genea, Balsamia, Hymenogaster, Melanogaster, Rhizopogon* [3]). All of these, except *Russula,* are forming only underground fructification. Consequently, the voles had to get fungi from beneath the ground.

Table 5.

The number of stomachs of voles (*Clethrionomys glareolus*) and mice (*Apodemus flavicollis*) in which the species of herbs and tree seeds were identified.

Species of plant	*Clethrionomys glareolus*				*Apodemus flavicollis*			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Oxalis acetosella	5	7	8	3	2	1	1	
Galeobdolon luteum	8	4	5	4	1	1	1	
Hepatica nobilis	7	6	4	2	1			
Viola silvestris		2	3	2		1	2	1
Hieracium murorum	3	5	2	2	2		2	
Mercurialis perennis	3	5						
Carex silvatica	2	3	2					
Pulmonaria obscura	2	2	2					
Mycelis muralis	4					2		
Anemone nemorosa	5							
Ajuga reptans		2			1			
Rubus hirtus		2						
Actaea spicata		2						
Hedera helix	2					1		
Asperula odorata				2				
No. of stomachs examined	86	54	40	29	47	33	30	15
Species of seeds								
Fagus silvatica	57	7	17	17	36	19	14	9
Quercus peduculata	6	14	2	2	4	5	5	2
Carpinus betulus	5	8	1		2			
Acer pseudoplatanus		5	1	3	3	5	1	1
Picea excelsa		3				3		
No. of stomachs examined	86	54	40	29	47	33	30	15

The species composition of tree seeds in the stomachs of voles was also determined (Table 5). As expected, most commonly found were the seeds of *Fagus silvatica, Quercus pedunculata, Carpinus betulus, Acer pseudoplatanus* and *Picea excelsa.*

[3]) The fungi were identified by Dr. W. Wojewoda, Dept. of Plant Taxonomy and Phytogeography, Jagiellonian University, Cracow.

The differences in quantitative composition of stomach contents of the bank voles were larger between "seed year" and "no seeds year" than between seasons (Fig. 3). During the heavy fall of beechmast this food was definitely prevailing in the stomachs making up 68.0% of contents.

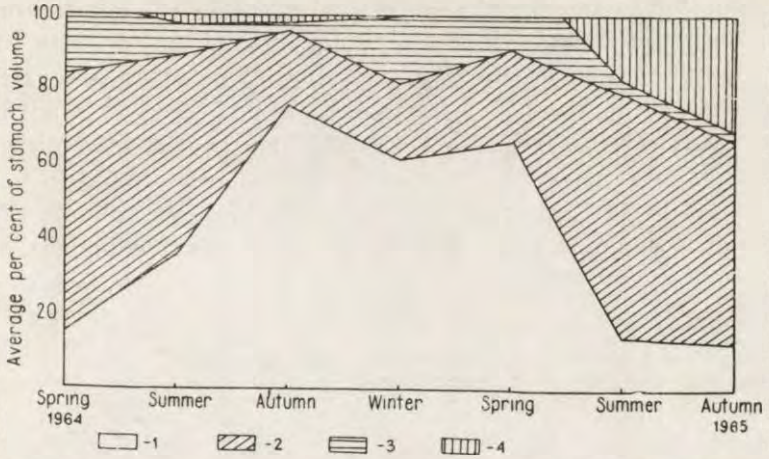

Fig. 3. Seasonal changes of the quantitative composition (by volume) of the stomach contents in voles (*Clethrionomys glareolus*) during the two years cycle (seed year and "no seeds year").
1 — seeds, 2 — green parts of plants, 3 — invertebrates, 4 — fungi.

Table 6.

The frequency of different food components in the stomachs of mice (*Apodemus flavicollis*) in per cent.

Seasons	No of stomachs	Per cent of stomachs containing:							
		Bark	Tree seeds	Fruits	Green parts of plants	Flowers	Roots	Fungi	Invertebrates
Spring 1965	47		97.1		17.1	6.4			48.5
Summer 1964	18		88.0	11.0	22.0			5.5	77.7
Summer 1965	15		100.0		43.3				26.6
Autumn 1964	20		90.0		40.0			10.0	70.0
Autumn 1965	10		30.0		70.0			30.0	90.0
Winter 64/65	15	6.6	73.3		13.3		13.3	6.6	40.0
Total	125	0.8	87.2	1.8	29.6	1.6	1.6	6.4	55.2

In the corresponding periods of "no seeds year" the tree seeds were amounting to only 19% of stomach contents. The voles were compensating for the scarcity of seeds by consuming green parts of plants and fungi (60.0% and 13.0%, respectively).

Considering the mean values of the periods of abundance and scarcity of beechmast, it appears that the quantitative share of greens and seeds

in the diet of voles is similar. Green parts of plants make up on average 44.0% and the seeds — 40.0%. The remainder are animal food (9%) and fungi (7%).

The stomachs of mice usually have much less diversified contents. Three main food components i.e. seeds, greens and invertebrates are present. Both the frequency (Table 6, Fig. 3) and quantitative composition (by volume) (Fig. 5) are changing slightly in the year cycle.

The frequency of seeds in the stomachs of mice caught in spring 1965 was very high (97.1%), what can be explained by the above mentioned abundance of beechmast. Green parts of plants were found in very few stomachs and invertebrates in approximately half of animals (Table 6, Fig. 4). In the summer 1964 the frequency of seeds was slightly lower,

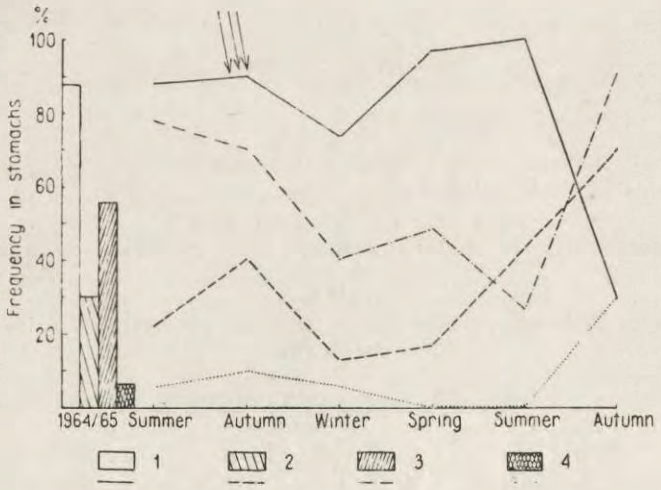

Fig. 4. Seasonal changes of the frequency of main food components in the stomachs of mice (*Apodemus flavicollis*) during two years cycle (seed year and "no seeds year").

Bars at the left — mean frequency during this period. Arrows — the period of heavy beechmast fall. 1 — seeds, 2 — green parts of plants, 3 — invertebrates, 4 — fungi.

while greens and especially invertebrates were more often found. In summer 1965 in spite of the lack of beechmast on the ground, it was still found in all studied stomachs. Apparently mice were using stores accumulated in the burrows when the seeds were abundant. In the autumn 1965 the frequency of seeds in mouse stomachs was three times lower than in autumn 1964. The frequency of greens and invertebrates was much less changed. However, in autumn 1965 fungi were present in nearly 30% of stomachs.

The mean frequency of basic food components during two studied years indicates that mice are consuming predominantly concentrated food: seeds (87.2%) and invertebrates (55.2% of stomachs).

Eight species of herb layer plants were identified in the stomach contents of mice (Tab. 5). Of these, most frequently found were: *Oxalis acetosella, Viola silvestris, Hieracium murorum, Galeobdolon luteum.* Among seeds most frequent were beechmast, acorns and seeds of *Acer pseudoplatanus.* The seeds of *Carpinus betulus* and *Picea excelsa* were only sporadically found (Table 5).

The quantitative composition was changing in the annual cycle and was different in the periods of abundance and scarcity of seeds (Fig. 5). In all seasons of both years studied the seeds were dominating. On the

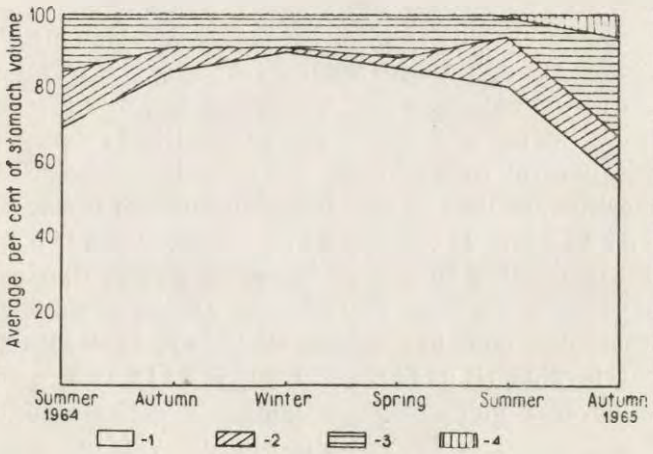

Fig. 5. Seasonal changes of the quantitative composition (by volume) of the stomach contents in mice (*Apodemus flavicollis*) in the two years cycle (seed year and "no seeds year").
1 — seeds, 2 — green parts of plants, 3 — invertebrates, 4 — fungi.

average they were making up about 74% of volume. The greens were making up 10% of volume, invertebrates — 15% and fungi — 1%. However, during the heavy fall of beechmast seeds amounted to 87% of the volume and during the scarcity of seeds — only to 69%. Mice were compensating for the deficiency of seeds by consuming more plants of the herb layer; 4% in the "seed year" and 13% in the "no seeds year".

Green parts of plants are consumed by mice least frequently in winter and most often in summer (Fig. 5).

IV. DISCUSSION

1. The Natural Food of Bank Vole and Yellow Necked Mouse

The natural food of voles and mice was studied by many ecologists and foresters in Europe (Sviridenko, 1940; Turćek, 1956; Novikov, 1959; Petrov, 1963; Tanton, 1965 and others). All of these authors agree that the bank vole is more polifagous than the yellow necked field mouse. Voles can consume both low energy (bulky) food: herbs, lichens, berries, fungi, buds, bark, roots and high energy (concentrated) food: seeds and invertebrates. Mice are eating mostly high energy food: tree seeds and invertebrates. This difference in the diet corresponds to differences in the anatomy of alimentary tract of these two species (Górecki & Gębczyńska, 1962).

Consequently, the natural food of voles can change drastically during the year and from year to year (for example years of heavy fall of seeds) and can be completely different in different ecosystems. The diet of voles in mixed wood and taiga (Naumov, 1948; Koškina, 1957) is different than in the studied beech forest and in other deciduous forests (Miller, 1954). On the other hand the variability of mouse diet is very restricted. The natural food of mice in the Ojców beech forest is, in general composition, similar to that in oak-hornbeam forest (*Querco-Carpinetum*) (Górecki & Gębczyńska, 1962; Sablina, 1953; Dinesman, 1961). Related species of the same genus: *Apodemus sylvaticus* L. and *Apodemus microps* Krat. & Ros. have similar prevalence of seeds in their diet both in England (Miller, 1954; Tanton, 1965) and in Czechoslovakia (Holišova, 1960; Holišova, *et al.*, 1962).

There are several methods of studying the food habits of small mammals (c.f. Myrcha, 1965). In the majority of studies concerning food of voles and mice only one method was used: the analysis of stomach contents or the laboratory "cafeteria test" ("choice test" — Chitty, 1954). Very few authors (Naumov, 1948; Miller, 1954) were using both methods concomittantly.

In this work both methods were used; the results are in general agreement and appear to complement each other. Studied rodent species were consuming tree seeds in comparable degree in the forest and in the laboratory. The results of "cafeteria test" were generally consistent with the results of stomach contents analysis. Consequently, it appears that cafeteria test represents well the actual food habits of studied animals. For example plant species that were most willingly consumed in experiments (*Anemone nemorosa, Galeobdolon luteum, Hepatica nobilis* and *Viola silvestris*) were most frequently found in the stomachs of voles and mice. However, comparing the results of "cafeteria test" (Table 3)

and frequency of plants in the stomach contents (Table 5) indicates that in laboratory the voles were consuming more plant species than were found in stomachs. Consequently, it appears that the "cafeteria test" indicates "potential" food of rodents, while the stomachs contain food that is "liked" and is easy to find in a given ecosystem. The number of potential food components would exceed the number of "liked" components. In studying the energy flow it seems very rewarding to employ both methods of studying food habits of herbivorous rodents.

2. Small Rodents Food Supply in the Beech Forest

Beech forest (*Fagetum carpaticum*) in the Ojców National Park is covering the northern slopes in valleys and gorges. The phytosociology of this forest was thoroughly studied and it is mapped on the "Vegetation map of Ojców National Park" (Medwecka-Kornaś, 1952; Medwecka-Kornaś & Kornaś, 1963). The primary net production was studied in two areas of this forest; the productivity of trunks, branches, leaves and seeds of trees was determined (Myczkowski, 1967). The food habits of rodents were studied on several hectares of this forest. The net production of above-ground parts of herbs in the Jamki gorge is about 250 kg of oven dry weight per ha yearly. This production consists mostly of *Asperula odorata* and also *Carex silvatica, Actaea spicata, Sanicula europaea, Viola silvestris, Asarum europaeum, Oxalis acetosella, Ajuga reptans, Galeobdolon luteum,* as well as many others (Rajchel, 1965).

The production of trees, except roots, in the vicinity of studied area (Chełmowa Góra) was estimated as approximately 10.3 tons/ha/year. Of this, the majority is trunks and branches (6,100 kg/ha), tree leaves amount to 2,900 kg/ha, seeds (in the year of good fall) — 44 kg/ha, the remainder being fall of flowers, twigs, buds etc. (Myczkowski, 1967). Consequently, the total production of trees and the herb layer is approximately 43,000,000 kcal/ha/year (cf. Table 7).

The main purpose of this study was to determine what part of the primary net production of the beech forest is available to rodents as food. To answer this question it is necessary to consider the production of forest "from the point of view of the vole and the mouse". It is necessary to make certain simplifications. Such estimation can consider only the above-ground parts of plants assuming that roots are usually not available to rodents. The estimation will consider only the production i.e. yearly increase of vegetation disregarding the supply of timber and bark produced in preceding years. The food supply of the beech forest has to be estimated separately for the vole and for the mouse as their food habits are different.

The balance of food components available to rodents is given in the Table 7 (in caloric values). The total production of herb layer was estimated as roughly 250 kg without considering the decrease of vegetation caused by rodents and invertebrates. In the studied forest this correction was estimated to be 20 to 30 kg of oven dry weight/ha/year (Grodziński, *et al.*, *in litt.*).

Table 7.

The food supply for small rodents in the beech forest and annual primary net production of this ecosystem.

Kind of food	Net production kg/ha/year dry weight	Caloric value kcal/g	Food of voles		Food of mice	
			kg/ha/year	kcal/ha/year $\times 10^3$	kg/ha/year	kcal/ha/year $\times 10^3$
1. Herb layer vegetation	275[1])	3,940[2])	233	918	130	512
2. Tree leaves	2,900[3])	4,630[4])	145	671	70	324
3. Tree twigs (Trunks and branches)	840[3]) (6,100)	4,267[5])	25	107		
4. Tree seeds	44[6]) (5—80)	7,212[7])	28[8]) (3—50)	202 (22—360)	28[8]) (3—50)	202 (22—360)
5. Fungi	5[9])	4,290[10])	3	13	2	9
6. Invertebrates	10[11])	5,363[5])	7	38	7	38
Plant food of the primary production (1—4)	10,3 ton[12]) 43,000,000 kcal		431 (406—453)	1,898 (1,718—1,956)	228 (203—250)	1,038 (858—1,196)
Total food supply (1—6)			441 (416—463)	1,949 (1,769—2,007)	237 (212—259)	1,035 (905—1,243)

[1]) from Rajchel (1965), corrected for the consumption by rodents. [2]) from Kaźmierczakowa (1967); average caloric values of the above ground parts of plants in April, June and October. [3]) from Myczkowski (1967); yearly fall of leaves and twigs of trees (in parenthesis-yearly production of trunks and branches). [4]) from Myczkowski (1967); mean caloric values of the beech leaves in summer. [5]) The caloric value of twigs and insects is given according to Golley (1961). [6]) The fall of beechmast according to Myczkowski (1967); in parenthesis — fluctuations of beechmast fall in different years. [7]) Caloric value of beechmast according to authors determination in the calorimetric bomb. [8]) Proportion of edible parts in seeds according to Górecki & Gębczyńska (1962). [9]) Standing crop of fungi was estimated from the data of Wojewoda (personal communiction) cf. calculations in the text. [10]) Caloric value of fungi fructifications was estimated from the data of Rudowska-Koprowska (1954). [11]) The production of terrestial invertebrates was calculated from the data of Kaźmierczak (1967). [12]) Total values of net production of the trees and the herb layer according to Rajchel (1965) and Myczkowski (1967).

From the total production of herb layer the prevailing majority can be the potential food of voles. Fruits, berries and seeds are also an excellent food for this species. However, from 275 kg of total production of these plants it is necessary to subtract the production of species that were never eaten by voles in "cafeteria test" experiments (Table 3) and never found in their stomachs. The resulting figure is 233 kg of oven dry weight available in the herb layer vegetation.

Only small fraction of herb layer vegetation can be considered the potential food for mice. Summing up all plants that were found in mice stomachs (Table 5) and eaten in the experiments (Table 3) will result maximally in the value of 130 kg of oven dry weight per 1 ha.

The trees in the beech forest can offer seeds, leaves and bark of twigs to the studied species of rodents. The yearly production of leaves was determined by Myczkowski (*l.c.*) as 2,900 kg/ha. The voles in experiments were consuming some leaves and buds of beech, oak and hornbeam and definitely liked the leaves of *Sorbus aucuparia*. The mice were eating some buds of the same tree species and of *Corylus avellana*. Considering that the leaves of small bushes and low branches can be the potential food of voles, one can assume that at least 5% of leaves is available to voles. This estimation would not be valid for the mouse. Mice can reach leaves much easier but they consume much less of them.

The bark of twigs and bushes is consumed by voles and mice only when there is very little choice. Twigs and bark that are available to rodents were estimated to amount to 20—30 kg/ha/years.

The seeds of deciduous trees are the best and the most willingly eaten food that rodents can find in the forest. The heavy fall of beechmast occurs in Ojców *Fagetum carpaticum* forest once in several years. In 1964 the fall of seeds was 44 kg/ha (Myczkowski, *l.c.*). Of this 28 kg is edible for rodents.

The proportion of primary net production that is available to rodents can be estimated by summing up all decribed above plant food components. The resulting values are : 1,898,000 kcal/ha/year for the bank vole and 1,038,000 kcal/ha/year for the field mouse. It appears that from the immense primary production of beech forest (43,000,000 kcal/ha/year) only 2.4% is available to mice and 4.4% to voles. The energy available to the populations of both species is 4.4%.

Fungi, being decomposers, are not included in the primary production. However, they are important component of the diet of rodents. The estimation of production (or even crop) of fungi in the beech forest is not available. Wojewoda (personal communication) determined that the density of fungi fructification in the *Fagetum carpaticum* in Ojców is maximally 3750/ha. Most numerous are: *Marasmius lupuletorum*,

M. Wynnei, M. fusco-purpureus, Mycena pura, Xerocomus chrysenteron, and *Ondemansiella radicata.* The dry weight of one fructification is roughly 0.2 to 4.0 g. The average weight was assumed to be approximately 0.5 g as smaller species are dominating in the beech forest. Consequently, assuming the average density of fructification as 1000/ha the oven dry weight of one standing crop is about 500 g. The fungi in Ojców occur frequently only during four months period (July trough October). If they are growing intensively during only half of this period and their fructification last on average one week, their yearly production would be 8 to 10 times larger than single crop, namely 4 to 5 kg/ha/year.

In the Table 7 it is assumed that all of the above-ground fructification can be consumed by voles and mice, although in fact it is not so. However, forest rodents (especially voles) were consuming many fungi with under-ground fructification The production of these is very difficult to estimate.

In addition to plant food, the beech forest is offering rodents various kinds of animal food. Both mice and voles are readily utilizing animal food (cf. Figs. 3, 5). It appears that mainly small invertebrates occuring on the forest floor are available to small rodents. The average standing crop of terrestial invertebrates is roughly 1.8 kg of dry weight/ha during the spring, summer and autumn (Kaźmierczak, 1967). It is impossible to estimate the production from the average standing crop as reproductive cycles of involved invertebrate species are extremely diversified. However, assuming turn-over of 5 to 6 one can speculate that the production would be at least about 10 kg dry weight/ha/years. From this value roughly 1/3 has to be subtracted to correct it for *Carabidae* and other beetles that usually are not consumed by rodents.

The total food supply for rodents in the beech forest (both plant and animal food) is about 1,949,000 kcal/ha/year. Depending on the fall of beechmast it can vary from year to year ranging from 1,769,000 to 2,007,000 kcal/ha/year. The food available to rodents during the year corresponds to over million kcal/ha/year for mice and nearly two millions kcal/ha/year for voles (Table 7). In comparison with other studied forest ecosystems (Górecki & Gębczyńska, 1962; Grodziński, 1961, 1963, *in litt.*) these values appear high and it is difficult to estimate how precise they actually are.

The comparison of our results with the data concerning meadow communities seems to be of some interest. The primary net production of the beech forest is 3 to 4 times higher than the production of above-ground parts in the grassland ecosystem. In spite of this, on the old fields or meadows herbivorous rodents (*Microtus)* have much more of easily available food (Golley, 1960; Pearson, 1964). Also seed-

-eating rodents (*Peromyscus, Rheithrodontomys*) have more food in grassland ecosystems than in the deciduous forest (Odum, *et al.*, 1962; Pearson, 1964). Although forests have much higher total production than the meadow ecosystems, they appear to offer less food to rodents.

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STOSUNKI POKARMOWE GRYZONI A ZASOBNOŚĆ LASU BUKOWEGO

Streszczenie

Aby ocenić jaka część produkcji pierwotnej netto lasu bukowego jest dostępna dla gryzoni zbadano stosunki pokarmowe nornicy rudej, *Clethrionomys glareolus* (Schreber, 1780) i myszy leśnej, *Apodemus flavicollis* (Melchior, 1834) w lesie *Fagetum carpaticum* w Ojcowskim Parku Narodowym koło Krakowa. Posługiwano się równolegle dwoma metodami, z których pierwsza — doświadczenia żywieniowe testem wyboru pokazuje, które naturalne pokarmy mogą być zjadane przez gryzonie, druga natomiast — analizy żołądków — pozwala przekonać się bezpośrednio jakie pokarmy są naprawdę zjadane w lesie bukowym. Doświadczenia żywieniowe przeprowadzono łącznie na 85 gryzoniach, którym w trzech porach roku podawano do wyboru naturalne pokarmy dostępne w lesie bukowym. Stopień zjadania oceniano w 4 stopniowej skali. Ponadto dokonano mikroskopowej analizy 334 żołądków (Tab. 1) nornic i myszy, które odłowiono w lesie bukowym w cyklu dwóch lat. W żołądkach oceniono frekwencję poszczególnych składników pokarmowych, a także ich udział ilościowy (objętościowy).

Przeprowadzone w cyklu rocznym doświadczenia żywieniowe wykazały znaczną polifagiczność nornic, które mogą odżywiać się zarówno pokarmami objętościowymi jak i treściwymi. Nornice zjadały w trakcie doświadczeń prawie wszystkie nasiona i owoce drzew i krzewów, oraz większość roślin runa. Gałązki, pączki i liście drzew stanowiły dla nornic pokarm zjadany w ostateczności (Fig. 1, Tab. 2, 3).

Analizy zawartości żołądków wykazały, iż skład pokarmu nornic uzależniony jest od aktualnej bazy pokarmowej w lesie. Wyrazem tego jest zmieniająca się frekwencja i udział ilościowy poszczególnych składników w cyklu rocznym, jak również w okresie roku nasiennego i nienasiennego. W okresie urodzaju nasion nornice chętnie wybierają pokarm treściwy, natomiast w innych okresach mogą drastycznie zmienić swoją dietę. Niedobór pokarmów treściwych nornice rekompensują zjadając większe ilości roślin runa, grzybów i pokarmów pochodzenia zwierzęcego. W żołądkach nornic dominują ilościowo zielone części roślin i nasiona (średnio 44 i 40% objętości treści pokarmowej), reszta przypada na pokarmy zwierzęce i grzyby (9 i 7%) (Fig. 3).

Mysz leśna w przeciwieństwie do nornicy odznacza się węższą specjalizacją pokarmową. Doświadczenia żywieniowe wykazały, że jedynym odpowiednim pokarmem dla niej są nasiona, oraz owoce drzew i krzewów. Rośliny runa, krzewinki, liście i pączki drzew mogą stanowić tylko znikomy dodatek do diety myszy leśnych (Fig. 1, Tab. 3).

Analizy treści pokarmowej żołądków myszy wykazały, że w warunkach naturalnych zjadają one nasiona i drobne bezkręgowce, znacznie rzadziej rośliny runa i grzyby. Nasiona stanowią średnio 74% objętości ich pokarmu, bezkręgowce 15%, zielonki 10% i grzyby około 1%. W okresach nasiennych nasiona drzew wypełniają żołądki w 87%, podczas gdy w okresach nienasiennych w 69%. Z braku nasion myszy zjadają większe ilości pokarmu zwierzęcego i roślin (w okresach nasiennych 19 i 4%, a w nienasiennych 18 i 13%) (Fig. 5).

W lesie bukowym potencjonalnym pokarmem nornic są rośliny runa i nasiona drzew, także grzyby, owady, oraz pewna część liści, pączków i gałęzi drzew. Pokarmem myszy mogą być przede wszystkim nasiona drzew i owady, także część grzybów i nieliczne rośliny runa. Zasobność pokarmową lasu bukowego dla nornicy oceniono na 1.949.000 kcal/ha/rok podczas gdy dla myszy tylko na 1.085.000 kcal/ha/rok. Pokarmy dostępne dla gryzoni stanowią zaledwie 4.4 i 2.4% rocznej produkcji pierwotnej netto badanego lasu (Tab. 7).