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

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Food and Feeding Habits of Rodents in a Deciduous Forest

[With 4 Table & 2 Figs.]

The food habits of small rodents, *A. flavicollis* and *C. glareolus*, dominating in a *Tilio-Carpinetum* deciduous forest in the Niepołomicka Forest near Kraków, were studied in 1967—1969. Two methods were employed: stomach content analysis and food test preference. Altogether 376 stomachs were analysed. Seeds (62—90%) were most often found in the stomachs of mice, while green plant, fungi, invertebrates and fruits constituted only a small proportion parts. In voles, seeds constituted 19 to 55%, green plant parts 38 to 65%, fruits 9 to 20%, invertebrates 2.5 to 16% and fungi 8 to 12% of the stomach content volume. Voles consumed both seeds and the green parts of herb layer plants, while the mice ate mainly seeds. Changes in food habits of mice and voles were observed in various seasons in relation to the occurrence of natural food in the forest. Knowing the primary net production of the deciduous forest, it was calculated that the food available for voles constitutes 6.8 to 16.9%, and for mice 0.9 to 11.7% of this value. It was concluded that the abundance of a given type of food does not determine its choice by rodents, but that this depends mainly on food habits of the animals.

I. INTRODUCTION

In investigations of energy flow through an animal population the primary production of the ecosystem is usually compared with the amount of food taken from it by the animals. Such studies concerning small rodents were carried out in various ecosystems: abandoned fields (Golley, 1960; Odum, Connell & Davenport, 1962), meadows (Pearson, 1964), beech forest (Drożdż, 1966), low peat-bog (Gębczyńska, 1970), desert shrub community (Chew & Chew, 1970), and taiga forest (Grodziński, 1971).

The purpose of this investigation has been to estimate the degree of utilization of food by the rodents studied in a deciduous forest of *Tilio-Carpinetum* type, and to establish whether the choice of a given type of food depends on its amount and availability in the terrain. The food supply of *Tilio-Carpinetum* forest has been also estimated.

II. MATERIAL AND METHODS

Red bank voles, *Clethrionomys glareolus* (Schreber, 1780), and yellow-necked field mice, *Apodemus flavicollis* (Melchior, 1830), were trapped in the *Tilio-Carpinetum* stand in the Niepołomice Forest near Kraków (50°07'N, 20°23'E). In all seasons of the year two methods were employed: microscopic analysis of stomach contents and food preference tests of rodents.

Stomach contents were analysed by separating them into particular fractions (green parts of plants, seeds, fruits, invertebrates and fungi), and estimating their relative volume. Five microscopic slides were prepared from each fraction, and fraction composition was determined on the basis of 5 fields of vision from each slide. For the identification of plant species, histological slides and drawings of the epiderm were employed (cf. Williams, 1962; Holišova, Pelikan & Zejda, 1962; Drożdż, 1966).

The food habit experiments were conducted in four seasons of the year using the test of choice which depends on supplying the animals in separate cages with

Table 1

Number of stomachs of *C. glareolus* and *A. flavicollis* analysed in different seasons.

Seasons	*C. glareolus*	*A. flavicollis*
Spring (Apr.—June), 1967, 1968, 1969	126	34
Summer (July—Sept.), 1969	14	25
Autumn (Oct.—Nov.), 1967, 1968	102	52
Winter (Dec.—March), 1968	9	14
Total	251	125

3 to 5 types of different food and estimating the degree of its utilization in an arbitrary scale from 0 to 3 (Górecki & Gębczyńska, 1962; Drożdż, 1966; Watts, 1968; Gębczyńska, 1970).

Food preference was investigated in 105 rodents (52 *C. glareolus* and 53 *A. flavicollis* in series consisting of 10 to 15 animals). Contents of 376 stomachs were analysed (Table 1).

III. RESULTS

3.1. Food Preference

The preference of natural forest foods by *C. glareolus* varied with seasons. Fourteen of 22 tested plant species were consumed by voles to a degree above the second stage of the scale (Table 2). Most consumed were: *Anemone nemorosa* L., *Mycelis muralis* (L.) Dum., *Oxalis acetosella* L., *Ranunculus lanuginosus* L.; *Asarum europaeum* L. and *Carex brizoides* L. were omitted. Voles consumed both leaves and immature seeds of the herb layer plants (Fig. 1). They utilized some buds and bark from tree twigs supplied.

Field mice showed a more narrow food choice. Herb layer plants were consumed only reluctantly. Only *Mycelis muralis* (L.) Dum., and *Ranunculus lanuginosus* L. were utilized above scale number one. The remaining plants of the herb layer were negligibly consumed, and from trees, only some buds were eaten (Table 2). When herb layer plants and their seeds were supplied seed consumption by the rodents was considerably greater (Fig. 1).

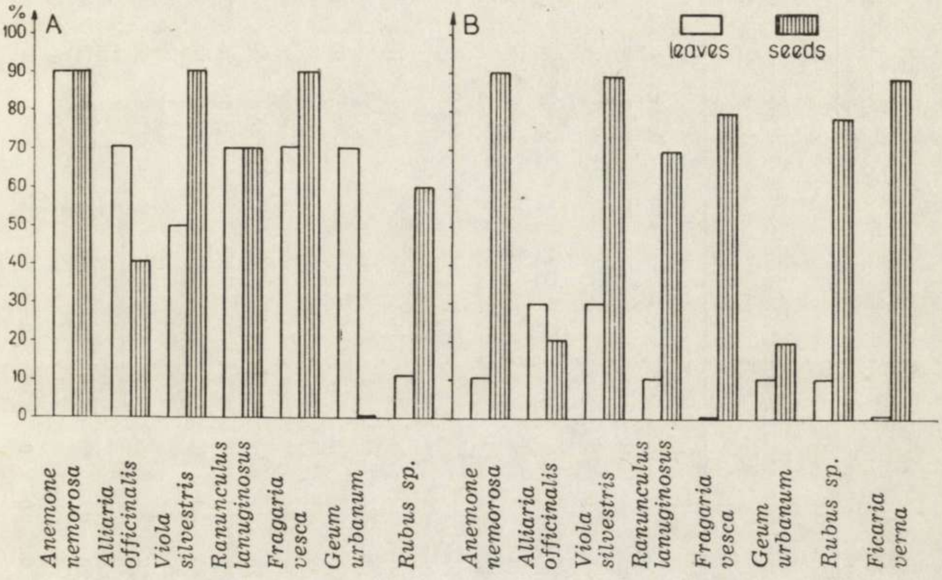

Fig. 1. Consumption of herb layer plants and their seeds by *C. glareolus* (A) and *A. flavicollis* (B).

Since both species consume both immature and mature seeds of herb layer plants it may be supposed that in spring (in the absence of other foods) field mice may especially utilize immature seeds remaining on plants. Tree and shrub seeds (except *Fraxinus excelsior* L.) are willingly consumed. The rodents consumed only stones from *Rosa* sp. fruits, leaving the pulp, the reverse was observed in the fruits of *Sambucus nigra* L. (Table 2).

3.2. Analysis of Stomach Contents

The following categories of food could be distinguished in the stomachs of mice and voles: seeds, fungi, green parts of plants, fruits, and foods of animal origin.

Table 2

Food preference of *C. glareolus* and *A. flavicollis* expressed in a scale of four degrees.

	C. glareolus								*A. flavicollis*							
	Spring		Summer		Autumn		Winter		Spring		Summer		Autumn		Winter	
	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%
HERB LAYER PLANTS																
Anemone nemorosa L.	3.0	100	—	—	—	—	—	—	0.3	10	—	—	—	—	—	—
Mycelis muralis (L.) Dum.	3.0	100	2.8	90	—	—	—	—	2.0	60	2.8	90	—	—	—	—
Oxalis acetosella L.	3.0	100	3.0	100	—	—	—	—	0.7	20	0.4	10	0.4	10	0.3	10
Ranunculus lanuginosus L.	2.9	100	2.2	70	2.1	60	—	—	1.2	30	0.3	10	+	5	—	—
Geum urbanum L.	2.5	80	2.4	80	—	—	—	—	0.3	10	0.3	10	—	—	—	—
Majantheum bifolium (L.)	2.4	80	2.6	80	2.2	70	—	—	+	5	0	0	0	0	—	—
Ficaria verna Huds.	2.3	70	—	—	—	—	—	—	+	5	—	—	—	—	—	—
Fragaria vesca L.	2.3	70	2.4	80	—	—	—	—	+	5	+	5	—	—	—	—
Galeobdolon luteum Huds.	2.3	70	1.9	60	1.1	30	1.5	40	0.4	10	0.6	20	0.4	10	0.8	20
Glechoma hederacea L.	2.3	70	1.3	40	1.4	40	—	—	+	5	0.5	10	0.4	10	—	—
Asperula odorata L.	2.1	60	1.8	50	1.3	40	—	—	0.4	10	0.3	10	0.3	10	—	—
Pulmonaria obscura Dum.	2.1	60	0.5	10	0.4	10	—	—	0.8	20	0.4	10	0.3	10	—	—
Alliaria officinalis Andrz.	2.0	60	2.3	70	1.2	40	0.9	30	0.7	20	0.7	20	—	—	—	—
Mercurialis perennis L.	1.7	50	0.8	20	—	—	—	—	0.8	20	1.1	30	—	—	—	—
Viola silvestris Rchb.	1.7	50	2.4	70	1.2	40	0.9	30	1.0	30	0.8	20	0.3	10	0,4	10
Impatiens noli-tangere L.	1.6	50	1.5	40	—	—	—	—	0.5	10	0.6	20	—	—	—	—
Cardamine amara L.	1.7	50	1.7	50	1.6	50	—	—	0.4	10	0.4	10	0.3	10	—	—
Ajuga reptans L.	1.1	30	2.0	60	1.8	50	2.0	60	0.8	20	0.7	20	0.5	10	0.8	20
Aegopodium podagraria L.	1.0	30	—	—	—	—	—	—	0.4	10	—	—	—	—	—	—
Circaea lutetiana L.	0.8	20	0.6	20	0.6	20	—	—	0.6	20	0.8	20	0.4	10	—	—
Asarum europaeum L.	+	5	+	5	+	5	+	5	0	0	0	0	0	0	0	0
Carex brizoides L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

GREEN PARTS OF TREES AND SHRUBS																
Rubus sp.	2.0	60	0.5	10	—	—	1.8	50	0.4	10	0.5	10	—	—	+	5
Carpinus betulus L.	+	5	+	5	+	5	+	5	+	5	+	5	+	5	+	5
Tilia cordata Mill.	+	5	+	5	+	5	+	5	+	5	+	5	+	5	+	5
Quercus robur L.	+	5	+	5	+	5	+	5	+	5	+	5	+	5	+	5
SEEDS AND FRUITS																
Fragaria vesca L.	—	—	3.0	100	—	—	—	—	—	—	2.7	90	—	—	—	—
Viola silvestris Rchb.	3.0	100	—	—	—	—	—	—	3.0	100	—	—	—	—	—	—
Anemone nemorosa L.	3.0	100	—	—	—	—	—	—	3.0	100	—	—	—	—	—	—
Ranunculus lanuginosus L.	—	—	2.9	100	—	—	—	—	2.5	70	2.5	70	—	—	—	—
Alliaria officinalis Andrz.	1.5	40	1.5	40	—	—	—	—	0.7	20	0.7	20	—	—	—	—
Rumex sp.	—	—	+	5	+	5	—	—	—	—	+	5	0	0	—	—
Geum urbanum L.	—	—	0	0	0	0	0	0	—	—	0.6	20	0.6	20	0.6	20
Rubus sp.	—	—	2.8	90	2.9	100	—	—	—	—	0.6	20	0.6	20	—	—
Sambucus nigra	—	—	2.4	70	1.9	60	—	—	—	—	1.0	30	0.9	30	—	—
Crategus sp.	—	—	—	—	2.1	60	2.1	60	—	—	—	—	1.7	50	1.7	50
Rosa sp.	—	—	—	—	2.0	60	1.8	60	—	—	—	—	1.2	40	1.2	40
Prunus spinosa L.	—	—	—	—	1.6	50	—	—	—	—	—	—	0.9	30	—	—
Tilia cordata Mill.	—	—	—	—	3.0	100	3.0	100	—	—	—	—	3.0	100	3.0	100
Quercus robur L.	—	—	—	—	3.0	100	3.0	100	—	—	—	—	3.0	100	3.0	100
Carpinus betulus L.	—	—	—	—	2.9	100	2.9	100	—	—	—	—	2.7	90	2.8	90
Fraxinus excelsior L.	—	—	—	—	0.5	10	0.5	10	—	—	—	—	0.5	10	0.5	10

\+ — feeding experiments they were described as »trace« and the value of 5% was assumed.

In spring green parts of plants constituted 38 to 65%, seeds 19 to 55% and invertebrates 7 to 16% of the stomach volume in voles (Fig. 2). Rather large variations in the proportion of particular constituents during consecutive years were caused by abundant fall of acorns in autumn 1966; these acorns constituted easily available food for the rodent in the

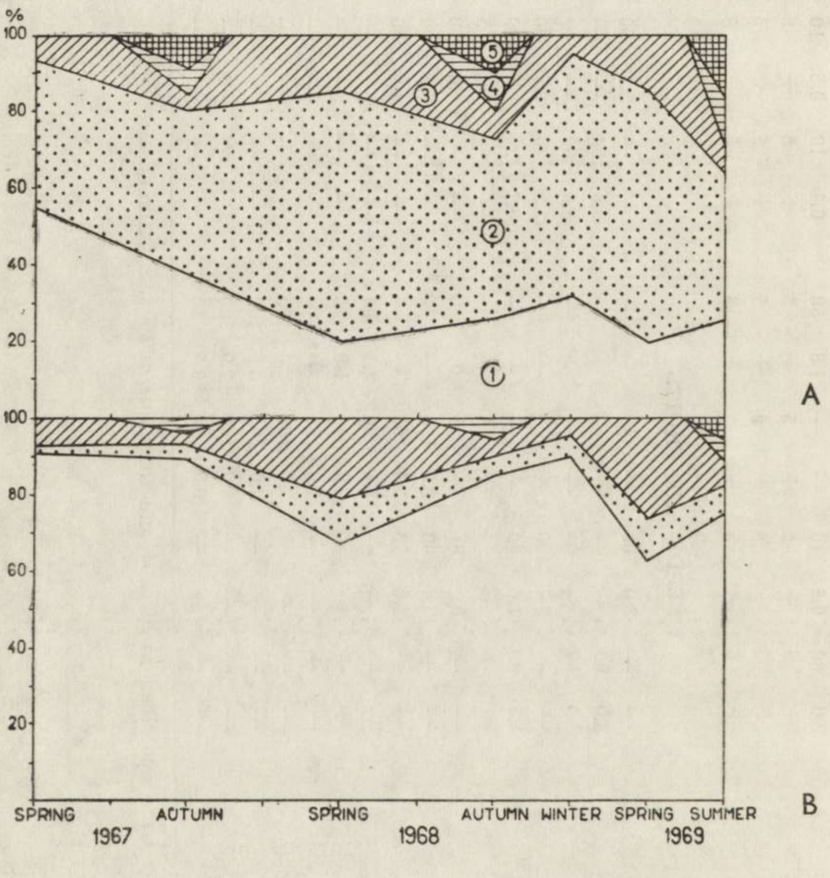

Fig. 2. Seasonal changes in the stomach content of *C. glareolus* (A) and *A. flavicollis* (B).
1 — Seeds, 2 — Plants, 3 — Invertebrates, 4 — Fungi, 5 — Fruits.

next year. On the other hand, the voles compensated for the lack of seeds in 1968 and 1969 by consuming invertebrates and green layer plants (Fig. 2).

The most often identified were: *Anemone nemorosa* L., *Oxalis acetosella* L., and *Pulmonaria obscura* Dum., hence these plants which along with *Mycelis muralis* (L.) Dum., and *Ranunculus lanuginosus* L., were preferred by voles in the feeding experiments.

Seeds predominated the stomach contents in spring (62 to 90%), while invertebrates constituted 8 to 12% and green plant parts were 8 to 26%. In case of seed deficiency the food was supplemented mainly with invertebrates, and to a lesser extent with green plants part (Fig. 2), mostly *Mycelis muralis* (L.) Dum., *Mercurialis perennis* L., and *Anemone nemorosa* L.

In summer, fruits, seeds, fungi and invertebrates constituted 17, 26, 12 and 7% respectively, the stomach content of voles while green plant remains were considerably reduced. Fruits and seeds of *Viola silvestris*

Table 3

Abundance of herbaceous plants and preference of them (%) by *C. glareolus*.

pecies	Abundance	Preference, %
Carpinus betulus L.	51.26	5
Quercus robur L.	42.71	5
Aegopodium podagraria L.	27.70	30
Anemone nemorosa L.	17.70	100
Impatiens noli-tangere L.	11.25	50
Ficaria verna Huds.	9.23	70
Glechoma hederacea L.	7.73	70
Circaea lutetiana L.	3.16	30
Tilia cordata Mill.	2.77	5
Carex brizoides L.	2.28	0
Viola silvestris Rchb.	1.72	50
Alliaria officinalis Andrz.	0.46	60
Ranunculus lanuginosus L.	0.04	100
Geum urbanum L.	0.03	80
Ajuga reptans L.	0.03	30
Fragaria vesca L.	0.03	70
Cardamine amara L.	0.02	50
Asperula odorata L.	0.02	60

Rchb., *Ranunculus lanuginosus* L., *Fragaria vesca* L. and *Rubus sp.* were most often encountered in the stomach, and most willingly selected in feeding experiments.

In the summer seeds constituted over 70% of the stomach volume of mice. Invertebrates and green parts of plants comprised 5 and 9% of the volume, respectively.

In 1967 and 1968 the autumn seed crop was very small and green parts of herb layer plants represented 50% of the stomach volume in voles seed content was 26 to 37%. On the other hand, mouse stomach contained nearly 90% seeds. A similar proportion was observed in the winter (Fig. 2).

3.3. Relationship between Food Habits of Rodents and Food Abundance

In order to determine whether rodents select the plants most often encountered in a habitat, the density of individual species of herb layer plants was compared with the test preference results. The comparison was made only for the bank vole on the basis of 12 phytosociological communities (Braun-Blanquet scale) during the spring on the area studied (B a n a s i k, unpubl. data).

Average percentage of cover was quantified according to of the B r a u n - B l a n q e t scale (1951). Table 3 shows the mean density of cover of the terrain by herb layer plants and consumption of these plants by voles in feeding experiments. The calculated coefficient of correlation $r = .1391$ is not significant. This permits the conclusion that the preference of a given plant by the animal is not a simple function of plant abundance (density of area cover) but depends on food habits of the rodents.

IV. DISCUSSION

The Niepołomicka Forest represents a typical *Tilio-Carpinetum* stand dominated by *Quercus robur* L., *Carpinus betulus* L. and *Tilia cordata* Mill. The total wood production amounts to 6.4 t dry wt/ha year, and of this approximately 6 t dry wt/ha year correspond to parts above the ground (D z i e w o l s k i, unpubl. data). Tree leaves and shrubs constitute over 3 t dry wt/ha year, and fallen tree seeds were estimated as 5.3 kg dry wt/ha year (B a n d o ł a, unpubl. data). The production of herb layer plants, in which dominate *Aegopodium podagraria* L., *Anemone nemorosa* L., *Impatiens noli-tangere* L., *Symphytum tuberosum* L., *Glechoma hederacea* L., *Circaea lutetiana* L. and *Milium effusum* L., was estimated as 602.36 kg dry wt/ha year (B a n a s i k, unpubl. data). The total production of trees, shrubs and herb layer plants amounts in this forest to 43.13 million kcal/ha year with a low seed crop, and increases to 48.41 million kcal in a year with a high seed crop (Table 4).

By knowing the total production of the *Tilio-Carpinetum* Niepołomicka Forest and food habits of the small rodents predominating there it is possible to estimate that part of the forest's net production which constitutes the available food supply of these animals. Such estimation requires, however, that the following simplified assumtions be made: (1) only the annual production of wood is taken into consideration, and the timber accumulated in previous years is ignored (2) the production of subsurface plant parts is ignored (3) those plants not consumed by the rodents in feeding experiments and not found in the stomach contents are omitted from the analysis.

Due to different food habits of the rodent species studied, the balance was obtained separately for red bank voles and field mice. Table 4 shows the estimated total production of trees and herb layer plants. The available herb layer food was approximately 2.0×10^6 kcal/ha year for voles, and $.3 \times 10^6$ kcal/ha year for mice. The total leaf production in the *Tilio-Carpinetum* forest is 3 t dry wt/ha year. Assuming that only 5% of leaves from the lowest twigs is available for the voles this amounts to $.74 \times 10^6$ kcal/ha year. The supply of the bark and twigs from trees and shrubs consumed in the absence of other food by voles was similary estimated in the beech forest (D r o ż d ż, 1966) as 20 to 30 kg dry wt/ha year. Seeds constitute an important and highly caloric food for rodents; their production varies from 5.3 kg dry wt/ha year poor

Table 4

Primary production of the deciduous forest of *Tilio-Carpinetum* type and food supply for the studied rodents in kg of dry wt/ha year and 10^6 kcal/ha year.

Food	Primary production		Available food	
	kg dry wt/ha year	kcal/ha year	Voles kcal/ha year	Mice kcal/ha year
Wood[1]	5962	25.8	0.1	—
Leaves[2]	3026	14.8	0.74	—
Herb layer plants[3]	602.36	2.55	2.0	0.3
Fungi and invertebrates	—	0.05	0.05	0.05
Tree seeds[2] *	5.3	0.03	0.03	0.03
Tree seeds[2] **	1205.3	5.31	5.31	5.31
Heavy mast year, Total	10795.66	48.46[6]	8.20	5.66
Light mast year, Total	9595.66	43.18	2.92	0.38

[1] Above-ground parts only — after D z i e w o l s k i (unpubl. data), [2] after B a n d o ł a (unpubl. data), [3] after B a n a s i k (unpubl. data), [4] Assumed as for the beech forest, [5] A correction for plant consumption by the animals was taken into consideration, [6] Caloric values of acorns after G r o d z i ń s k i & S a w i c k a - K a p u s t a, 1970.

* Year with poor seed crop, ** Year with heavy seed crop.

crop to 1200 kg dry wt/ha year in good seed crop year. The data on the food available for rodents are slightly underestimated by not including fungi and invertebrates consumed by these animals. Assuming that the biomass of these foods is similar to that in the beech forest (D r o ż d ż, 1966), the total food available for small rodents in a poor seed crop year would amount to 2.92×10^6 kcal/ha year for the bank vole and $.38 \times 10^6$ kcal/ha year for the field mouse, while the corresponding figures for a year with heavy crop of tree seeds are 8.20 and 5.66×10^6 kcal/ha year, respectively (Table 4). Hence almost 6.8% of the total primary production of the *Tilio-Carpinetum* forest constitutes the available food the bank vole but only .9% for the field mouse. In a year with heavy seed crop these values are 16.9% for the vole and 11.7% for the mouse. Heavy seed crop years occur more often in a *Tilio-Carpinetum* forest, however, and the herb layer is more abundant than in the beech forest. It may be thus supposed that despite the relatively large fall of beechmast observed rodents find a better food supply in a *Tilio-Carpinetum* type forest.

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STOSUNKI POKARMOWE DROBNYCH GRYZONI W GRĄDZIE PUSZCZY NIEPOŁOMICKIEJ

Streszczenie

W grądzie Puszczy Niepołomickiej koło Krakowa badano przyzwyczajenia pokarmowe *C. glareolus* i *A. flavicollis*, które stanowią 93% wszystkich drobnych gryzoni na tym terenie. Posługiwano się równolegle dwoma metodami: testem wyboru i analizą treści żołądków gryzoni. Pierwsza z nich daje odpowiedź na pytanie jaki pokarm może być zjadany przez gryzonie, druga — jaki pokarm faktycznie jest przez nie zjadany. Ogółem przeanalizowano 376 żołądków (Tabela 1).

W żołądkach myszy przez cały rok dominowały nasiona 62%—90%, bezkręgowce stanowiły 4,5%—26%, zielone części roślin 2,1%—12% oraz grzyby i owoce po około 5% objętości żołądka. W żołądkach nornic nie stwierdzono wyraźnej dominacji jednego typu pokarmu nad innymi: nasiona stanowiły 19%—55%, bezkręgowce 2,5—16%, zielone części roślin 38%—65%, owoce 9%—20% i grzyby 8%—12% objętości żołądka.

Doświadczenia żywieniowe wykazały, że nornice jadły chętnie nasiona roślin runa i nasiona drzew z tym, że nasiona *Fraxinus excelsior* mniej chętnie niż inne oraz wiele spośród roślin runa — najchętniej *Anemone nemorosa, Mycelis muralis, Oxalis acetosella* i *Ranunculus lanuginosus*. Zdecydowanie nie jadły *Carex brizoides*. Myszy najchętniej wybierały nasiona roślin runa i drzew z tym, że nasiona *Fraxinus excelsior* słabiej i dopiero po zjedzeniu nasion wybierały nieliczne spośród roślin runa np. *Mycelis muralis* czy *Ranunculus lanuginosus* (Tabela 2, Ryc. 1).

Aby przekonać się, czy gryzonie wybierają pokarm, którego aktualnie jest najwięcej przeprowadzono porównanie gęstości pokrycia terenu przez rośliny runa (zdjęcia fitosocjologiczne) z wynikami testów wyboru. Stwierdzono, że nie obfitość pożywienia determinuje jego wybór przez gryzonie, lecz jest to uwarunkowane obyczajami pokarmowymi zwierząt (Tabela 3). Produkcja netto lasu grądowego Puszczy Niepołomickiej oszacowana jest na ponad 43 mln kcal/ha × rok w roku nienasiennym i ponad 48 mln kcal/ha × rok w roku nasiennym (Tabela 4). Ilość pokarmu dostępnego dla gryzoni waha się w zależności od opadu żołędzi od 6,8%—16,9% produkcji pierwotnej dla nornicy i 0,9%—11,7% produkcji pierwotnej dla myszy.

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