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Food Conditions for Small Rodents in a Deciduous Forest

Stosunki pokarmowe drobnych gryzoni w lesie liściastym

[With 8 Figs. and 11 Tables]

I. PROBLEM

The role played by food in the mechanism controlling the size of populations of small rodents in the forest is not quite clear. It is known from numerous studies on the forest rodents that increased food supplies may bring about an increase in the number of these animals. It has been stated many a time that in mixed forests the number of voles and field mice augments evidently after the so-called "rich seed years" (Naumov, 1948; Adamczewska, 1961, and others). However, it is not clear whether the food supply of a forest may be the factor limiting the number of rodents or, in other words, whether the forest may run short of the food available for these animals.

The opinions of several authors who dealt with this problem are very divergent (Hamilton, 1941; Miller, 1954; Novikov, 1959). The solution of the question can be attempted by calculating the bioenergetic balance (Pearson, 1948), which, including only small mammals and their plant food in the forest community, is a fractional balance.

The calculation of the food balance for small mammals of a forest must be based on the determination of (1) their metabolism rate and bioenergetics, (2) number of these animals in the forest, (3) their food preference and (4) food supply provided by the forest (Grodziński, 1961).

Studies of this type were undertaken as a team work in the Department of Organic Evolution of the Jagiellonian University and carried out in a *Querceto-Carpinetum* community in the Wolski Wood near Kraków in 1959—1961. This is a climax community well-known to the botanists as regards its phytosociology (e.g. Medwecka-Kornaś, 1952).

The small mammals of the Wolski Wood have been already worked out (Kowalski 1950). *Clethrionomys glareolus* (Schreber 1780), *Apodemus flavicollis* (Melchior 1834) as well as *Sorex araneus* Linnaeus 1758 and *Apodemus agrarius* (Pallas 1771) predominate here decidedly.

The study presented in this paper deals with the food preference and diurnal food consumption in the bank vole, *Clethrionomys glareolus* (Schreber 1780) and yellow-necked field mouse (*Apodemus flavicollis* (Melchior 1834) in the annual cycle. The other purpose of the investigations was to determine the food supplies of the Wolski Wood for small mammals in the phenologically different seasons of the year. The metabolism rate and bioenergetics of small rodents in this wood constitute the subject of another publication (Grodziński 1962).

II. LOCALITY, MATERIAL AND METHODS

The Wolski Wood near Kraków, 427 hectares in area, covers one of the southernmost hills (270—358 m. a.s.l.) of the Kraków—Wieluń Jurassic Ridge. A well-developed community of *Querceto-Carpinetum medioeuropaeum* Tüxen 1936 (Medwecka-Kornaś, 1952), situated on the northern slopes of the hill near the reserve of Panieńskie Skały, was chosen for studies on the food conditions of rodents. The wood abounds in natural hiding-places for small mammals. Its food supplies available for rodents were estimated three times: in winter, at the passage from spring to early summer, and in autumn (Fig. 1). Determination of supplies was limited to the forest floor only, this being the most important layer to small mammals.

Ten samples of the herb layer vegetation and litter were collected from the 50×50 centimetre squares of the forest floor. The fresh plants in the samples were estimated in weight units (Dąbrowski, 1953), and the seeds were picked out of the samples dried for 24 hours and then weighed. Caloric value was found for all seeds; for this purpose the eatable matter content was calculated for each kind of seeds prior to their being combusted in Berthelot's bomb calorimeter.

The rodents used for laboratory studies were caught in box live traps in the Wolski Wood except mouse No. 22, which was caught in the neighbouring deciduous thicket. Catching was carried out in open plots for about 6 months in 4 main seasons of the year (Fig. 1.).

A total of 50 bank voles and 41 yellow-necked field mice were used for investigations.

During the feeding experiments the rodents were kept in large glass jars with a calibrated receptacle, glass feeding pot and a little cotton wool in each. The food, always in excess, various kinds of which were offered to animals so that they might

have their choice, was changed every day. Five series of experiments were carried out, and the foods used for them were those occurring in the Wolski Wood at the time of the particular experiment (Fig. 1). In winter the animals were given seeds, in the prevernal season seeds and twigs, towards the end of spring and at the beginning of summer herbs and twigs with fresh leaves on them, and in autumn green parts and seeds.[1])

The diurnal food consumption was determined in weight units (seeds and part of plants) or according to the four-grade scale (twigs and remaining plants) similar to those used by Naumov (1948), Miller (1954) and Sviridenko (1961).

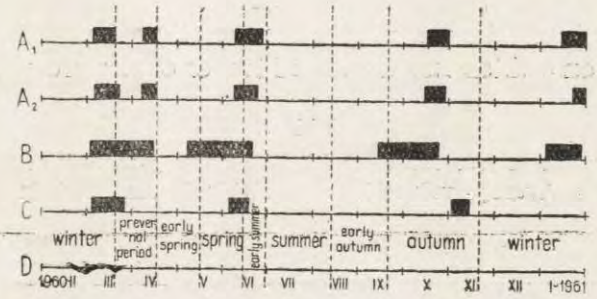

Fig. 1. Graph indicating time and length of laboratory experiments and field studies. A_1 — feeding experiments with *Clethrionomys glareolus* (Schreber), A_2 — feeding experiments with *Apodemus flavicollis* (Melchior), B — catches of small mammals in *Querceto-Carpinetum* forest, C — collecting of litter and herbs from the squares of the *Querceto-Carpinetum* forest floor, D — phenologic seasons of year.

During all these feeding experiments the animals were carefully weighed several times. The experiments were made at a temperature ranging between 16 and 21° C (in various seasons) and relative humidity between 60 and 80%. Control experiments at a temperature of 14° C and relative humidity of 95% were also carried out. Feeding experiments provide information on the food preference in the rodents examined, as well as render it possible to calculate their diurnal caloric requirements. The diurnal energy consumption thus calculated is not very accurate (Turček, 1956). It is why the determination of gaseous metabolism was applied as an accessory method. The oxygen consumption in voles and mice was measured at a temperature of 20° C in the Kalabukhov apparatus modified by Skvartzov (1957), working on the closed-circuit principle. The oxygen consumption measured during morning hours may be converted roughly into diurnal energetic requirement (Grodziński, 1961), assuming the respiratory quotient, R.Q., equal to 0.8 (Pearson, 1947), at which the caloric value of 1 l. of O_2 corresponds to 4.8 kg. cal.

The structure of the alimentary canal of the rodents in question was also studied to know their ability to absorb different foods. The relations between the lengths of

[1]) The seeds were supplied by the District Forest Administration in Kraków.

particular portions of the dissected alimentary canal were determined with special attention given to the small intestine and caecum.

The feeding experiments were carried out on 43, measurements of the alimentary canal on 48, and those of metabolism on 35 specimens of voles and mice.

III. RESULTS

1. Winter

In the Wolski Wood the phenological winter lasts from the end of November to about mid-March. However, the ground is not covered with snow all this time. In 1959/60 the snow sheet lay for 50 days and in 1960/61 for 42 days. The snow layer is generally of small thickness (5—20 cm) and rests on a thick substratum of leaves of the preceding year.

Table 1.

Diurnal consumption of tree seeds by *Clethrionomys glareolus* in the winter series of experiments. Average values for 10 individuals examined, in g. (cf. Fig. 2).

Vole No. / Seeds	1	2	3	201	203	204	205	214	216	217	Avg.
Carpinus betulus	0.48	0.90	0.61	0.27	0.20	0.21	0.08	0.23	1.30	0.50	0.477
Quercus sessilis	0.78	1.09	1.07	1.10	0.36	1.04	0.30	0.65	0.45	1.40	0.824
Fagus silvaticus	0.68	2.16	0.10	1.36	1.41	0.90	1.32	2.64	1.86	1.40	1.383
Tilia cordata, 1 - 3											0.291
Acer platanoides, 201 - 217	0.42	0.27	0.19	0.55	0.21	0.40	0.04	0.36	0.11	-	0.237
Water	5.63	5.05	3.80	5.10	5.30	4.00	4.60	5.80	5.60	not measured	4.986
Total seed consumption	2.35	4.42	1.97	3.28	2.18	2.50	1.74	3.88	3.72	3.30	2.935
Seed consumption per 1g. of body weight	0.12	0.17	0.13	0.14	0.13	0.11	0.10	0.29	0.22	0.15	0.149
Body weight	19.79	26.62	14.89	23.75	16.70	23.40	16.60	19.35	15.65	22.20	19.664

Table 2.

Diurnal consumption of tree seeds by *Apodemus flavicollis* in the winter series of experiments. Average values for 9 individuals, in g.

Mouse No. / Seeds	21	22	01	02	04	06	08	09	11	Avg.
Carpinus betulus	0.17	0.18	0.12	0.05	0.10	-	0.24	0.13	0.02	0.112
Quercus sessilis	0.51	1.21	2.10	1.21	1.22	1.52	1.05	0.73	1.55	1.232
Fagus silvaticus	2.83	0.84	2.20	2.58	2.05	2.34	2.05	2.18	2.40	2.163
Acer platanoides 01 - 11										0.170
Tilia cordata, 21 , 22	0.79	0.85	0.20	0.34	0.02	0.13	0.02	0.20	0.06	0.812
Water	7.20	4.25	not measured	1.80	2.00	2.00	1.50	3.00	2.00	3.000
Total seed consumption	4.30	3.08	4.62	4.18	3.39	3.99	3.36	3.24	4.03	3.798
Seed consumption per 1g. of body weight	0.14	0.10	0.16	0.14	0.13	0.14	0.11	0.10	0.16	0.132
Body weight	30.80	31.35	28.75	29.35	25.45	27.65	29.15	31.50	25.70	28.855

In the winter small rodents forage under snow as well as on its surface. Under snow they find mainly seeds, while on the surface they may catch insects or collect the seeds of the trees seeding in this season of the year. They also fairly often bite off the bark from trees and shrubs. At the beginning of winter voles and mice have good stores of seeds in their nests and avail themselves of seeds occurring in the layer of leaves. These supplies, however, run short as the winter time passes and the most critical period, as far as food is concerned, comprises the end of winter and the prevernal period, which came about mid-March in both years. It is why the samples of litter were collected from the forest floor and their food supplies available for rodents determined in March 1960.

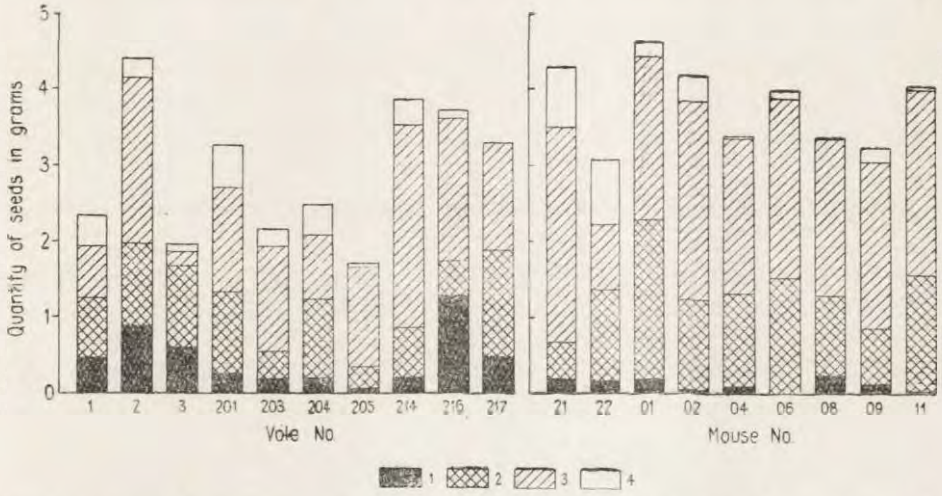

Fig. 2. Diurnal consumption of tree seeds by voles *(Clethrionomys glareolus)* and mice *(Apodemus flavicollis)* in the winter series of experiments. Average diurnal values for 10 voles (Nos. 1—217) and 9 mice examined (Nos. 21—11).

1 — *Carpinus betulus;* 2 — *Quercus sessilis;* 3 — *Fagus silvatica;* 4 — *Tilia cordata* (voles 1—3, mice 21,22) and *Acer platanoides* (voles 201—217, mice 01—11).

The average number of seeds of hornbeam, oak, beech, lime, maple and sycamore maple found in 1 sq. m. of the litter amounted to 102, with a total weight of 5.564 g. This figure was composed of 3.800 g. of hornbeam seeds, 0.472 g. of acorns, 0.316 g. of beech mast, 0.736 g. of seeds of maple and lime, and 0.240 g. of sycamore maple. Besides the seeds, small invertebrates (earthworms, snails, myriapods, beetles and *Apterygota*) and plants represented by germinating seedlings of hornbeam or oak and by sprouts of *Chaerophyllum* sp. occurred fairly abundantly in the litter.

The laboratory experiments on winter food preference were carried out in high winter (Jan. 23—28, 61) and towards the end of winter

(March 10—20, 60) (Fig. 1). The rodents were given the kinds of seeds which were present on the floor of the forest at that time except for those of sycamore maple. The diurnal consumption of seeds by 1 bank vole (Table 1) ranged from 1.710 to 4.420 g. with an average of 2.935 g. The fluctuation will be smaller, if the diurnal seed consumption is converted into the value for 1 g. of the body weight of the vole. This lies within 0.105 and 0.287 g. of seeds and the average is 0.149 g. (Table 1). Most of the bank voles ate beech mast (averaging 1.383 g.) and acorns (0.824 g.) very readily, the remaining seeds being used less willingly.

The diurnal consumption of seeds by the yellow-necked field mouse (Table 2) fluctuated between 3.077 and 4.620 g. with an average of 3.789 g. When calculated for 1 g. of the body weight of the mouse, it averaged 0.132 g. of seeds per 24hrs. It will be seen clearly from Figs. 2 that in the 19 specimens of bank voles and field mice examined there were great individual variations in their preference for food types. The majority of the voles consumed beech mast most readily with acorns following; some of them, however, behaved reversely. Great differences were also found in the amounts of hornbeam seeds eaten.

All the yellow-necked field mice (except No. 22) ate beech mast most readily and then acorns. The eating of maple and hornbeam seeds showed great individual differences. Mouse No. 22, coming from a young *Querceto-Carpinetum* wood of Sikornik, presented an interesting case. It took acorns and lime seeds most readily, beech mast coming in second. This might be explained by the food habits it had acquired in the young wood of Sikornik, where fruiting beeches were lacking whereas oaks and limes prevailed.

2. Spring and Summer

In the Wolski Wood the spring lasts about three months, from mid-March to mid-June, and the summer about two months, from mid-June to mid-August. The spring may be divided into three distinct periods: "prevernal period", "early spring" and "high spring" (Krotoska, 1961). In 1960, the prevernal period began in the Wolski Wood between 15-th and 20-th of March and lasted until April 15, being followed by a month's spell of the early spring, which in mid-May passed into the high spring ending in the first half of June. Then came two summer months, the first three weeks of which, in June, may still be distinguished as "early summer" (Fig. 1).

The development of the herbaceous layer in the *Querceto-Carpinetum* community of the Wolski Wood comes very early. The first shoots of herbs appear no later than the prevernal period. The rapid growth of vegetation on the floor of the forest takes place in the early spring, the

maximum of density and flowering being reached by the herbs at the end of the early spring and during the high spring.

At that time also the foliage of trees and shrubs arrives at the final stage of development, to a high degree shutting off the light from the forest floor. This results in a remarkable reduction of the density of the herb layer on the shaded floor of the forest.

The biomass of the vegetation of the forest floor at the stage of its full development (at the break of the early summer) averaged 716.430 g. per 1 sq.m. This figure included mainly *Poa nemoralis* (123.670 g.), then *Asarum europaeum* (82.320 g.), *Lilium martagon* (67.200 g.) and *Chaerophyllum sp.* (63.920 g.). The amount of *Polygonatum multiflorum*, hardly 15.240 g. per sq.m., was the smallest. The remaining plants — *Ranunculus longinosus, Phyteuma spicatum, Milium effusum, Viola silvestris, Lamium maculatum, Polygonatum verticillatum* and *Mycelis muralis* — occurred in amounts of the same order, their biomass fluctuating between 22.400 and 33.680 g. per sq.m.

The laboratory experiments on the food preference and diurnal food consumption in bank voles and yellow-necked field mice were carried out in the prevernal period (Apr. 7—12), as well as at the end of the spring and beginning of the summer (June 10—27). Thus, the poorest period in plant foods and the richest one were picked out of these two seasons for study.

During the experiments in the prevernal period the voles and mice were offered twigs of hornbeam, oak, beech, lime and birch with limited amounts of seeds of hornbeam and maple (4 g. in all). The diurnal consumption of these foods was calculated as the average of the data obtained with two voles and two mice in six days. The voles ate on an average 2.969 g. of twigs with preference for lime (averaging 1.597 g.). The twigs of beech and oak were taken in considerably smaller amounts and those of hornbeam and birch least. Of seeds they chose maple (0.378 g.), the consumption of hornbeam seeds being only 0.238 g. Both individuals lost weight remarkably in the course of the six-day series of experiments (5.500 and 7.430 g.). The field mice ate as little as 0.664 g. of twigs per day, of which lime with 0.491 g. was the most important food. They browsed on the twigs of beech, birch and oak far less.

Thus, twigs do not seem to be the main food for bank voles nor for field mice even in the prevernal period.

At the end of the spring and beginning of the summer feeding experiments were conducted on 10 bank voles and 4 field mice for 17 days (June 10—27, 60). The experiments consisted of 2 series. In the first series the animals were provided with all the herbs and leafed twigs of trees

Table 3.

Food preference shown by *Clethrionomys glareolus* in relation to herbs and trees at the end of spring. Quantities of plant foods eaten by the vole determined according to the 4-grade scale: +++ — food eaten in 50—90%, ++ — food eaten in 20—50%, + — food eaten in less than 20%, 0 — food left completely uneaten.

Food type \ Vole No.		1	2	3	4	juv.	5	6	7	8	9	Per cent average
Trees	Carpinus betulus	+	+	+	0	–	–	–	–	–	–	10
	Quercus sessilis	0	0	+	–	–	0	++	+	0	0	10
	Fagus silvaticus	+	0	+++	+	–	++	0	0	+	0	20
	Tilia cordata	+++	++	+++	+++	–	+++	+++	+++	+++	+++	90
	Acer platanoides	+	0	+++	++	+++	++	++	+++	++	++	50
Fresh herbs	Pulmonaria obscura	+++	–	+++	+++	+++	+	–	+	–	–	70
	Milium effusum	–	–	–	–	–	+++	–	++	–	–	70
	Asarum europaeum	++	–	–	+++	–	++	–	0	–	–	50
	Lilium martagon	+++	–	–	+++	–	–	–	–	–	–	90
	Poa nemoralis	+	–	0	0	–	+	–	–	–	–	10
	Viola silvestris	+++	–	–	+++	+++	–	–	–	–	–	90
	Hedera helix	++	–	–	+++	–	+++	–	+++	–	–	80
	Lamium maculatum	+++	–	+++	+++	+++	–	–	–	–	–	90
	Polygonatum verticillatum	–	–	–	–	–	+++	–	+++	–	–	90
	Chaerophyllum sp.	–	–	–	–	–	+++	–	++	–	–	70
	Mycelis muralis	+++	–	–	+++	+++	–	–	–	–	–	90
	Oxalis acetosella	+++	–	+++	+++	+++	–	–	–	–	–	90
	Convalaria majalis	–	–	–	–	–	+++	–	+	–	–	60
	Vaccinium myrtilus	+	–	+++	+++	–	+++	–	+++	–	–	80

Table 4.

Food preference shown by *Apodemus flavicollis* in relation to herbs and trees at the end of spring. Quantities of plant foods eaten were determined according to the 4-grade scale as in Table 3.

Food type \ Mouse No.		1	22	3	4	Per cent average
Trees	Carpinus betulus	+	++	++	–	40
	Quercus sessilis	+	++	+	–	30
	Fagus silvaticus	+	++	+	–	30
	Tilia cordata	++	++	+++	–	60
	Acer platanoides	+	++	++	–	40
	Acer pseudoplatanus	–	+++	–	–	90
Fresh herbs	Pulmonaria obscura	+	0	++	++	30
	Milium effusum	–	–	+	++	30
	Asarum europaeum	0	+	+	++	20
	Lilium martagon	+++	+++	–	++	80
	Poa nemoralis	0	++	++	–	30
	Viola silvestris	+++	+++	+++	++	80
	Hedera helix	+	0	+	–	10
	Lamium maculatum	++	+	+	++	40
	Polygonatum verticillatum	–	–	++	–	50
	Chaerophyllum sp.	0	0	+	+	10
	Mycelis muralis	+++	+++	+++	++	80
	Oxalis acetosella	+++	+++	+++	++	80
	Convalaria majalis	0	+	+	++	20
	Vaccinium myrtilus	++	+	++	–	40

Table 5.

Quantative consumption of green plant matter at the end of spring for 8 bank voles (*Clethrionomys glareolus*) in two series of experiments (A, B). Amounts of foods eaten are given in g. per day.

Vole No. / Fresh herbs	Given in g.	1	2	3	4	5	6	7	8	Avg.
					A					
Lamium maculatum	2.00	1.90	2.00	2.00	1.50	1.65	1.25	2.00	1.50	1.725
Mycelis muralis	2.00	2.00	1.75	1.25	1.60	2.00	1.45	1.90	2.00	1.743
Viola silvestris	2.00	2.00	1.60	1.50	1.70	1.50	1.40	1.55	1.45	1.587
Oxalis acetosella	2.00	1.85	2.00	2.00	1.80	1.55	1.90	2.00	2.00	1.888
Lilium martagon	1.00	1.00	0.82	0.65	0.50	1.00	0.45	0.65	0.35	0.677
Total	9.00	8.75	8.17	7.40	7.10	7.70	6.45	8.10	7.30	7.620
					B					
Pulmonaria obscura	2.00	1.60	1.95	1.30	2.00	1.80	1.90	1.30	1.60	1.618
Asarum europeum	1.00	0.25	0.30	0.50	0.80	0.45	-	0.30	0.15	0.343
Chaerophyllum birsulum	2.00	1.90	1.50	2.00	1.65	1.35	1.40	1.65	1.90	1.668
Convalaria majalis	1.00	0.55	0.80	0.70	1.00	0.40	0.55	0.20	0.30	0.500
Millium effusum	1.00	0.55	0.20	0.25	0.50	0.60	0.30	0.25	0.45	0.387
Total	7.00	4.85	4.75	4.75	5.95	4.60	4.15	3.70	4.40	4.317
Average for A + B	8.00	8.83	6.46	6.08	6.50	6.15	5.30	6.90	5.86	6.068

Table 6.

Quantative consumption of green plant matter by *Apodemus flavicollis* at the end of spring in two series of experiments (A, B). Amounts of foods eaten are given in g. per day.

Mouse No. / Fresh herbs	Given in g.	1	22	3	Avg.
			A		
Lamium maculatum	2.000	1.745	2.000	1.490	1.745
Mycellis muralis	2.000	1.150	1.150	0.980	1.093
Viola sylvestris	2.000	0.980	0.790	1.215	0.993
Oxalis acetosella	2.000	0.380	1.830	0.470	0.893
Lilium martagon	1.000	0.660	0.065	0.490	0.372
Total	9.000	4.915	4.835	4.645	5.096
			B		
Asarum europaeum	2.000	1.125	0.640	0.725	0.830
Chaerophyllum sp.	2.000	0.980	0.300	0.130	0.470
Convalaria majalis	1.000	0.660	0.205	0.235	0.366
Pulmonaria obscura	2.000	0.130	0.000	0.810	0.313
Milium effusum	1.000	0.320	0.065	0.490	0.291
Total	8.000	3.215	1.210	2.390	2.270
Average for A + B	8.500	4.050	3.500	3.500	3.683

occurring at that time. Four different diets were made up of 14 plant species and 5—6 tree species, and tried in turn for 12 days. The degree of their consumption was determined according to the 4-grade scale (Table 3 and 4).

Only 10 herbs (those eaten most readily by rodents) were used for the second series. During the first two days the bank voles and field mice received *Lamium maculatum*, *Mycelis muralis*, *Viola silvestris*, *Oxalis acetosella* and *Lilium martagon* (Tables 5 and 6, "A"), and for the following two days their diet included *Asarum europaeum*, *Chaerophyllum sp.*, *Convalaria majalis*, *Pulmonaria obscura* and *Milium effusum* (Tables 5 and 6, "B").

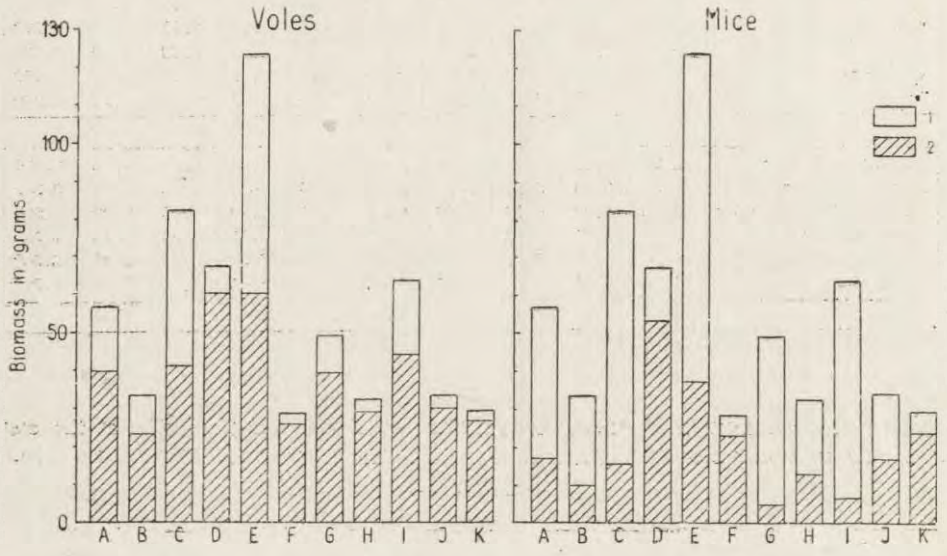

Fig. 3. Herb supplies of the floor of the *Querceto-Carpinetum* forest at the end of the spring and preference shown by *C. glareolus* and *A. flavicollis* in relation to these herbs.

1 — biomass of herbs, in g., 2 — preference for a given herb shown as per cent of its biomass. A — *Pulmonaria obscura*, B — *Milium effusum*, C — *Asarum europaeum*, D — *Lilium martagon*, E — *Poa nemoralis*, F — *Viola silvestris*, G — *Hedera helix*, H — *Lamium maculatum*, I — *Chaerophyllum sp.*, J — *Polygonatum verticillatum*, K — *Mycelis muralis*.

The diurnal consumption of fresh plants was determined in weight units (Table 5 and 6). Out of trees the lime twigs were taken most readily, while of herbs *Lilium martagon*, *Viola silvestris*, *Lamium maculatum*, *Mycelis muralis* and *Oxalis acetosella* were apparently preferred. *Poa nemoralis* was used by the voles very little. The results of the quantitative feeding experiments were very alike (Table 5). Part "A" of the Table shows that the voles ate similar, large amounts of *Oxalis acetosella*, *Mycelis muralis*, *Lamium maculatum* and *Viola silvestris*, that of *Lilium mar-*

tagon being somewhat smaller. In part "B" the voles consumed relatively much more of *Pulmonaria obscura* and *Chaerophyllum sp.*, and markedly less of *Convalaria majalis, Asarum europaeum* and *Milium effusum.* At the diet composed of 5 "less liked" herbs the voles ate up on an average 4.517 g. of plants per day, i.e. by 40% less than at the diet of "preferred" herbs.

The field mice (Table 4) picked leaves and bark from twigs of lime (60%) and sycamore maple (90%) most readily, and much less readily the remaining tree species. There were some individual differences in herb consumption; however, all the animals chose *Lilium martagon, Mycelis muralis, Oxalis acetosella* and *Viola silvestris* most readily (all were consumed in 80%). The remaining herbs were eaten to a slightly lower degree, and *Asarum europaeum, Convalaria majalis, Hedera helix* and *Chaerophyllum sp.* were taken in decidedly small amounts (10—20%).

During the second part of experiments the diurnal consumption of herbaceous plants averaged 3.683 g. (Table 6). The mice ate 5.096 g. per day of "preferred" plants (Table 6, "A") and only 2.270 g. of "less liked" plants (Table 6, "B"). Of the "preferred" plants they took *Lamium maculatum* in the first place and of the "less liked" ones *Asarum europaeum* was consumed comparatively best. In both series great individual variations were found in the consuption of particular foods as well as in the diurnal consumption of all foods.

Considering the food requirements of bank voles and field mice in relation to the supplies of the forest floor (Fig. 3), it has been ascertained that both voles and mice eat, as a rule, nearly all plants occurring in the forest, though they show a distinct preference for some species of these plants.

3. Autumn

Autumn begins in the Wolski Wood in the middle of August and lasts until the second half of November. The herb layer of the *Querceto-Carpinetum* forest is very poor, but rodents find a large abundance of plant food, above all, in the form of tree seeds. The seeds of hornbeam, lime, maple, oak and sycamore maple begin to fall in August and fall all through the autumn till December, with the maximum intensity in September, October and November.

The supply of fresh seeds and herbs on the forest floor was estimated towards the end of the autumn (Nov. 5—10, 60). Though the year 1960 was not a "rich seed year" for oak nor for beech, an average of 21.100 g. of fresh seeds was collected from 1 sq.m. of the forest floor. This amount was composed mainly of the seeds of sycamore maple (8.720 g.) and then

of the nuts of hornbeam (4.080 g.), beech mast (3.840 g.), acorns (2.520 g.), seeds of maple (1.550 g.) and lime (0.400 g.). In the herb layer, plants were already scarce at that time and occurred irregularly. On the average only 125.560 g. of fresh biomass fell to 1 sq.m., the amount being 6 times

Table 7.

Food preference shown by 10 bank voles (*Clethrionomys glareolus*) examined, in relation to fresh seeds and herbs in autumn. "A" — at 18° C, "B" — at 14° C. Quantities of foods eaten were determined according to the 4-grade scale as in Table 3.

Food type	Vole No.	1	2	3	4	5	6	7	8	9	10	Per cent average
							A					
Fresh seeds	Carpinus betulus	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
	Quercus sessilis	+++	+++	+	+++	+++	++	++	++	+++	+++	70
	Fagus silvaticus	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
	Acer platanoides	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
Fresh herbs	Pulmonaria obscura	+++	+	++	++	+	+	+	+++	+++	+	50
	Milium effusum	++	0	+++	++	0	0	++	++	+++	++	40
	Mercurialis perennis	-	-	-	++	+++	-	+++	+++	+++	++	60
	Viola silvestris	+++	++	+++	+++	+++	+++	+++	+++	+++	++	80
	Lamium maculatum	+++	+	+	++	+	+	++	++	+	0	30
	Chaerophyllum sp	+++	++	+++	0	+	0	+++	+	++	+	40
	Mycelis muralis	++	+++	+++	+++	0	++	+++	+++	+++	+++	70
	Majanthemum bifolium	0	+++	++	++	+	0	++	++	++	+	40
	Oxalis acetosella	+++	+++	++	+	+++	+++	+++	++	++	++	70
							B					
Fresh seeds	Carpinus betulus	+++	+++	+++	+++	+++	+++		+++		+++	90
	Quercus sessilis	+++	+++	+++	+++	+++	+++		++		+++	60
	Fagus silvaticus	+++	+++	+++	+++	+++	+++		+++		+++	90
	Acer platanoides	+++	+++	+++	+++	+++	+++		+++		+++	90
Fresh herbs	Pulmonaria obscura	+++	++	+++	+	+++	+++		++		++	70
	Viola silvestris	+++	+++	++	+++	+++	+++		++		+++	30
	Lamium maculatum	+++	++	+++	++	++	++		+++		+++	70
	Oxalis acetosella	+++	+++	++	+++	+++	+++		+++		+++	80

smaller than that of the biomass of the herb layer at the peak of development, i.e. at the end of spring. Late in the autumn only 4 plant species were found, of which *Pulmonaria obscura* with 59.200 g. per 1 sq.m. was the most abundant and was followed by *Lamium maculatum* (32.000 g.), *Chaerophyllum sp.* (19.760 g.) and *Asarum europaeum* (14.600 g.). The average amount of plants and seeds per 1 sq.m. was 146.680 g., the richest out of the 10 squares examined having as much as 604.600 g.

In the laboratory the bank voles and yellow-necked field mice were examined for food preference in relation to the fresh seeds and herbs present in the forest at that time. The experiments were made in two series (Oct. 18—28, 60) on 10 voles and 10 mice (Table 7 and 8). As it was important to embrace the influence exerted by the temperature upon the

diurnal food consumption in autumn in the experiments, one series ("A") was conducted in the laboratory room at a temperature of 18° C and the other ("B") in the cellar at a temperature of 14° C. In both series the voles and mice were given diets of 4 kinds of fresh seeds (hornbeam, beech, oak and maple) and 4—5 fresh herbs.

Table 8.

Food preference shown by 10 yellow-necked field mice (*Apodemus flavicollis*) examined, in relation to fresh seeds and herbs in autumn. "A" — at 18° C, "B" — at 14° C. Quantities of foods eaten were determined according to the 4-grade scale as in Table 3.

Food type	Mouse No. 1	2	3	4	5	6	7	8	9	10	Per cent average
A											
Fresh seeds: Carpinus betulus	++	+++	++	++	+++	+++	+++	+++	+++	+++	80
Fresh seeds: Quercus sessilis	+++	+++	+++	+++	+++	+++	++	++	+++	+++	80
Fresh seeds: Fagus silvaticus	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
Fresh seeds: Acer platanoides	+++	++	+	+++	+++	+++	+++	+++	+++	+++	80
Fresh herbs: Pulmonaria obscura	++	+	0	+	+	+	++	+	0	0	20
Fresh herbs: Milium effusum	+	0	+	+	0	-	-	-	-	-	10
Fresh herbs: Mercurialis perennis	+	+	+	+	+	-	-	-	-	-	20
Fresh herbs: Viola silvestris	+	+	0	++	++	+++	++	+++	+	+++	70
Fresh herbs: Lamium maculatum	0	+	0	+	++	0	0	0	0	0	10
Fresh herbs: Chaerophyllum sp.	++	+	++	+	++	-	-	-	-	-	40
Fresh herbs: Mycelis muralis	+++	++	+++	+++	++	-	-	-	-	-	80
Fresh herbs: Majanthemum bifolium	+	+	++	+	+	-	-	-	-	-	20
Fresh herbs: Oxalis acetosella	+	+	0	+	0	0	0	++	0	+	10
B											
Fresh seeds: Carpinus betulus	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
Fresh seeds: Quercus sessilis	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
Fresh seeds: Fagus silvaticus	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
Fresh seeds: Acer platanoides	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	90
Fresh herbs: Pulmonaria obscura	0	0	0	++	++	0	0	+	0	++	20
Fresh herbs: Viola silvestris	++	0	0	+	++	++	+++	++	0	+++	40
Fresh herbs: Lamium maculatum	0	0	0	0	+	0	++	+	0	0	10
Fresh herbs: Oxalis acetosella	+	0	0	+	++	+	+++	++	0	++	30

In the laboratory room (Table 7, "A") the voles ate on the average 90% of the seeds of hornbeam, beech and maple and 70% of the acorns. Of herbs they rather readily ate *Mercurialis perennis* and *Viola silvestris* (80% of either), then *Oxalis acetosella* and *Mycelis muralis* (70%), *Pulmonaria obscura* (50%). *Milium effusum, Chaerophyllum sp.* and *Majanthemum bifolium* (40%). The experiments carried out in the cellar (Table 7, "B") showed that voles ate a little more seeds and fresh herbs at a lower temperature. Individual variations in the consumption of seeds and fresh herbs were relatively small both in the laboratory room and in the cellar.

The field mice in the laboratory room used fresh seeds most readily (Table 8, "A"), beech mast being consumed on an average in 90% and the seeds of hornbeam, oak and maple in 80%. Of plants they took *Mycelis muralis* and *Viola silvestris* best.

In the cellar (Table 8, "B") all the seeds offered were eaten in 90%. Of the 4 herb species the mice ate *Viola silvestris* most readily. Comparing the results obtained in the laboratory room with those from the cellar, it will be seen that the diurnal consumption of seeds at the lower temperature was only slightly larger. Instead in the cellar the mice ate somewhat less fresh herbs.

IV. DISCUSSION OF RESULTS

The diet of bank voles and field mice was studied frequently, by various methods and from various points of view. Foresters (Capecki & Gabryel, in manuscript) thoroughly tabulated damages caused by different rodents in the Central European forests. Many ecologists analysed the contents of the stomachs of bank voles and field mice (Naumov, 1948; Sablina, 1953; Miller, 1954). Field studies included the determination of the amounts of various foods eaten up from special feeding-tables (Naumov, 1948), while in laboratories voles and mice were examined for food choice in relation to the seeds of trees and shrubs (Miller, 1954; Turček, 1956; Sviridenko, 1961).

The results of the foregoing works and those of our study agree as to the polyphagousness and food requirements plasticity of the bank vole and, to a lower degree, field mouse. Qualitatively, the diets of both these animals change very essentially during the annual cycle (Naumov, 1948; Dinesman, 1931). In the spring and early in the summer bank voles feed mainly on green plant matter and seeds, whereas field mice are fond, first of all, of seeds and next of insects and green plant matter. In the high summer seeds and insects predominate in the stomachs of mice, berries and greens being only complementary. At that time the diet of voles consists mainly of green plant matter and some amount of seeds. In the autumn the feeding habits of both animals become similar with tree seeds prevailing (Naumov, 1948; Dinesman, 1961).

The field mouse thus eats nutritious foods chiefly, and the vole both nutritious and voluminous ones. This could be distinctly seen also from our experiments, for the bank vole fed on green plant matter more readily (7.620 g. per day of "preferred" plants and 4.517 g. of "less liked" plants) than the field mouse did (5.096 g. and 2.270 g. respectively). The voles also browsed considerably more fresh twigs (2.969 g. per day) than the field mice (0.664 g.). However, both rodents consumed seeds intensively

(on an average 3.789 g. and 2.935 g. per day respectively). These variations in food preference between voles and mice are connected with the somewhat varying structures of the alimentary canal in these animals. The size of the small intestine, in which most fats and proteins are absorbed, and that of the caecum, where cellulose is digested with the help of bacteria, are here particularly important. Table 9 shows clearly that the bank vole's alimentary canal is more "all-round" having the well-developed small intestine as well as caecum. The alimentary canal of the field mouse is more specialized and is characterized by the well-developed intestine but reduced caecum.

Table 9.

Lenghts of intestines in the alimentary canals of the rodents examined.

Species	Number of alimentary canales measured	Average lenght of body, in mm.	Total lenght of intestines, in mm. M	Total lenght of intestines, in mm. σ	Lenght of small intestine, in mm M	Lenght of small intestine, in mm σ	Lenght of caecum in mm. M	Lenght of caecum in mm. σ
Clethrionomys glareolus	20	93.1	592.0 ±	160	363.7 ±	124	97.0 ±	29
Apodemus flavicollis /adult/	16	96.9	475.3 ±	70	309.3 ±	55	49.6 ±	11
Apodemus flavicollis /young/	12	82.8	411.2 ±	71	278.7 ±	53	44.1 ±	11

The foods of the bank vole and yellow-necked field mouse vary rather considerably also with the type of the forest (Sablina, 1954; Novikov, 1959; Dinesman, 1961). In the *Querceto-Carpinetum* forest bank voles and field mice readily eat seeds, fruits and berries of all the tree and shrub species making up this community (Capecki & Gabryel, in manuscript; Novikov, 1959; Sviridenko, 1961; Dinesman, 1961). Voles and mice crop also bark, sprouts and buds of main trees of this community (Capecki & Gabryel, in manuscript; Dinesman, 1961). The present experiments have showed that both these species of rodents eat nearly all herbs occurring in the herb layer of the forest of this type. The diet composed of herbs only is, however, insufficient for the field mouse and also, to a lower degree, for the bank vole. Therefore, the bank vole and field mouse can use all the get-at-able foods that are produced by the deciduous forest at various seasons of the year.

In order to answer the question put at the beginning of this paper, whether the food supplies can limit the number of small mammals in the forest directly, it is necessary to compare the food requirements of the small mammal community with the food supplies provided by the forest.

The food balance of this type has been already worked out for the American forest mammals (Hamilton, 1941; Pearson, 1948) and it has been recently calculated for the *Querceto-Carpinetum* forest by Grodziński (1961).

The bioenergetic balance was calculated for small mammals in the Wolski Wood in the prevernal period of 1960, for this season is critical so far as food is concerned. The diurnal energy dissipation can be determined very accurately for the rodents examined from the measurements of gaseous metabolism, or less accurately from the diurnal food consumption. Oxygen consumption in a vole with a mean body weight (21.400 g.) averaged 5.3704 cu.cm. of O_2/g. × hour at 20°C. Similarly oxygen consumption in a field mouse with a mean body weight (29.262 g.) amounts to 4.3880 cu.cm. of O_2/g. × hour.

Table 10.

Eatable matter content and caloric value of tree seeds. Caloric values determined in Berthelot's bomb calorimeter.

Tree seeds	Eatable parts, in %	Uneatable parts, in %	kg.cal./g of eatable parts
Carpinus betulus	15.54	84.46	6.213
Quercus sessilis	85.76	14.24	5.595
Fagus silvatica	62.78	37.22	6.487
Acer platanoides	55.48	44.52	2.093

Table 11.

Results of catches of small mammals carried out by the trap/day method in the Wolski Wood in the winters of 1960 and 1961.

Species	No. of specimens caught	Per cent share of catch	Per cent
C. glareolus	19	1.064	38.76
A. flavicollis	9	0.504	18.37
S. araneus	11	0.616	22.45
S. minutus	6	0.336	12.24
A. agrarius	4	0.224	8.16
Total	49	2.744	100.00

At the respiratory quotient, RQ, equal to 0.8 (Pearson, 1947) the caloric value of 1 l. of O_2 corresponds to 4.8 kg.cal. Thus the oxygen consumption in bank voles and field mice corresponds to 0.0281 and 0.0241 kg.cal./g. × hour respectively. Hence at the end of winter the diurnal energy consumption amounts to about 13.24 kg.cal. for the adult bank vole and 14.79 kg.cal. for the field mouse.

The diurnal requirement of energy calculated from the food consumption was 14.76 kg.cal. in the bank vole and 15.59 kg.cal. in the field mouse. This value was obtained by multiplying the diurnal seed consumption in the winter series of experiments (Tables 1 and 2) by the caloric values of these seeds determined by their combustion in Berthelot's bomb calorimeter (Table 10). The number of calories

thus computed was already decreased by 5%, allowing for the assimilation coefficients (B y k o v et al., 1957).

The diurnal metabolism calculated from the food consumption is therefore slightly higher (by 1.52 and 0.8 kg.cal.) than that obtained from the oxygen consumption. It is due, among other things, to the fact that during the feeding experiments the animals stayed in the somewhat lower temperature (18°C) than the temperature at which the metabolism measurements were made (20°C).

Similar figures were obtained from feeding experiments by T u r č e k (1956) and G r o d z i ń s k i (1962). At the diet composed of beech mast the field mouse ate 17.68 kg.cal. per day and at the acorn diet 14.26 kg.cal. Hence the average diurnal consumption was 15.96 kg.cal. (T u r č e k, 1956). On the other hand, at the standard diet including an apple and oats the bank vole takes 13.08 kg.cal. in its food (G r o d z i ń s k i, 1962).

The evaluation of the size of small mammals population of a forest is methodically very difficult. G r o d z i ń s k i (1961) estimated it at about 40 animals per hectare in the *Querceto-Carpinetum* forest at the end of the winter and beginning of the spring.

Table 11 presents the results of the catches done by the trap/day method in the Wolski Wood in the winters of 1959/60 and 1960/61. The bank vole and next the shrew and field mouse predominated over other small mammals of the forest floor. Our catches rather resembled those done by K o w a l s k i (1950) in the same wood in 1946—1948. The only large difference concerned the share of shrews, which made hardly 7.8% of the mammals caught, according to K o w a l s k i, against 34.24% in our catches .The latter figure was made up by *Sorex araneus* L. (22.45%) and *Sorex minutus* L. (12.24%), which in 1946—1948 was not found at all.

The diurnal energy dissipation calculated for all the bank voles inhabiting 1 hectare of the forest is about 251.6 kg.cal. day × hectare (17 voles × 14.8 kg.cal.) and for the field mice about 146.4 kg.cal (8 mice × 18.3 kg.cal.). These calculations allow for low temperature, mobility, group effects and other factors affecting the metabolism. The energy dissipation for the whole community of small mammals in the deciduous community of the Wolski Wood in the prevernal period approximated to 625 kg.cal./hectare × day (G r o d z i ń s k i, 1961). The critical food period lasts in the Wolski Wood for 2—3 weeks, when the winter passes into the prevernal period. To survive this period the community of small mammals with a density of 40 individuals per hectare needs about 12,500 kg.cal./hectare in the form of food.

At the end of the winter the value of diverse foods, such as plants (D ą b r o w s k i, 1953), seeds and insects (N o v i k o v, 1959), on the floor of the *Querceto-Carpinetum* forest exceeds 30,000 kg.cal./hectare (G r o-

dziński, 1961). At the same season of 1960 there was as much as 55.640 kg/hectare of seeds of broadleafed trees only, in the Wolski Wood. This figure multiplied by the coefficients of eatability and caloric value (Table 10) gives 75,750 kg.cal./hectare of very nutritious food, of which all forest rodents and most shrews are fond (Novikov, 1959; Sviridenko, 1961).

If in the prevernal period small mammals fed on seeds only, they would find 6 times as large amount of them as they could consume during the critical 3-week period (they will use hardly 16.5% of the seed supply). The consumption of seeds by other larger mammals and birds [e.g. *Sciurus vulgaris* L., *Oryctolagus cuniculus* (L.) and *Garrulus glandarius* L.] is very small in view of the small number of these animals living in the Wolski Wood.

The balance offered above proves evidently that food cannot be the factor limiting the size of the population of small forest mammals directly (i.e. by starvation) in the spring. Even if the error of the balance resulting from inaccuracy were very great, e.g. up to $\pm 50\%$, the food resources of the forest would exceed the requirements of small mammals by many times. On the other hand, the abundance of food can affect the size of the forest rodent population only indirectly, e.g. increasing their fertility (Naumov, 1948; Adamczewska, 1961), or diurnal activity and mobility (Grodziński, 1962).

V. SUMMARY

Food supplies of a climax *Querceto-Carpinetum* wood available for small rodents were studied in the different phenological seasons of 1960—1961. Food preference and diurnal food consumption in *Clethrionomys glareolus* (Schreber 1780) and *Apodemus flavicollis* (Melchior 1834) were investigated in the laboratory.

1. In the winter, bank voles and field mice feed mainly on tree seeds, which are still present in an amount of 5.564 g./sq m. at the end of this season. Bank voles eat on the average 2.935 g. of seeds per day and field mice 3.789 g. Both rodents choose beech mast and acorns most readily.

2. The prevernal season is a critical time for rodents so far as food is concerned; later on, in the spring and summer the *Querceto-Carpinetum* forest secures them a large abundance of green foods and insects. The biomass of the herb layer reaches 716.43 g./sq.m. at the peak of development. In principle, both rodents may eat all the herbs of the herb layer and crop tree twigs. Bank voles consumed 2.969 g. of twigs per day and field mice hardly 0.664 g. Towards the end of the spring bank voles used 7.620 g. of fresh herbs per day and field mice 5.096 g., a strong liking for some herbs being noticeable.

The diet composed of herbs or twigs only is apparently insufficient for the field mouse and, to a lower degree, for the bank vole.

3. In the autumn there is a large quantity of fresh seeds (21.100 g./sq.m.) on the floor of the *Querceto-Carpinetum* forest, whereas the herb layer is impoverished considerably (125.560 g. of biomass per 1 sq.m.). Bank voles and field mice relish

fresh seeds of the main trees. Of the herbs the vole and field mouse show preference for *Mercurialis perennis, Viola silvestris* and, in the case of the bank vole, also for *Oxalis acetosella* and *Mycelis muralis*. A drop in temperature by several degrees causes an increase in the consumption of high-caloric seeds.

4. The bank vole and field mouse are polyphagous animals and they change their diet during the annual cycle and in varying biotopes. The field mouse mainly eats foods of high nutritive value, the bank vole both of high nutritive value and of large volume. This fact is determined by the structure of their alimentary canals, that of the bank vole being more "all-round".

5. The food balance for the small mammal community in the *Querceto-Carpinetum* forest shows that food conditions cannot limit the number of these animals directly. The period of 2—3 weeks at the passage from the winter to the prevernal season is the most critical spell as regards food. The bioenergetic balance of this period is as follows:

(A) The diurnal consumption of energy by the bank vole amounts in the field to 14.8 kg.cal., by the field mouse to 18.3 kg.cal., and by the whole community of small mammals with a density of 40 individuals per hectare to 625 kg. cal. Thus, to survive 20 days small mammals need 12,500 kg.cal.

(B) At that time the quantity of tree seeds only on the floor of the forest corresponds to 75,750 kg.cal. Therefore, if the small mammals fed merely on seeds, they would use hardly 16.5% of the supply.

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STRESZCZENIE

W latach 1960—1961 zbadano zasobność pokarmową klimaksowego lasu *Querceto-Carpinetum*, w pokarmy dostępne dla drobnych gryzoni w różnych fenologicznie porach roku. W laboratorium zbadano wybiórczość pokarmową i dobowe zużycie pokarmu przez *Clethrionomys glareolus* (Schreber 1780) i *Apodemus flavicollis* (Melchior 1834).

1. W zimie nornice rude i myszy leśne odżywiają się głównie nasionami drzew, których z końcem zimy w lesie jest jeszcze 5,564 g/m². Nornice rude mogą zjadać średnio 2,935 g nasion na dobę, a myszy leśne 3,789 g; oba gryzonie najchętniej wybierają bukiew i żołędzie.

2. Przedwiośnie pod względem pokarmu jest okresem krytycznym dla gryzoni, potem w czasie wiosny i lata las *Querceto-Carpinetum* zapewnia im dużą obfitość pokarmów zielonych i owadów. Biomasa runa w pełni jego rozwoju osiąga 716,43 g/m². Oba gryzonie mogą w zasadzie zjadać wszystkie rośliny zielone z runa, oraz ogryzać gałązki drzew. Nornice rude zjadały w ciągu doby 2,969 g gałązek, a myszy leśne zaledwie 0,664 g. Z końcem wiosny nornice rude zużywały 7,620 g świeżych roślin a myszy leśne 5,096 g, przy czym zaznaczała się wyraźna wybiórczość pokarmowa w stosunku do różnych roślin.

Dieta złożona z samych roślin lub gałązek jest wyraźnie niewystarczająca dla myszy leśnej, a w mniejszym stopniu i dla nornicy.

3. Jesienią na dnie lasu *Querceto-Carpinetum* jest dużo świeżych nasion (21,100 g na m^2) natomiast runo znacznie ubożeje (125,560 g biomasy/m^2). Nornice i myszy zjadają chętnie w tym czasie świeże nasiona głównych drzew. Z roślin nornica ruda i mysz leśna najchętniej zjadają *Mercurialis perennis, Viola silvestris*, a nornica ruda także *Oxalis acetosella i Mycelis muralis*. Obniżanie temperatury o kilka stopni powoduje zwiększoną konsumpcję wysokokalorycznych nasion.

4. Nornica ruda i mysz leśna są zwierzętami polifagicznymi, zmieniającymi pokarm w cyklu rocznym i w różnych biotopach. Mysz leśna zjada jednak głównie pokarmy treściwe, podczas gdy nornica zarówno treściwe jak i objętościwe. Jest to zdeterminowane budową ich przewodu pokarmowego, który u nornicy rudej jest bardziej "wszechstronny".

5. Z bilansu pokarmowego dla zespołu drobnych ssaków w lesie *Querceto-Carpinetum* wynika, że pokarm nie może w prosty sposób ograniczać liczebności tych zwierząt. Najkrytyczniejszym pokarmowo okresem jest 2—3 tygodni na przełomie zimy i przedwiośnia. Bilans bioenergetyczny dla tego okresu zamyka się w następujących cyfrach:

(A). Dobowe zużycie energii przez nornicę rudą w terenie wynosi 14,8 Kcal, przez mysz leśną 18,3 Kcal, przez cały zespół drobnych ssaków przy zagęszczeniu 40 osobników na ha — 625 Kcal. Na przetrwanie 20 dni trzeba więc drobnym ssakom 12.500 Kcal.

(B). Samych tylko nasion drzew znajduje się w tym czasie na dnie lasu aż 75.750 Kcal, zatem gdyby drobne ssaki żywiły się tylko nasionami, to zdołają je wyeksploatować zaledwie w 16,5%.

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