Zofia GĘBCZYŃSKA

Bioenergetics of a Root Vole Population*

[With 11 Tables & 5 Figs.]

Studies made over a period of three years were used as a basis for assessing the bioenergetic indices and food relations of *Microtus oeconomus* (P a l l a s, 1776). In addition an estimate was made of the energy flow through a root vole population in the light of the net production of the peat-bog in which this population lived. The daily energy budget in summer is 0.581 kcal/g, and in winter correspondingly 0.510. Thus in the study population one root vole consumes an average of 14.06 kcal on a summer day, and 11.37 in winter. The value of the digestibility coefficient of food in spring and summer is aprroximately 69%, and in autumn 73.9%. Value of food assimilation differs from this coefficient by 1.5 to 2.5%. In summer, therefore, food consumption is 20.92 kcal/day which is equal to about 4.9 g of dry plant mass. In winter this value is 15.92 kcal/day, that is 3.8 g of dry mass. On account of the high population numbers the value of energy flow over the course of the year is considerable, and is about 375,000 kcal/hectare. Nevertheless this constitutes only a negligible part (about 3.1%) of net production assessed as 11,929,864.7 kcal/ha/year. The great majority of plant biomass is formed by species preferred and consumed by *M. oeconomus*. Thus the abundance of the food supply for this vole greatly exceeds its requirements over the whole year. Despite the fact that species does not cause visible damage in an association of annual plants, it is a serious pest of young trees, although gnawed bark forms only a supplement to its basic diet.

1. INTRODUCTION

The root vole, *Microtus oeconomus* (P a l l a s, 1776), is a species less numerous in Poland than other rodents, since the southern limit of its range passes through Poland (K o w a l s k i, 1964). It has, however, a very wide geopraphical range, and inhabits vast areas of the northern part of the Euro-Asiatic continent (F e t i s o v, 1958), where it plays an important role as a pest of field and forest cultures and of meadows (S n i g i r e v s k a y a, 1961; T a s t, 1964; 1966; 1968).

This vole is a typical herbivore, and the green parts of plants form its basic diet. It eats seeds, roots of herbs and grasses and also the bark of trees only in late autumn or winter. Even at these times of the year, however, green parts of plants constitute the basic component of the food of this species (B a r a b a s h - N i k i f o r o v, 1946; K a r a s e v a, N a r-s k a y a & B e r n s t e i n, 1957; L a v r o v a, P r o k h o r o v a & L i s t, 1960; S n i g i r e v s k a y a, 1961; T a s t, 1966).

In investigations of the energy flow through a herbivores population it is most convenient to refer the amount of energy intake by this population to the energy contained in the plant production which forms the food supply of this species. For this purpose it is necessary not only to determine the metabolism rate and bioenergetics of the herbivore, but also its food relations and population numbers. It is also essential to assess the primary production of the plant association forming the food supply.

Data on the metabolism rate of *M. oeconomus* are scanty, and limited to the results obtained during the arctic summer period in Alaska (G r o-d z i ń s k i, 1966) and the approximate values given by B a s h e n i n a (1967; 1968). It was therefore necessary to estimate the energy requirements of this species and at different times of the year. The average daily metabolism rate (*ADMR*) and experiments on intensivity of heat · production for maintenance of body temperature and social temperature regulation formed the basis for calculating the daily energy budget (*DEB*) of the root vole.

Measurements of the amount of plant mass permitted of simplifying assessment of net primary production. It was thus possible to estimate

the amount of food available for the rodents, that is, food easy to find, and also preferred and consumed.

It can be assumed that in a study area covered by grass vegetation almost all species of plants were easy to find, although, as shown by the cafeteria test, not all of them were equally readily chosen and consumed by the root voles. In order to determine the degree to which food is utilized by this species assessment was made in further experiments of its digestibility coefficient and assimilation level.

Observations and experiments were carried out on a population of root voles living in an area which was to a certain extent naturally isolated. Studies were simultaneously made there on the numbers and succession of small mammals (B u c h a l c z y k, 1967; B u c h a l c z y k & P u c e k, 1968), which gave an accurate picture of this »island« population. This made it possible to calculate the energy balance of the whole root vole population.

The aim of the present study was therefore not only to ascertain the energy requirements of the root vole but also its food relations. After assessing the food supply and knowing the numbers of the study population it became possible not only to determine the bioenergetics of the population but also to evaluate the role which this population plays in the study area.

2. STUDY AREA

The investigations were carried out in a drained peat-bog situated in the interior of a tree stand. It lies at an altitude of 120 m a.s.1 in the Augustów Forest ($\varphi = 53°22'$ N; $\lambda = 23°22'$ E). This area is surrounded on all sides by woods — on the north and east by pine woods, on the south and west by a narrow belt of grassland beyond which there is also a pine wood (Fig. 1). The whole area of the peat-bog is about 34 ha, and it is situated in a local depression collecting the excess rainwater from the forests which surround it.

In 1961 an expert grassland survey was made which showed, on the basis of the species of plants occurring there, that this area belongs to typical marshland. This was also confirmed by drilling and soil exposures [1]. The great majority are soils of organic origin belonging to the hydromorphic soil group. The soils occurring there are mainly peat soils, peat mud and humus. There are also small amounts of peat soils of mineral origin. Depth of the peat varies from 0.3 to 1.6 m.

The area was drained in 1962 and intersected by dikes. Before this was done the place was extremely boggy on account of the silting up of the main drain. After draining, ploughing and cultivating the glade grass was sown along the paths and roads which were constructed. The habitat still forms, however, a peat-bog

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[1] Data on the species composition of the vegetation in this locality in 1961, and also on the origin and composition of the soils, were taken from the expert survey made by the Department of Meadow and Pasture Cultivation of the Higher School of Agriculture in Olsztyn, commissioned by the District State Forest Board in Bialystok.

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association with the addition of grass sown there and certain species of plants accidentally carried there.

Since 1963 the central part of the glade, measuring 15.75 ha in area, has been used for experimental cultures of different species of trees: birch, alder, ash, maple, poplar, oak and osier and also pine and spruce. These cultures are planted in
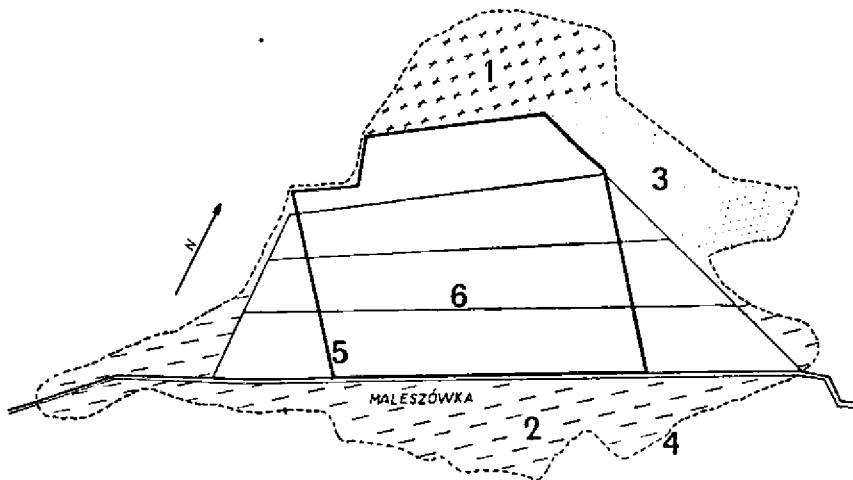

Fig. 1. Map of the study area.
The extend of the study area is shown by the thick line. 1 — cultivated fields. 2 — meadows, 3 — forest cultures, 4 — limit of forest, 5 — border of experimental area, 6 — drainage ditches.

Fig. 2. General view of the study area in early spring.
Young pine and spruce trees among grass — *Agrostis vulgaris.*

single-species or mixed belts, in various combinations of species and numbers (Fig. 2). Whenever any of the species is killed by frost it is immediately replaced by a different species, e. g. poplar in the east part of the area was replaced by spruce trees several years old. The belts vary in width from 8 to 20 m. The various parts of the cultures are separated from each other by roads. The whole experimental area is thus covered by herb vegetation and the sown grasses and sedges, and is weeded only in the immediate vicinity of the young trees.

3. MATERIAL

The study area was inhabited almost exclusively by root voles. Only small numbers of other small mammals — mainly Soricidae — were caught (B u c h a l c z y k & P u c e k, 1968).

Table 1.

Number of root voles used in experiments in different season.

. Eksperiments	Spring	Summer	Autumn	Winter	Total
Measurements of oxygen consumption:					
ADMR	20	20	16	19	75
RMR	36	35	36	41	148
Measurements of food consumption:					
Cafeteria test	23	17	21	—	61
Digestibility and assimilation of food	20	18	28	—	66
Total	99	90	101	60	350

A total number of 350 root voles, caught from 1966—1968 at different seasons of the year, were used for laboratory investigations (Table 1).

4. METHODS

4.1. Investigation of Amount of Plant Biomass

The harvest method was used for investigations of the state of plant biomass forming the potential food of the root vole. It consists in direct measurements of plant biomass on exactly defined areas at established periods of the year (T r a c z y k, 1968). The investigations were made in four seasons: in spring, high summer, autumn and at the end of winter, immediately after the snow had partly disappeared, but before the soil had thawed out. This was the only possible way of making measurements characterising the winter period. In the depth of winter the thick snow cover made it impossible to take samples of plants. The time chosen was also convenient on account of the fact that it is a period in which the amount of green parts of plants is smallest and the root vole's food supply is consequently smallest.

Thirty samples were taken in each of these seasons within the study habitat. Each of the samples, from a circular area equal to 1000 cm², was chosen at random. Within these circular areas the whole plant mass was cut with scissors as close as possible to the soil and the cut parts of plants and also dead material carefully collected. Material from the samples was separated into two categories: green biomass, .and dead parts. The samples segregated in this way were placed in paper bags and dried in a drier at a temperature of 85°C to an air-dry state, which took from 48 to 72 hours. They were next weighed with accuracy to 0.1 g.

The parts below groud were not examined on account of the difficulty as to methods. This was not of any real significance, however, in determining the abundance of the root vole's food supply, as only the root of the dandelion (*Taraxacum officinale*) is of any importance during the winter as an addition to the green parts of plants which form the basic food during this period. On this account a quantitative estimate of dandelion roots was made in winter.

Calculation was next made from all samples of the average value per 1000 cm² and the results converted to the value per hectare.

Additional calculation was made for spring and the end of winter of the percentages of the various species forming the given association.

4.2. Measurements of Oxygen Consumption

The oxygen consumption rate constituted the measure of metabolism in these experiments. Measurements of this value were made in the four main seasons of the year (Table 1). The captured root voles were taken to the laboratory at Białowieża (about 230 km away). Previous to each experiment the animals were acclimatized to laboratory conditions for 2 to 4 days. The temperature in the laboratory rooms was fairly constant over the year and varied from 16 to 20°C. Light conditions were similar to those of the natural rhythm, that is, in autumn and spring the length of day was about 11—12 hours, winter 8—9 hours, and summer 16—17 hours. Both during the animals' acclimatization period in the laboratory and during the 24-hour experiments the root voles were fed on a mixture of moistened oat grains and red beet supplied *ad libitum*.

In all seasons measurements were made both of the average daily metabolism rate (*ADMR*) and resting metabolism rate (*RMR*). The first of these values was obtained from 24-hour measurements of oxygen consumption in large 14.4 l metal chambers in a respiration apparatus of the Kalabukhov-Skvortzov type (K a l a-b u k h o v, 1951; S k v o r t z o v, 1957). The respiration chambers had a nesting compartment and a run, separated by a partition with two holes in its lower part. Material for the nest (cottonwool), an exercise drum and feeding box were all accessible (G ę b c z y ń s k i, 1963). The root voles, however, only sporadically made use of the exercise drum, and even then their attempts were very shortlived. The 24-hour experiments were made at a constant temperature of 20°C, which is recommended as the standard temperature for measurements of *ADMR* of rodents (G r o d z i ń s k i, 1965) [2].

Resting metabolism rate was also measured in a Kalabukhov-Skvortzov type respirometer in small glass chambers, in which the animals were placed in wirenetting cages measuring $4 \times 4 \times 8$ cm, which greatly restricted their activity. During these experiments, which lasted one hour, the root voles were kept with-

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[2] G r o d z i ń s k i W., 1965: Program of bioenergetic studies concerning the productivity of small rodents. Unpubl.

out food. In all seasons RMR was measured at different temperatures for 148 individuals (Table 1). The voles were weighed before and after each respiration experiment, and the mean weight obtained from these measurements used for calculations.

4.3. Evaluation of Food Preferences

Food preferences were evaluated by means of the »cafeteria test«. The root voles were placed singly in metal cages measuring $45 \times 25 \times 15$ cm, without litter, which made it possible to clear away all the uneaten parts of plants. Cottonwool was provided for the nest.

The experimental voles were fed daily on mixtures consisting of 5—7 species of herb plants, grasses and branches of young trees, in different combinations. The degree of consumption was next determined, using a 4-degree scale for this purpose, in which 0 — indicated that a certain plant was not eaten; 1 — consumption up to about 20% of the whole (not readily eaten); 2 — 20—50% (readily eaten) and 3 — 50—90% (very readily eaten) (G ó r e c k i & G ę b c z y ń s k a, 1962). The higher values in the ranges of the degrees were taken for calculation. The averages obtained were rounded up to whole tens in order to avoid suggesting excessive quantitative accuracy of the results of this method, the aim of which is mainly a qualitative evaluation of the tested foods. Each set of plant food was fed to the animals for a period of 4—6 days. The plants used for the experiments were collected from the area in which the study population of M. oeconomus lived. The animals were not given water in these experiments on account of the high natural moisture content of the food given them, which fully satisfied their water requirements.

In this way a list was obtained of herbs, grasses and young trees eaten by the root vole in three seasons: spring (May), summer (July) and autumn (October), (Table 1). A total of 94 experiments were made, 42 in spring, 34 in summer and 18 in autumn, on 61 animals.

4.4. Investigation of Digestibility and Assimilation of Food

The investigations were made using the balance method, which consists in supplying the animals daily with a known amount of food and collecting the whole of their faeces and urine (D r o ż d ż, 1966; 1968a). The experiments were carried out in three seasons on 66 adult voles of both sexes (Table 1). On account of the large volume of the food used it was put into the cage twice daily — morning and evening. The food put into the cages consisted of those species of plants which occurred in the area inhabited by the root vole and which they readily ate in the preference tests made.

The animals were caught immediately before the start of the experiments, and were then placed for 4—6 days in metal cages without litter. They were fed on the same food during this period as they recived later during the proper experiment. During this time the animals accustomed themselves to their new feeding conditions, and the whole of their alimentary tract became completely filled with the test food. This assumption was based on the finding that in related herbivorous rodents the average period for which contents remained in the alimentary tract was not more than 17.5 hours (K o s t e l e c k a - M y r c h a & M y r c h a, 1964).

The actual experimental period lasted 7 days. The animals were then placed singly in metabolic cages (D r o ż d ż, 1968b).

The voles were weighed before the preliminary period and before and after the experiments, which were carried out at a temperature of $18° \pm 2°C$ and with a natural light rhythm.

Faeces and urine was collected daily at a uniform time and dried in a drier for 3 days. The caloric value of food and of urine and faeces were determined in a Berthelot system calorimeter (G ó r e c k i, 1965).

5. RESULTS

5.1. Total Amount of Plant Biomass

The total amount of plant biomass is subject to certain fluctuations over the course of the years (Table 2). Maximum values occurred in the spring of 1968 and winter of 1969. In the summer of 1966 and 1967 a reduction of about 19 % was found in the amount of biomass per hectare, its values being very similar in the two consecutive years. The greatest differences in amount of plant mass occurred between two successive winters — 1968 and 1969, when they are as much as 55 % (Table 2).

Table 2.

Amount of air dry green biomass and dead parts of plants at different seasons.

Season, month, year	Green parts			Dead parts		Total
	kg/ha	%	kcal/ha	kg/ha	%	kg/ha
Spring, May 1968	2,940 0	81.9	12,658,758.0	647.0	18.1	3,587.0
Summer, July 1966	1,867.3	61.1	7,870,669.0	1,040.2	38.9	2,907.5
Summer, July 1967	1,996.1	70.1	8,413,561.5	850.7	29.9	2,846.8
Autumn, October 1966	577.4	22.2	2,404,011.6	2,030.5	77.8	2,607.9
Winter, March-April 1968	106.0	4.3	455,651.0	2,388.0	95.7	2,494.0
Winter, March-April 1969	169.1	4.3	726,893.0	3,720.0	95.7	3,889.1

In comparison with variations in total amount of biomass the seasonal variations in green mass are far greater. While in spring the green parts form over ⁴/₅ of the whole, by summer this is only ²/₃. In autumn when the mass of vegetation dies, living parts form only ¹/₅ of the entire plant mass. The amount of green plants determined immediately after snow disappears forms only 4.3 % of the whole plant mass (Table 2). At the end of winter in 1968, when the total amount of biomass was far smaller than in 1969, the relative percentage of green plants was exactly the same as in the winter of 1969 (Fig. 3). The mass of green plants is always greatest in spring, but undergoes considerable, but also gradual, decrease in successive seasons of the year. It is always smallest during the final part of the winter, regardless of the year in which measurements were made (Table 2).

The participation of dead plants in the total amount of plant biomass is relatively great in all seasons, and both its percentage and absolute amount increases from spring to winter. In the spring of 1968 there was 647 kg of dead mass per hectare, while at the end of winter of the following year this amount had increased by almost six times as much. For purposes of comparison it may be added that the amount of green parts during this period decreased by more than 17 times (Fig. 3). The percentage of dead parts in the whole of plant biomass thus changes to an even greater degree. When in spring they form about 18% of the whole, by the end of winter they increase in amount to almost 96% (Table 2).
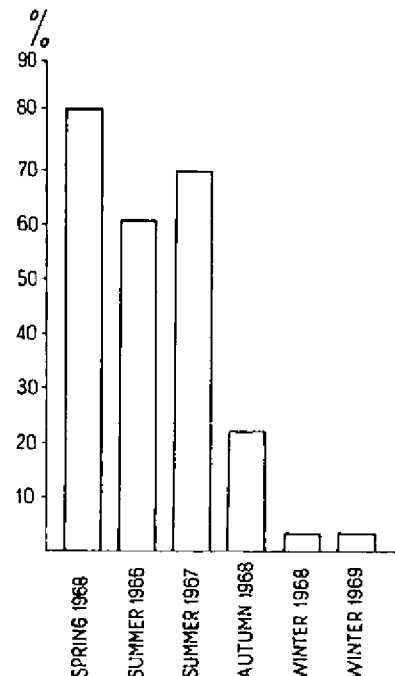
Fig. 3. Relative percentage of green mass in the total amount of biomass depending on season and year.

The caloric values of 1 g of dry green plant mass varies slightly over the growing season and are as follows: in May — 4.307 kcal, in July — 4.215 kcal, in October — 4.162 kcal and at the end of March and beginning of April — 4.299 kcal. These data were used to estimate the caloric values of green plant mass in these months. It is thus obvious that the slight variations in the caloric value of plant mass cause the energy reserves of food mass to be directly correlated with its amount. Thus also the energy value of potentially available food is highest in spring, since during this period it is over 12.65 mln kcal/ha and is lowest in winter, being in 1968 only 0.45 mln kcal/ha, and in 1969 slightly more, 0.73 mln kcal/ha (Table 2). The other periods of the year are characterized by intermediate caloric value of the food available for root voles.

5.2. Participation of Plant Species in Formation of Green Mass
in Spring and Winter

Additional assessment was made of the percentage of different species of plants for the height of spring and the end part of the winter, that is, seasons in which the green plant mass reaches extreme values. This made it possible to trace which species dominate quantitatively in creating biomass and whether this phenomenon depends on the season. In turn this permitted of assessing the number of species more or less readily eaten by the voles.

The above measurements were made in the spring of 1968 and the end of winter 1969 (Table 3). In spring the plant association of the peat-bog examined consisted of 25 species of plants, of which only 9 are represented in the winter aspect of this habitat. In winter, however, 7 further plants were added (Table 3), so that during this period the plant association of the peat-bog consisted of 16 species in all.

In spring the participation of 4 species of plants — *Agrestis vulgaris, Stellaria palustris, Dactylis glomerata* and *Senecio vernalis* — is greater than 5% and gives a combined figure over 73%. If a fifth species — *Stellaria uliginosa* — is added to this, although forming less than 5%, then taken together these species form almost ⁴/₅ of the biomass. The remaining 20 species form percentages varying between 3.75 and 0.04%. It must however be emphasised that *Agrostis vulgaris* occurs very numerously (37.1%) in the spring aspect of this association and thus differs considerably from the other species (Table 3). This species of grass forms an almost identical percentage (36.2%) in winter and during this period also differs considerably from the species next in order to it in numbers — *Taraxacum officinale*, although its amount expressed in kg/ha decreased by exactly 18 times in comparison with the spring period.

In winter only one other species of grass — *Dactylis glomerata* — forms a similar percentage to that in spring (Table 3). The remaining species dominating in spring — *Stellaria palustris* and *Senecio vernalis* — do not occur at all in winter, and *Stellaria uliginosa* occurs to a lesser extent than in spring. The second winter species in order of numbers is *Taraxacum officinale*. In summer it forms a negligible percentage, but as it withstands winter well and its numbers decrease by only twice as much, it forms the second species in order of numbers during this period. As mentioned above, this is the only species, the roots of which play certain part in the food of the root vole during this period. The amount of roots, or strictly speaking the parts below ground, expressed in kg of dry mass, is larger than that of the parts above ground (leaves and upper part of root — Table 3). A root usually attaining over 15 cm in

length is most certainly not eaten in its entirety, since root voles were not observed to dig away soil to this depth. If we accept that only 1/3 of the root mass is available to them, even so this makes it over 12 kg/ha.

The participation of *Ranunculus repens* and *Cerastium vulgatum* also increases considerably in winter in comparison with spring. In winter, as in spring, 5 species of plants formed percentages less than 5% (Table

Table 3.

Participation of different species in the total amount of green plant mass.

Species	Spring 1968		Winter 1969	
	kg/ha	%	kg/h	%
1. *Agrostis vulgaris* With.	1091.0	37.11	61.2	36.19
2. *Stellaria palustris* Ehrh.	496.1	16.87	—	—
3. *Dactylis glomerata* L.	347.0	11.80	14.3	8.46
4. *Senecio vernalis* W. K.	204.1	6.94	—	—
5. *Stellaria uliginosa* Murr.	134.7	4.58	2.5	1.48
6. *Gnaphalium silvaticum* L.	110.1	3.75	—	—
7. *Cirsium arvense* L.	95.3	3.24	—	—
8. *Stellaria media* L.	85.4	2.90	1.8	1.06
9. *Ranunculus repens* L.	57.4	1.95	10.0	5.92
10. *Cerastium vulgatum* L.	54.5	1.85	12.4	7.33
11. *Taraxacum officinale* Web.	54.0	1.84	25.6	15.14
T. *officinale* — roots	—	—	37.8 *)	—
12. *Knautia arvensis* (L.)	48.0	1.63	—	—
13. *Urtica dioica* L.	39.1	1.33	3.1	1.84
14. *Cardamine pratensis* L.	39.1	1.33	—	—
15. *Capsella bursa pastoris* (L.)	19.1	0.65	—	—
16. *Iris pseudoacorus* L.	17.8	0.60	—	—
17. *Erisimum cheiranthoides* L.	13.8	0.47	—	—
18. *Rumex acetosa* L.	8.1	0.27	—	—
19. *Veronica beccabunga* L.	7.6	0.26	—	—
20. *Malachium aquaticum* Fr.	5.3	0.18	—	—
21. *Rorippa amphibia* (L.)	4.0	0.14	6.2	3.66
22. *Achillea millefolium* L.	4.0	0.14	—	—
23. *Veronica chamaedrys* L.	2.2	0.07	—	—
24. *Caltha palustris* L.	1.7	0.06	—	—
25. *Stachys palustris* L.	0.6	0.04	—	—
26. *Galium palustre* L.	—	—	8.4	4.96
27. *Moss*	—	—	7.7	4.55
28. *Erigeron acer* L.	—	—	6.8	4.02
29. *Crepis* sp. L.	—	—	6.0	3.55
30. *Agrostis stolonizans* Bess.	—	—	1.8	1.06
31. *Pedicularis* sp. L.	—	—	0.7	0.42
32. *Succisella inflexa* (Kluk) Beck	—	—	0.6	0.36
Total	2940.0	100.0	169.1	100.0

*) Assessed amount of roots.

3) and all these species occurred in spring, although only *Agrostis vulgaris* and *Dactylis glomerata* dominated in both these seasons. In all the five species mentioned form 77% of green mass.

Species occurring only in the spring aspect of the peat-bog are relatively small in numbers, although the total amount of biomass during this period is several times lower than in spring. Only two of the eight species

occurring in winter each form less than 5% of the mass, while the percentage of the remaining species is even smaller.

The winter aspect of the plant association differs considerably from the spring aspect in respect of composition and percentages of the various species. The decidedly dominating species of grass (*Agrostis vulgaris*), despite the extremely great variations in quantity, is not subject to any changes in this respect.

5.3. Average Daily Metabolism Rate (ADMR)

Oxygen consumption measured over whole 24-hour periods forms a good basis for calculating the energy requirements of these rodents (G ę b c z y ń s k i, 1966; G r o d z i ń s k i, 1966; G r o d z i ń s k i & G ó - r e c k i, 1967; G ó r e c k i, 1968). It is expressed as average daily metabolism requirement both in ccm of oxygen per gram of body weight per hour, and in kcal/g/hour [3]).

Average daily metabolism rate is lowest in the root vole in spring (Table 4). During this period the body weight of the group of animals

Table 4.

Average daily metabolism rate in the root vole at different seasons.

Season	n ($\male\male+\female\female$)	Body weight, g $\pm$ S.D.	ADMR		Metabolic body size, $kg^{3/4}$	$kcal/kg^{3/4}$ per day
			ccm/g/hr$\pm$S.D.	C. v.		
Spring	20 (11+ 9)	37.02 ± 2.27	3.31 ± 0.55	13.6	0.085	166.07
Summer	20 (11+ 9)	22.13 ± 6.00	4.49 ± 0.43	9.3	0.057	200.82
Autumn	16 (8+ 8)	26.01 ± 7.84	4.31 ± 0.89	20.6	0.064	201.78
Winter	19 (9+10)	21.11 ± 5.32	3.65 ± 0.85	23.3	0.055	161.38

examined was highest. In spring, in May, only old adult animals, that is, the heaviest were caught. In the other periods of the year animals with different body weights were taken for experiments to ensure that all weight groups of the study population were represented. It is for this reason that the standard deviation of body weight in the spring group is far smaller in comparison with other seasons. Root voles are characterized by maximum oxygen consumption in summer. These values for autumn and winter come between values for spring and summer and do not greatly differ from each other (Table 4).

In order to determine exactly in which period of the year the voles' metabolism is greatest the values obtained were expressed in kcal/kg$^{3/4}$

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[3]) In calculations of this kind it was accepted that the respiration coefficient *RQ* in rodents is 0.8, with which the caloric equivalent of oxygen is 4.8 kcal/l.

per day. Such conversion made it possible to compare the metabolism of animals irrespective of their body weight, freeing as it were data on energy metabolism from the relation which is present between the size of the animal examined and metabolism calculated per unit of body weight. Oxygen consumption values calculated in this way are suitable for both interspecific and intraspecific comparisons (K l e i b e r, 1968). It thus also became possible to compare results obtained for different seasons. Minimum metabolism, expressed in kcal/kg$^{3/4}$, characterized the root vole in winter and spring (Table 4). Maximum energy metabolism rate is exhibited by *M. oeconomus* in autumn and summer, both these

Table 5.

Oxygen consumption in different seasons depending on ambient temperature.

Season	Temp. °C	Body weight		RMR		n	%
		g ± S. D.	kg$^{3/4}$	ccm/g/hr±S.D.	kcal/kg$^{3/4}$/hr		
Spring	6	42.45 ± 7.67	0.094	6.74 ± 1.18	14.61	12	147.3
	15	47.30 ± 8.40	0.102	5.53 ± 1.07	12.31	12	124.1
	25	40.64 ± 7.75	0.091	4.63 ± 0.57	9.92	12	100.0
Summer	6	21.22 ± 2.62	0.055	7.36 ± 1.12	13.63	9	151.9
	16	20.17 ± 2.51	0.053	5.56 ± 0.95	10.16	12	113.3
	25	20.10 ± 2.06	0.053	4.93 ± 1.37	8.97	12	100.0
Autumn	10	22.55 ± 2.46	0.058	7.06 ± 0.76	13.18	12	140.7
	15	25.91 ± 7.10	0.064	5.75 ± 0.78	11.17	12	119.2
	25	24.95 ± 7.24	0.062	4.85 ± 1.66	9.37	12	100.0
Winter	0	19.92	0.053	9.48	17.10	2	340.0
	8	31.17 ± 5.14	0.075	5.72 ± 0.43	11.41	12	226.8
	15	28.40 ± 6.21	0.069	4.17 ± 1.65	8.24	15	163.8
	25	39.60 ± 6.17	0.090	2.38 ± 0.35	5.03	12	100.0

values being almost equal, as it is the case when winter is compared with spring. ADMR in summer and autumn is about 11% higher than in winter and spring, and this difference is statistically significant (P < 0.001; Student's tests), whereas there are no statistically significant differences between values for summer and autumn, and spring and winter.

5.4. Heat Production in Different Ambient Temperatures

Measurements of resting metabolism rate (RMR) at different temperatures were made in all seasons (Table 5). This permitted of evaluating the relation between oxygen consumption rate and ambient temperature

in different seasons and expressing it by both absolute and relative change depending on temperature. It was then possible to calculate additional energy losses at low temperatures, that is, for periods spent outside the nest.

As the body weight of the voles examined, as in the case of measurements of ADMR, was different, the results obtained were expressed not only in ccm O_2/g per hour, but were also converted to kcal/kg$^{3/4}$ per hour (Table 5). This conversion permitted of establishing that the values of RMR of voles in winter are lower than in other seasons and that these differences are statistically significant (P < 0.001; Student's test). The differences between the other seasons, on the other hand, are slight (Table 5; Fig. 4) and statistically non-significant.
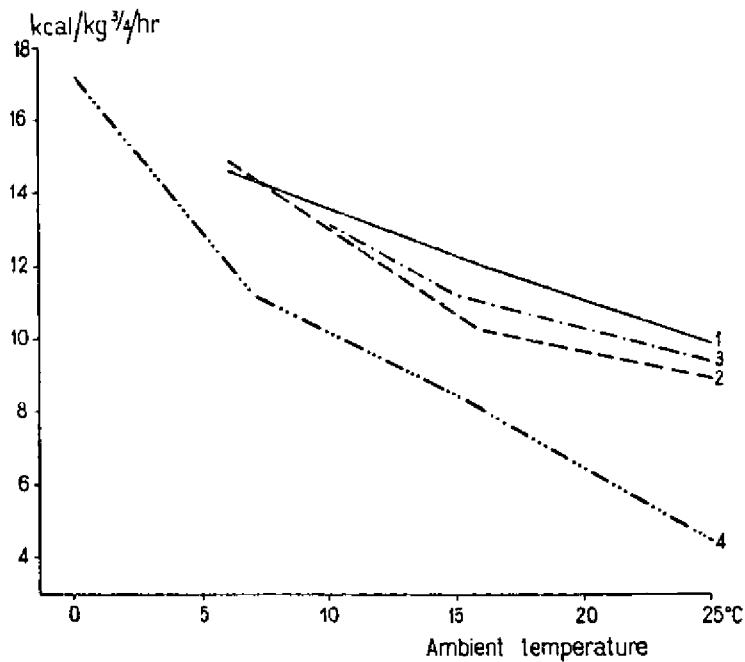

Fig. 4. Resting metabolism rate of the root vole.
1 — spring, 2 — summer, 3 — autumn, 4 — winter.

Voles exhibit maximum increased metabolism rate, depending on the ambient temperature, in winter, within limits of 0 to 8°C (Fig. 4). In this range of temperatures change in metabolism is 5.69 kcal/kg$^{3/4}$ per hour, that is, 0.71 kcal/kg$^{3/4}$ per hour per 1°C. Between 8 and 15°C it is correspondingly only 0.45 kcal/kg$^{3/4}$ per 1°C, and an even lower rate of metabolism changes takes place between 15 and 25°C, when it is only 0.32

kcal/kg$^{3/4}$. The rate of heat production in different ambient temperatures is slightly lower in other seasons (Fig. 4). The most weakly expressed metabolic reaction to a change in ambient temperature is observed in summer between 16 and 25°C, when it is only 0.13 kcal/kg$^{3/4}$ per hour per 1°C.

5.5. Social Temperature Regulation

The effect of the size of the group of voles on the rate of heat loss was studied. Groups consisting of pairs, or three individuals of one sex, were kept in cages for at least one week before the experiment, to enable the animals to get accustomed to each other. Attempts at forming groups of 4 individuals of one sex were not successful, as the voles fought each other and as a rule bit each other to death.

Oxygen consumption was measured in a Kalabukhov-Skvortzov apparatus for an hour at a temperature of 20°C. Groups of voles were kept in respiration chambers of 9 l capacity, without food or nesting material, that is, under conditions similar to experiments on heat production in

Table 6.

Oxygen consumption at a temperature of 20°C in spring by root voles aggregated in groups of different sizes. n — number of measurements.

Group size	n	Mean weight of group, g	ccm/g/hr	kcal/kg$^{3/4}$ per day
1	20	37.0	3.31	166.1
2	10	74.6	2.97	177.3
3	6	126.7	2.83	194.8

different ambient temperatures. It was impossible to restrict movements in such a group, because the voles, when placed in a narrow container behaved restively and often bit each other, which increased general activity. Oxygen consumption was therefore calculated only during periods in which they kept together in a group and behaved quietly.

It was found that oxygen consumption by animals concentrated in a group is lower than in individuals kept singly. During spring this difference was 10.3 % in the case of two individuals kept together, and in a group of three, 14.5 % lower. After converting these values to metabolic size of body it turned out that a group of three individuals has higher heat losses than a pair of voles (Table 6).

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5.6. Daily Activity Rhythm

Measurements of oxygen consumption over full 24-hour cycles permitted of simultaneous evaluation of the daily activity cycle of *M. oeconomus*. The activity model calculated in this way was set out in two--hour intervals (Fig. 5), although measurements of oxygen consumption were made every hour. By accepting two-hour intervals it was possible to determine the general activity rhythm in the study population of root voles.
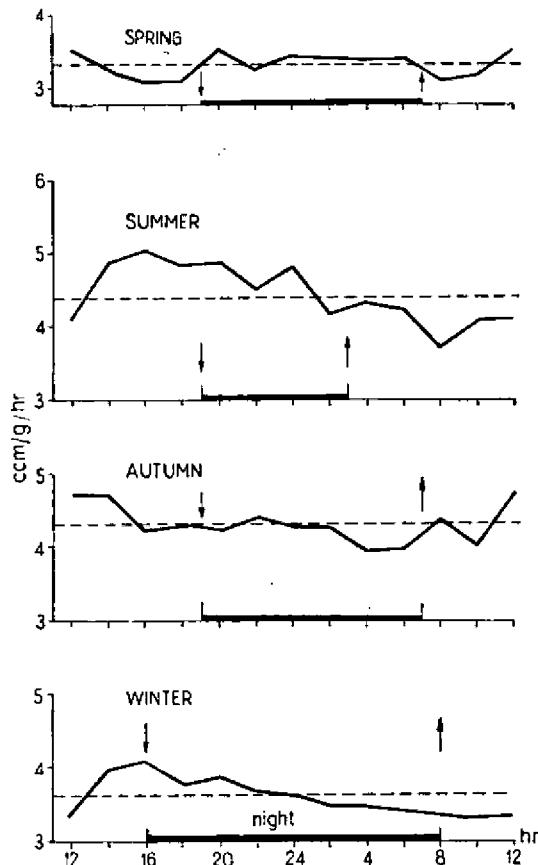
Fig. 5. Daily rhythm of oxygen consumption in the root vole. Dotted line indicates the mean value of daily metabolism in the given season. Arrows indicate the beginning and end of night.

These animals are characterized by relatively small daily amplitude of the average maximum and minimum oxygen consumption. This relation is lowest in spring (1.18), and highest in summer (1.39). The values for autumn and winter are intermediate and similar to each other (Table 7). *M. oeconomus* is a species active over the whole day, almost regardless of the season. It is only in summer that relative differences in activ-

ity are observed, when the maximum occurs during afternoon and evening hours (Fig. 5).

The fact that the activity of root voles has many phases is also shown by the slight differences between mean metabolism during night hours

Table 7.

Parameters of daily activity calculated from O_2 consumption.

Season	ccm/g/hr min	ccm/g/hr max	Max : min ratio	ccm/g/hr Day	ccm/g/hr Night	Night : day ratio
Spring	3.02	3.56	1.18	3.19	3.43	1.07
Summer	3.72	5.16	1.39	4.46	4.56	1.02
Autumn	3.76	4.85	1.29	4.42	4.22	0.95
Winter	3.30	4.29	1.30	3.62	3.70	0.98

in comparison with daytime hours. In spring and summer this index is very slightly higher than 1.0, whereas in autumn and winter it is slightly lower than 1.0 (Table 7).

5.7. Food Preference

The degree of the root vole's food preferences for different species of plants was assessed in three seasons — in spring, summer and autumn (Table 8).

In spring the animals were given 27 species of plants, 2 species of which were trees — birch and poplar. The food consisted of the stalks and leaves of herb plants and blades of grass, and in the case of trees — the thin branches from which the voles bit the buds, leaves and to a slight extent the bark. In this season, as in summer and autumn, the animals exhibited a marked preference for *Taraxacum officinale*. This species was as a rule consumed almost in its entirety, only small amounts of the thickened parts of leaf stalks and ligneous parts of roots being left. Degree of consumption was therefore evaluated as 3. The rodents began eating other species from the young and juicier parts of the plants.

There are other species in spring which belong to very readily eaten plants, that is, more than 50% of which were consumed (Table 8). None of them belong to *Gramineae*. A further eleven species are readily eaten, and it is only in this category that two species of grass are included, the remaining species being herb plants. The final 9 species used for these experiments on food preferences in spring can be considered as not readily eaten, and they include the two species of trees. Not a single species was found at this time of the year which was not eaten at all by the voles.

In summer the list of tested plants was far longer and included 33 species (Table 8). Only 6 species on this list, however, were considered as very readily eaten, that is, one species less than in spring. During summer only 3 species of those evaluated in spring as very readily eaten

Table 8.

Food preferences of root voles in different seasons*).

Species	Spring			Summer			Autumn		
	n	Avg.	%	n	Avg.	%	n	Avg.	%
1. *Taraxacum officinale* Web.	10	3.0	90	17	3.0	90	19	3.0	90
2. *Senecio vernalis* W. K.	10	2.7	80	10	1.3	30	16	2.0	50
3. *Stellaria palustris* Ehrh.	20	2.5	70	13	1.7	40	21	2.4	60
4. *Stellaria media* L.	10	2.5	70	10	2.6	70	8	2.7	80
5. *Stellaria uliginosa* Murr.	10	2.3	60	10	2.3	60	—	—	—
6. *Urtica dioica* L.	10	2.3	60	—	—	—	—	—	—
7. *Rumex acetosa* L.	10	2.2	60	—	—	—	—	—	—
8. *Cerastium vulgatum* L.	10	2.0	50	10	1.9	50	—	—	—
9. *Veronica beccabunga* L.	10	1.9	50	10	1.9	50	—	—	—
10. *Malachium aquaticum* Fr.	10	1.6	40	14	2.0	50	—	—	—
11. *Agrostis vulgaris* With.	10	1.7	40	10	1.0	20	24	2.2	60
12. *Cardamine pratensis* L.	10	1.6	40	10	1.5	40	—	—	—
13. *Dactylis glomerata* L.	20	1.7	40	10	1.6	40	16	2.3	60
14. *Ranunculus repens* L.	20	1.8	40	10	1.7	40	—	—	—
15. *Rorippa amphibia* (L.)	10	1.7	40	—	—	—	20	1.4	30
16. *Achillea millefolium* L.	10	1.3	30	10	1.9	50	—	—	—
17. *Knautia arvensis* (L.)	10	1.5	30	10	1.5	30	13	2.4	70
18. *Cirsium arvense* (L.)	10	1.5	30	—	—	—	—	—	—
19. *Capsella bursa pastoris* (L.)	10	1.0	20	—	—	—	—	—	—
20. *Veronica chamaedrys* L.	10	1.1	20	10	1.1	20	—	—	—
21. *Erysimum cheiranthoides* L.	10	0.9	20	10	0.8	20	—	—	—
22. *Caltha palustris* L.	10	1.0	20	—	—	—	—	—	—
23. *Gnaphalium silvaticum* L.	10	0.9	20	10	0.9	20	—	—	—
24. *Stachys palustris* L.	10	0.7	10	10	1.1	20	—	—	—
25. *Betula verrucosa* Ehrh.	10	0.6	10	10	0.7	10	—	—	—
26. *Alnus glutinosa* (L.)	10	0.4	10	—	—	—	—	—	—
27. *Iris pseudoacorus* L.	10	0.7	10	—	—	—	—	—	—
28. *Viola arvensis* Murr.	—	—	—	11	2.9	90	—	—	—
29. *Vicia cracca* L.	—	—	—	10	2.1	60	—	—	—
30. *Tussilago farfara* L.	—	—	—	12	2.2	60	—	—	—
31. *Veronica longifolia* L.	—	—	—	10	1.9	50	13	2.3	70
32. *Agrostis alba* L.	—	—	—	10	1.3	30	—	—	—
33. *Verbascum* sp. L.	—	—	—	10	1.4	30	—	—	—
34. *Mentha arvensis* L.	—	—	—	10	1.4	30	—	—	—
35. *Festuca rubra* L.	—	—	—	10	1.4	30	—	—	—
36. *Chamaenerion angustifolium* (L.)	—	—	—	16	1.2	30	11	2.7	80
37. *Phelum pratense* L.	—	—	—	10	1.4	30	—	—	—
38. *Potentilla anserina* L.	—	—	—	12	0.9	20	—	—	—
39. *Linaria vulgaris* (L.)	—	—	—	12	0.9	20	—	—	—
40. *Scirpus silvaticus* L.	—	—	—	10	0.6	10	—	—	—
41. *Calamagrostis epigeios* (L.)	—	—	—	10	0	0	10	0	0

*) It was found that in several supplementary experiments the following species of plants are very readily eaten in winter: *Galium palustre* L., *Erigeron acer* L., *Crepis* sp. L.; readily eaten: *Succisella inflexa* (Kluk) Beck.; not readily eaten: *Agrostis stolonizans* Bess., *Pedicularis* sp. L.

remainded in that category. Two — *Senecio vernalis* and *Stellaria palustris* — were estimated only as readily eaten in summer, as opposed to the spring assessment. Additions to the species very readily eaten in summer were *Viola arvensis*, *Vicia cracca* and *Tussilago farfara*.

The majority is formed by species which were shown by preference tests to be readily eaten by root voles. There are sixteen species on this list, and 11 of them are species which also occur in spring. All the plants readily eaten in summer were also readily or very readily eaten in spring. An exception to this is *Stachys palustris*, which was not very readily eaten in spring (10%), but proved to be a little more readily eaten in summer (30%).

Eight species were considered as not readily eaten, and of these 4 were included in the spring experiments, when only 3 were not readily eaten. *Agrostis alba* was readily eaten in spring, contrary to the summer, when the voles did not readily eat it. It was also found that *Calamagrostis epigejos* is the only species which is not eaten at all by *M. oeconomus*.

In autumn the voles were given only 11 species of plants to choose from (Table 8), all of which had already occurred in either spring or summer. Despite the fact that this list of plants used in the experiments was the shortest, the number of very readily eaten species is greatest, i.e. 8 species. Of the remaining three two species are readily eaten, while *Calamagrostis epigejos* is not eaten at all.

It is clear from the above that the number of species very readily eaten in all seasons is similar, irrespective of the number of plants tested. There are more readily eaten plants in summer and autumn than very readily eaten species. These two groups in general form the majority of the plant association in all seasons. In spring the list of plants very readily and readily eaten by root voles consists jointly of 18 species, which forms 66.6% of the whole plant association in this period. In summer this percentage increases to 72.7%, and in autumn reaches as much as 90.9%. Thus species not readily eaten, or not eaten at all, by the voles, form only a small part of the plant association in the study area.

5.8. Digestibility and Assimilation of Food

Determination of the digestibility coefficient and assimilation level was made in three seasons (Table 9). The food given to the voles was very similar in all seasons and consisted of the green parts of grasses and herbs, mainly the leaves of *Taraxacum officinale*, leaves and stalks of *Stellaria media* and *Stellaria palustris*, and also blades of *Agrostis vulgaris* and *Dactylis glomerata*. The experiments were made in autumn

using two diets: natural (Series I) and culture (Series II). The culture diet included red beet and the roots of parsnips and carrots.

The value of the digestibility coefficient varies from about 69% to over 91% (Table 9). It exhibits the lowest value in spring and summer, and differs by only 1% in these periods. This difference is statistically non-significant (Student's t test, P > 0.05). In autumn in the experiment in which the animals were given similar food, but with the addition of the root of *Taraxacum officinale*, the digestibility coefficient rose to 74%. This difference between summer and autumn (I) is not significant (P > 0.6). On the other hand, during the autumn, when the voles were fed on a diet with lower cellulose content in the dry mass (series II), the difference in relation to the natural food (series I) is statistically highly significant (P < 0.001).

Table 9.

Digestibility coefficient and assimilation level depending on season and kind of food.

Roots of *Taraxacum officinale* were added to the animals food in experiment I in autumn; and carrot, beet and parsnip were given in experiment II.

| Season | n | Digestibility coefficient | | Assimilated energy |
		Avg. ± S. D.	C.v.	Avg. ± S. D.
Spring	20	69.7 ± 5.4	7.7	67.5 ± 9.5
Summer	18	68.7 ± 9.2	13.3	67.2 ± 8.2
Autumn				
I	20	73.9 ± 6.2	8.3	71.4 ± 10.0
II	8	91.4 ± 4.1	4.5	90.4 ± 4.7

There can be no doubt that the lower value of the digestibility coefficient in spring and summer is connected with the high indigestible cellulose content in the food. Reduction in the amount of cellulose causes simultaneous increase in assimilation of food.

The value of food assimilation differs from the digestibility coefficient by 1.5% to 2.5% (Table 9). This was the caloric value of the urine excreted by the voles.

6. DISCUSSION

The results obtained for daily oxygen consumption, heat production in different ambient temperatures and social temperature regulation, and also activity, made it possible to attempt to calculate the daily energy budget of the root vole. On the other hand calculation of the energy requirements of this population of voles had special features under the conditions described. A well-isolated habitat, relatively small

in area, covered by a homogenous plant association, was mainly inhabited by one species of rodent (B u c h a l c z y k & P u c e k, 1968). The plant association of the peat-bog consisted of grasses and herb annuals, which enabled a simple conversion of determined biomass to net production to be made. It was next also possible to assess which part of this production is food available to rodents and to what extent it can be utilized by them. Owing to these properties, which as it were created the conditions of the intended experiment, it was possible accurately to trace the development of the root vole population and its influence on the plant association of the peat-bog examined.

6.1. Net Primary Production

Despite the different attempts made at calculating primary production, it is the method of assessing the amount of organic substances produced by plants which is in most general use.

Primary production can be determined relatively easily, and certainly most accurately in aggregations composed of annual plants, since their structure and floristic composition are simplest (M e d w e c k a - K o r- n a ś, 1965). Lawn and meadow associations belong to such communities.

The peat-bog association consists of grasses and annual herbs and it was not therefore difficult to determine the amount of net production. As in the case of the grassland evaluation, the maximum amount of biomass les the amount recorded at the end of winter was taken as the net production value. In a grassland analysis it is sufficient to make a single finding during the year of the plant crop when there is the maximum amount of biomass, although these results are as a rule underestimated in relation to actual production (O d u m, 1960; S o c h a v a, L i p a t o v a & G o r s h k o v a, 1962). T r a c z y k (1968) calculated the net production of a meadow and found that there are fairly considerable differences between results depending on the method used. Acceptance of peak amount of biomass gives a lower result than when other methods are used. This is connected with the fact that growth and dying of different species of plants, and attainment by them of their maximum mass, does not take place at one and the same time. In this particular case it is not of course a question of the whole biomass, since its dead parts may originate even from several recent years (T r a c z y k, 1968). Nevertheless use is made of the method of calculating production from the amount and disappearance rate of dead parts (W i e g e r t & E v a n s, 1964). In the present case only the amount of the green parts of the difference in biomass in spring and winter was taken as net primary production. This value is 11,929,864.7 kcal/ha.

The amount of production undoubtedly also depended on the year, as is shown by the differences between winter 1968 and the winter of the following year. Differences between the summer of 1966 and of 1967 were however slight. O d u m (1960) found in old-field communities differences many times greater, depending both on the season and years, which is mainly due to the different amount of rainfall in the study area. W i e g e r t & E v a n s (1964), on the other hand, on the basis of observations made in this ecosystem over a period of several years, found that variations in the total amount of biomass from year to year are relatively small. Similarly the meadow associations examined by T r a-c z y k (1968) exhibited slight differences in successive years.

There are no data on variations in the biomass of the underground parts of plants and seeds which are necessary to full evaluation of the net production of a peat-bog. In the study habitat an evaluation of this kind was made only in order to estimate the amount of potential food of the root vole. On this account, of the underground parts of plants, measurement was made only of the amount of roots of Taraxacum officinale, which are included in the root vole's diet in late autumn and winter.

Assessment of net primary production by the harvest method also fails to take into consideration the amount of losses in biomass due to the effect of herbivorous animals. Thus it is necessary to add the amount of plants eaten by M. oeconomus to the results of net production of peat--bog.

6.2. Food Resources of the Root Vole

Although root voles cannot use the whole of plant mass as food no uniform method has as yet been established for estimating the amount of food potentially of use to rodents. G o l l e y (1960) assumed that in old--fields community the whole of the green mass above ground is available to Microtus pennsylvanicus (O r d, 1815). O d u m, C o n e l l & D a v e n-p o r t (1962) on the other hand took as the food supply of Peromyscus polionotus (W a g n e r, 1843) in a similar association only the seeds, which form slightly less then 7% of the whole above-ground production of live plants. Similarly P e a r s o n (1964) considered that only the seeds of meadow plants constitute food potentially available to three species of rodents — Microtus californicus (P e a l e, 1848), Reithrodontomys megalotis (B a i r d, 1858) and Mus musculus L i n n a e u s, 1758.

The food supply of mammals can best be assessed after obtaining an accurate knowledge of their food habits, and then referring them to net primary production. Available food means only those plants which are easy to find and are simultaneously preferred and eaten by animals (D r o ż d ż, 1966; G r o d z i ń s k i, 1968).

Practically speaking all the species of plants in the peat-bog association are easy for *M. oeconomus* to find, but not all are equally preferred (Table 8). The amount of available food also varied depending on the season, chiefly on account of the fact that over the yearly cycle the amount of live plant biomass varied enormously (Table 2). Calculation was therefore made of the amount of this food in periods extreme in respect of supply of green biomass, that is, in spring and winter. The percentage of the different species of plants in the total amount of live biomass is known in these two seasons (Table 3). We know the preferences for the different kinds of foods for spring, summer and autumn. In winter it was possible to make only an approximate test of preferences for several species of these plants which were not examined in other seasons. Therefore when calculating food available in winter in principle it was the date obtained in other seasons which were used for this purpose.

In spring 7 species of plants were considered as very readily eaten (Table 8). Jointly they give 1,021.5 kg of dry green mass per hectare. If we add to this 11 species of plants readily eaten during this period, then together with the previously mentioned species they give almost 3 tons per hectare (Table 10). The remaining species of plants form slightly more than 5% of the dry mass and are also eaten, although not readily. Thus in spring the whole green biomass may be considered as food available to the root vole.

On the basis of results obtained from experiments on food preference the amount of available food consumed was calculated. In spring, of the most readily chosen foods, the root voles ate on an average about 80% of the mass of these plant tissues, and thus there is as much as 700 kg/ha of the particularly preferred and fully consumed food. Root voles consume an average of 40% of the mass of plants considered as readily eaten, which also gives a figure of approximately 700 kg/ha. Only 15% of mass is eaten in the third group of plants, that is, 25 kg may be used in this way. Jointly this gives a figure of over 1.4 tons/ha of plant mass which may actually be consumed. There remained about 1.5 tons of available plants per hectare, but is probably not eaten. This consists of the parts of plants which the voles did not eat during experiments on food preferences. There is, however, no doubt that part of the plant tissues were not eaten because food was supplied *ad libitum* in the experiment, which reduces the estimated value of the amount of food both available and consumed. The percentage of very readily eaten plants is far higher in winter than in spring, and constitutes 4/5 of the total live biomass (Table 10). This, however, forms only 129.7 kg of dry mass per hectare and is almost 8 times smaller than

in spring. The percentage of readily eaten and not readily eaten plants, on the other hand, is far lower than in the period previously discussed (Table 10). In winter moss, which is inedible, must be deducted from total mass. It was assessed as forming 7.7 kg/ha during this period. Available food in winter (1969) was thus 161.4 kg/ha, that is, nine time less than in spring.

If we attempt, in the same way as for spring, to calculate the amount of plant mass which is consumed, it is found that 90.6 kg/ha of the group of most readily eaten species may be consumed. This value is 11.7 kg/ha for readily eaten species, and for food not readily eaten 0.4 kg/ha. Jointly this gives 112.9 kg of green biomass per hectare, that is 12 times less than in spring.

Table 10.

Amount of food available to the root vole in spring and winter.

Season	Very readily eaten		Readily eaten		Not readily eaten		Total	
	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%
Spring	1021.5	34.8	1753.2	59.6	165.3	5.6	2940.0	100.0
Winter	129.7	80.3	29.2	18.1	2.5	1.6	161.4	100.0

An even lower state of live biomass was recorded at the end of the winter in 1968 (Table 2). Calculation for this period of the amount of food mass which can be eaten shows that it is only 67.2 kg/ha. During the winter there is the addition of 12 kg/ha of the roots of *Taraxacum officinale*, a favourite and fully available food.

The amount of food available and eaten by the root vole is subject to considerable variations over the year and is closely correlated with the amount of green biomass, which is almost the only source of this food. Tree bark forms a certain supplement to the animals' diet, especially in late autumn and winter. In the peat-bog examined the voles gnawed bark and also occasionally the roots of young decidous trees (G ę b- c z y ń s k a, 1969).

6.3. Daily Energy Budget of the Root Vole

In order to construct the daily energy budget (*DEB*) it is possible to use, in addition to average daily metabolism rate (*ADMR*) other means of measuring it, such as, for instance, basal metabolism rate (M c N a b, 1963), or resting metabolism rate (P e a r s o n, 1960; G r o d z i ń s k i, 1961; M c N a b, 1963; T r o j a n & W o j c i e c h o w s k a, 1967a). It is

open to discussion which of these measures of metabolism permits of the most accurate calculation of the average daily energy requirements. Many ecologists and physiologists, however, are inclined to accept *ADMR* as the most convenient basis for these calculations (G r o d z i ń s k i & G ó r e c k i, 1967). Measurement of *RMR*, usually lasting for the best part of an hour, in small chambers which limit movement, give over-estimated results (G ę b c z y ń s k i, 1963).

On this account *ADMR* became the basis for calculating the daily energy budget of the root vole. Only the author's own measurements of daily oxygen consumption were taken as a basis in this case. Although G r o d z i ń s k i (1966) measured *ADMR* in the root vole it was a sub-species of the vole originating from Alaska, *i. e. M. oeconomus macfar-lani* (M e r r i a m, 1900), whereas animals taken from the north of Po-land are allocated to the subspecies *M. oeconomus stimmingi* (N e h-r i n g, 1899) (cf. W a s i l e w s k i, 1956). Comparison of results is also rendered difficult by the fact that G r o d z i ń s k i (1966) measured daily oxygen consumption at temperatures of 10 and 15°C, under the condi-tions of the arctic summer. If, however, we extrapolate his results to a temperature of 20°C, at which the experiments with *M. o. stimmingi* were carried out, then *M. o. macfarlani* under such conditions would use 4.241 ccm O_2/g/hour. This figure is astonishingly close to the present results for summer and autumn (Table 4). In order to make even more exact comparison of the results of experiments from Alaska and Poland, G r o d z i ń s k i's data were converted to kcal/kg$^{3/4}$, which evens out the slight existing differences in the average weight of the groups examined. When the results from Alaska are extrapolated as before to a temperatu-re of 20°C their agreement with data for summer and autumn is con-firmed. For *M. o. macfarlani* the caloric requirements per day are 197 kcal/kg$^{3/4}$, and for *M. o. stimmingi* — 200.8 (summer) and 201.8 (autumn).

This agreement may also be considered as largely fortuitous, since there can be no doubt that such great differences in physical and biotic habitat as there are between the Alaskan taiga and a peat-bog in northern Poland shape the bioenergetic relations in these two subspecies diffe-rently. Nevertheless this fact permits of the assumption that the root vole has similar physiological characteristics in this respect over the whole of its range. A confirmation of this would appear to be found in the data on the metabolism of *M. oeconomus* from the Moscow district, which were presented by B a s h e n i n a (1967; 1968). Exact comparison of her results is not, however, possible as this author does not give details of all the experimental conditions.

Although *ADMR* gives a general idea of the value of the daily energy requirements of the species examined, it is essential to set out certain

corrections supplementing this value. The first of them is connected with the daily activity cycle. We know little about the activity of the root vole and the cycles of its daily activity were defined on the basis of the daily course taken by oxygen consumption (G r o d z i ń s k i, 1966; own data). In Alaska the voles were slightly more active at night than during the day, since the proportion of oxygen consumption in these two daily periods was 1.07 (G r o d z i ń s k i, 1966). Under Polish conditions this proportion varied with the season and it was only in spring that it was the same as for the Alaskan subspiecies (Table 7). In summer it fell to 1.02 and in autumn and winter was respectively 0.95 and 0.98. Another detail which we do not know is average time the root vole spends outside

Table 11.

Daily energy budget (DEB) for the root vole on a summer and a winter day.

	Summer	Winter
ADMR (20°C) in the nest, including group effect (12.4%)	20 hr × 4.49 ccm/g/hr = 0.431 kcal/g/day	21 hr × 3.65 ccm/g/hr = 0.368 kcal/g/day
Metabolic rate during period of out-of-the-nest activity (17.4 or 0°C)	4 hr × 4.66 ccm/g/hr = 0.089 kcal/g/day	3 hr × 10.59 ccm/g/hr = 0.152 kcal/g/day
Cost of reproduction	14.1% ADMR = 0.061 kcal/g/day	—
Corrected ADMR values × average body weight	0.581 kcal/g/day	0.510 kcal/g/day
DEB in kcal/voles per day	0.581 × 24.2g*) = 14.06	0.510 × 22.3g**) = 11.37

*) Mean weight of 790 individuals caught in July and August; **) Mean weight of 51 individuals caught in February and March.

the nest, but in the majority of rodents it is similar and comes within limits of 15—25% of the day (e. g. B a s h e n i n a, 1962; G ó r e c k i, 1968). If we accept the value characteristic of Microtus arvalis (B a s h e-n i n a, 1962) then we obtain a result which shows that M. oeconomus spends from 20—21 hours out of the 24 in the nest. Comparison of these two herbivorous species would seem to be the more convenient in view of the fact that it is the quality of their food which determines the sum total of the rodents' activity (G r o d z i ń s k i, 1962).

In order to construct DEB it is also essential to know the temperature of the habitat in which the given species lives. It is necessary here to take into consideration other factors also (e. g. wind velocity, humidity)

which affect the degree of cooling (F e d y k & O l s z e w s k i, 1969) and the consequent rate of heat loss from the organism. We have hitherto not learnt how to make complex measurement of the extent of cooling, and therefore make use only of temperature.

The next correction which has to be taken into consideration in calculations of *DEB* results from the fact of increase in energy requirements in pregnant and nursing females. This phenomenon has been examined in respect of two species of small rodents — *Clethrionomys glareolus* (S c h r e b e r, 1780) and *Microtus arvalis* (P a l l a s, 1788) — (K a c z- m a r s k i, 1966; T r o j a n & W o j c i e c h o w s k a, 1967b; M i g u l a, 1969). In the case of *C. glareolus* this increases to as much as 24 % during the pregnancy period (K a c z m a r s k i, 1966) and in *M. arvalis* 32 % (M i g u l a, 1969). During lactation, however, the increase in energy requirements is far greater, being 92 % in the case of *C. glareolus* (K a c z- m a r s k i, l.c.) and 133 % in *M. arvalis* (M i g u l a, l.c.). The average increase in metabolism in females during the reproductive period is, according to these authors, 58 % in *C. glareolus* and 82.5 % in *M. arvalis*. In the case of the root vole use was made of the values calculated for females of *M. arvalis*.

Seasonal variations in *ADMR*, heat production in different ambient temperatures, climatic habitat factors and reproduction make it necessary to calculate *DEB* for at least the two most greatly differing periods of the year, *i. e.* summer and winter.

In summer *ADMR* is 4.49 ccm O_2/g/hour, which after conversion gives 0.517 kcal/g/day (Table 11). If we assume that the temperature in the nest in which the root vole spends about 20 hours in summer, is 17—19°C, then the increase in oxygen consumption connected with this is compensated for by social temperature regulation. Similar results were obtained for *C. glareolus* by G ó r e c k i (1968). It would seem that social temperature regulation in the case of rodents is an effective protective mechanism against cooling. At lower temperatures the animals readily aggregate and form a compact group, and the effect of social temperature regulation is higher than at temperatures near the neutral temperature zone (G ę b c z y ń s k i, 1969a, b).

During the reproductive season the average for all censuses made from May to the beginning of October during the period from 1966—1968 showed that sexually active females (*i.e.* pregnant and lactating) formed 34.3 % of all females. The sex ratio was almost ideally equal, 1:1 (B u- c h a l c z y k & P u c e k, in prep.). The appropriate correction was therefore calculated and converted to the average for the whole population. As pregnant and lactating females increase energy consumption by 82.5% the average value for the whole population is thus 14.1 % (Table 11).

In winter the average temperature for January is —8.0°, and for February —3.9° [4]). The root voles do not, however, emerge on to the surface of the snow but remain all the time in the zone under the snow where they find their food. In this zone air temperature falls slightly below 0°C only in a few cases, but is never lower than —1°C (C o u l i a- n o s & J o h n e l s, 1962). The wintering condions for the root vole at Biele are good, as the snow cover persists for a very long time in this area. For instance in the winter of 1966/67 snow laid for 96 days (from December 5th to March 10th), and thickness was up to 50 cm. In the winter of 1967/68 the duration of the snow cover was even longer, i.e. 109 days (December 5th — March 23rd), while the thickness of the snow cover was 39 cm.

The temperature of 0°C was therefore taken as the basis for calculation of the correction for the voles' heat production in different ambient temperatures during the time they spent outside the nest. In winter the sum total of the voles' activity is always lower than in summer (O s t e r- m a n, 1956; G r o d z i ń s k i, 1962; G ę b c z y ń s k i, 1964) and it was therefore taken that M. oeconomus spend only 3 hours outside the nest. Reproduction was not observed in winter and it was therefore unnecessary to calculate this correction (Table 11).

The voles' daily energy budget is higher in summer than in winter (Table 11). It must be mentioned here that this difference is almost exclusively connected with reproduction costs. If we omit this correction, then requirements will be almost uniform, and be 0.520 kcal/g/day in summer and 0.510 kcal/g/day in winter. When calculating energy consumption for a whole animal use was made of the average weight for the whole of the material caught during this period, although the weight of animals used for the respiration experiments is very similar to the average values for the population.

The above values relating to the daily energy budget of M. oeconomus are similar to those for other species of rodents, whether mice or voles (G ę b c z y ń s k i, 1966; D r o ż d ż, 1968b; G ó r e c k i, 1968; 1969). In all these species higher energy requirements were found in summer than in winter.

6.4. Energy Flow Through a Root Vole Population

In order to find a reply to the question as to what the energy requirements are of the population in the study area it was necessary to know

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its numbers. The Standard Minimum captures made enabled this value to be estimated (B u c h a l c z y k & P u c e k, 1968). Population numbers were subject to fairly great fluctuations in the study area, depending on the season and year, and varied from 56 to 131 individuals per hectare.

The daily requirements of the root vole are 14.06 kcal/day in summer. The amount of food consumed is, however, greater than this value, as not all the food eaten is digested and assimilated by the organism. After determining the level of food assimilation, which was 67.2% in summer, it is possible to calculate that the root vole must eat 20.93 kcal during the day in order to maintain its energy balance. This rodent therefore needs an average of 4.9 g of dry mass per 24 hours. If we multiply this figure by the number of individuals per hectare we can then ascertain how much food the root vole population eats over the 24-hour period, and in turn we can calculate what part of the available food is eaten by rodents.

In May, with relatively low numbers (56 individuals/ha) they eat 274.4 g of dry plant mass per 24-hours per hectare, which forms 0.009% of the available food and only 0.026% of the mass of readily eaten plants. In summer the amount of food is reduced and population numbers increase so that the animals use 0.034% of the available food. In autumn this percentage increases even further, and is then 0.045%.

It was not possible to estimate numbers in winter in view of the thick snow cover. It would, however, appear that despite the very great reduction in the amount of live plant biomass at this time of the year, the root voles had a food supply in excess of their requirements, especially as the roots of *Taraxacum officinale* and tree bark are eaten as well during this period.

All the above data make it possible to calculate the yearly balance of energy flow through the root vole population and to compare it with the net production of the peat-bog. Using the formula given by G o l l e y (1962) it was found that the value of this energy flow is 375,000 kcal/ha over the whole year. This forms 3.1% of net production. The effect of the root vole on the vegetation of the peat-bog examined is therefore slight. In reality this effect is even less than that given, since as already mentioned, the method used to assess net production gives over-low results. It is nevertheless large in comparison with the effect of rodents on other grass associations. On the mountain pastures in the Bieszczady Mountains, despite the lower net production, the rodents used only 1.03% of the food available (G r o d z i ń s k i et al., 1966). This difference results from the very great density of the root vole population in the study area. Population numbers in the Bieszczady Mountains were 15 individuals/ha, whereas in the present case this figure was many times higher.

6.5. Effect of Root Voles on the Vegetation

The above calculations show that the plant food eaten by root voles forms only a small part of the grasses and herbs growing in this area. The calculations thus confirmed long-term observations, which show that the root voles did not cause any visible damage to the annual plant associations. They are nevertheless pests in this area, as they formed a serious threat to forest cultures. After the peat-bog had been drained cultures of young deciduous trees were planted in the glade. In late autumn and winter the root voles gnawed the bark of these young trees, in particular round the root neck and the lower branches, and sometimes even gnawed the roots. The root voles completely destroyed 7% of the deciduous species of trees in this way and damaged from 48—67% of the young alders, maples, ash and osiers. They failed to bite pine and spruce only (G ę b c z y ń s k a, 1969; B u c h a l c z y k, G ę b c z y ń s k a & P u-c e k, 1970). In effect this results in considerable material losses in forest cultivation in this area.

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Zofia GĘBCZYŃSKA

BIOENERGETYKA POPULACJI NORNIKA PÓŁNOCNEGO

Streszczenie

Na podstawie trzechletnich badań oszacowano wskaźniki bioenergetyczne oraz stosunki pokarmowe (Tabela 1) nornika północnego, *Microtus oeconomus* (P a l l a s, 1776). Poza tym dokonano oceny przepływu energii przez populację tego nornika, na tle produkcji netto torfowiska niskiego (Ryc. 1, 2).

Ogólny stan biomasy roślinnej podlega wprawdzie niewielkim wahaniom w ciągu roku (Tabela 2) jednakże sezonowe zmiany masy zielonej są znaczne (Ryc. 3). Rośliny zielone stanowią na wiosnę około 80% biomasy, latem ich udział nieco się zmniejsza, jesienią wynosi już tylko około 20% a w końcowym okresie zimy spada do 4,3%. Sezonowo zmienia się również udział poszczególnych roślin, tworzących biomasę zieloną (Tabela 3). Zawsze jednak ilość pokarmu dostępnego (Tabela 10) pozostaje w dużym nadmiarze w porównaniu do zapotrzebowania przez norniki.

Dzięki pomiarom średniego metabolizmu dobowego (Tabela 4), można było określić wzorzec aktywności dobowej norników (Ryc. 5, Tabela 7). Oznaczono również wielkość metabolizmu spoczynkowego w różnych temperaturach, w poszczególnych sezonach (Ryc. 4, Tabela 5) oraz wielkość termoregulacji zespołowej (Tabela 6). Wszystkie te parametry pozwoliły na skalkulowanie dobowego budżetu energetycznego (Tabela 11). Budżet ten wynosi w ciągu dnia letniego 0,581 kcal/g a zimą odpowiednio 0,510. Tak więc jeden nornik zużywa latem w ciągu doby, średnio 14,06 kcal, w zimie natomiast tylko 11,37 kcal.

Określona została również wybiórczość pokarmowa badanego gatunku gryzonia (Tabela 8), a także wartość współczynnika strawności i poziomu asymilacji (Tabela 9). Wartość współczynnika strawności pokarmu na wiosnę i latem waha się około 69% a jesienią jest równa 73,9%. Wartość asymilacji jest niższa od tego współczynnika o 1,5 do 2,5%. Latem więc konsumpcja pokarmu osiąga 20,92 kcal na dobę, co równa się około 4,9 g suchej masy roślinnej. Zimą wartość ta wynosi 15,92 kcal/dobę, czyli 3,8 g suchej masy. Z uwagi na wysoką liczebność populacji, wielkość przepływu energii w ciągu roku jest duża i równa się około 375.000 kcal/ha. Tym niemniej stanowi to tylko znikomą część (około 3,1%) produkcji netto ocenionej na 11.929.864,7 kcal/ha na rok.

Mimo, iż nornik północny nie czynił widocznych szkód w zespole roślin jednorocznych na badanym terenie, to jest jednak groźnym szkodnikiem drzewek, choć ogryzana kora stanowiła tylko dodatek do jego diety.