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Net Production of Small Rodents in a Deciduous Forest *

[With 8 Table & 11 Figs.]

In deciduous stands (*Tilio-Carpinetum*) of the Niepołomicka Forest (Southern Poland) the numbers of rodents were estimated during four consecutive years (1967—71) by means of prebaiting and intensive removal method. Bank voles (*Clethrionomys glareolus*) and yellow-necked field mice (*Apodemus flavicollis*) constituted 92.5% of all rodents in this forest. Small rodents went in this period through a population cycle from a high density (32.1 vole and 5.9 mice per ha during the year on the average) to a low density (8.1 and 2.0 individuals, respectively). The mean number for the four year cycle amounts to 19.0 rodents/ha. When young animals staying in the nests are also taken into account the mean numbers should be increased by approximately 20%. The age of mice and voles was determined and then life tables were constructed and curves of individual growth were drawn. At high population density the mean life span of voles amounts to 2.2 and mice to 2.4 months, while at low density the corresponding figures are 2.6 and 3.3 months. The rate of body weight increase was lower in the year of mass occurrence. The turnover of individuals was also related to density and in the population of voles it ranged from 5.5 to 4.6 per year, while in the population of mice—from 5.0 to 4.0 per year. The turnover of biomass amounted on the average to 3.6/year in both populations. The number of rodents born during the year was estimated and the net production was computed from the curves of their growth and survival. In consecutive years the net production ranged from 755 to 2691 g/ha year, out of this 562 to 1977 g/ha year falling for voles and 177—755 g/ha year for mice. The mean year production of all rodents amounted to 1360 g, which corresponds to 1983 kcal/ha year. The net production of rodents was compared in a dozen or so forest and grassland ecosystems. A logarithmic describing the relationship between the production of a population and its mean year density was calculated on the example of voles population.

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I. INTRODUCTION

Deciduous forests of *Tilio-Corpinetum* type grow mainly on fertile soils. In Poland they occur both in lowland area and in the Carpathian foothills (Medwecka-Kornaś, 1966) constituting at present around 3% of our forests. These oak-hornbeam stands show the highest productivity among deciduous forests, and in respect of population density of small mammals they occupy the second place after alder forests (Aulak, 1967).

The oak-hornbeam stands of the Niepołomicka Forest are the subject of collective studies on the productivity and functioning of the forest ecosystem (Medwecka-Kornaś, 1973). Botanical studies include mainly estimation of the primary production and description of plant associations occurring there (Ferchmin & Medwecka-Kornaś, 1973). Studies on the energy flow through population of consumers include some insects, amphibian and birds (Medwecka-Kornaś, 1973), and among mammals — small rodents and deer (Bobek, 1971; Bobek, Weiner & Zieliński, 1972).

The main purpose of studies on the rodent populations was to estimate their assimilation and consumption, and also to determine the effect of these animals on the forest primary production. The net production constitutes only one element of the energy flow and corresponds to this part of assimilated energy which is incorporated into animal tissues (Petruszewicz & Macfadyen, 1970). In populations of small homeothermic animals production constitutes barely 2—5% of the costs of maintenance (Davis & Galley, 1963; Ryszkowski & Petruszewicz, 1967; McNeill & Lawton, 1970). Still it represents, jointly with animal numbers, a basic value for the whole balance of energy flow. The magnitude of net production is also very important for higher trophic links in the feeding chain.

The estimation of production represents a difficult and complicated task. It includes time-consuming determinations of numbers, complicated estimations of mortality, body weight increase and reproduction, which to be carried out in field conditions. There are known several methods of estimation of the net production, as reviewed by Petruszewicz & Macfadyen (1970). In theory the net production of a population can be determined in the simplest way according to the following formula (Petruszewicz, 1967):

$$P = B \cdot \theta_B \quad (1)$$

where B represents the mean state of biomass in a given unit of time, and θ_B — turnover of biomass. In practice, however, calculations by

means of this formula are very difficult, since the turnover of biomass cannot be directly estimated in the population. Hence for calculations the rotation of individuals (Θ_N) is being used, but its value usually exceeds the turnover of biomass (Petrušewicz *et al.*, 1969; Bobek, 1971). For the studies of productivity of a rodent population Petrušewicz (Petrušewicz *et al.*, 1969) introduced a graphical method of the net production estimation as elaborated earlier by Allen (1950) and Nees & Dugdale (1959). This method requires the numbers of born individuals to be known, as well as drawing their growth—survivorship curves. In the production estimated in such way one can distinguish the production due to reproduction and growth, as well as the degree of realization of the potential production (Petrušewicz & Walkowa, 1968).

The present study was aimed at the estimation by this method of the net production of small rodents in *Tilio-Carpinetum* of the Niepołomicka Forest. The most abundant rodents in these forests are bank voles, *Clethrionomys glareolus* (Schreber, 1780) and field mice, *Apodemus flavicollis* (Melchior, 1834). The field studies were carried out for six consecutive years during which voles and mice completed the population cycle. Due to this it was possible to follow population parameters and investigate production at different stages of rodent density. Part of these studies has been earlier published as a communication (Bobek, 1971).

II. STUDY AREA, MATERIAL AND METHODS

The Niepołomicka Forest is situated to the East of Kraków in the Wisła Valley (50° 07'N, 20° 23'E) and covers the area of 10,846 ha. It consists mainly of pine forests, and to a smaller extent of deciduous forests of *Tilio-Carpinetum* type (Ferchmin & Medwecka-Kornaś, 1972). These forests constitute a separate complex of 1,975 ha in area and they were the place of the present study on the productivity of small rodents. During six years (1966—71) 3,445 rodents were trapped there. The rodents were captured with snap traps by means of prebaiting and intensive removal — »Standard Minimum Method« (Grodziński, Pucek & Ryszkowski, 1966). The trapping was carried out mainly on one plot of 5.76 ha where in April and October (1967), or in June and October (1968—1971), standard series of trappings were completed. Each series included 5 days of prebaiting and 5 days of trapping. The Standard Minimum method was also employed during additional trappings on other plots, or on smaller 2.25 ha plots (Babińska & Bock, 1969). Moreover, a few trappings were accomplished on a trapline, in which the bait was at first left at some points and then traps were set at every 15 m. During six years of investigations altogether 25 series of trappings were carried out, mainly as Standard Minimum on 5.76 ha plot (13 trappings), censuses on 2.25 ha plots (8 trappings), and four series of trappings on the trap line. Due to this arrangement in some years (e.g. 1969 and 1970) trappings were carried out almost every month (Fig. 1).

In the trapped material of 3,445 rodents there dominated *C. glareolus* (65.9%) and then *A. flavicollis* — 26.7%. The remaining 7.5% included mainly *Apodemus agrarius* (Pallas, 1771), *Pitymys subterraneus* (de Selys-Longchamps, 1835), *Microtus agrestis* (Linnaeus, 1761) and common dormice, *Muscardinus avellanarius* (Linnaeus, 1758), Table 1. Apart from rodents also 177 shrews were trapped (*Sorex araneus* Linnaeus, 1758, and *Sorex minutus* Linnaeus, 1776), but they were not included in the present study.

All the trapped animals were weighed and the state of their reproductive organs was evaluated. The age of 2243 voles and 895 mice was estimated with the accuracy of approximately one month. For young bank voles (below 3 months) the age was estimated from the tooth shape (Mazák, 1963), while for older ones the length of M_1 roots was determined with micrometer calipers (Pucek & Zejda, 1968). The age of field mice was estimated on the basis of the degree of upper molars wear (Adamczewska-Andrzejewska, 1967).

Only the animals captured during the first 3—4 days of trappings were employed in the calculations, since in the estimation of numbers by the method of maximum

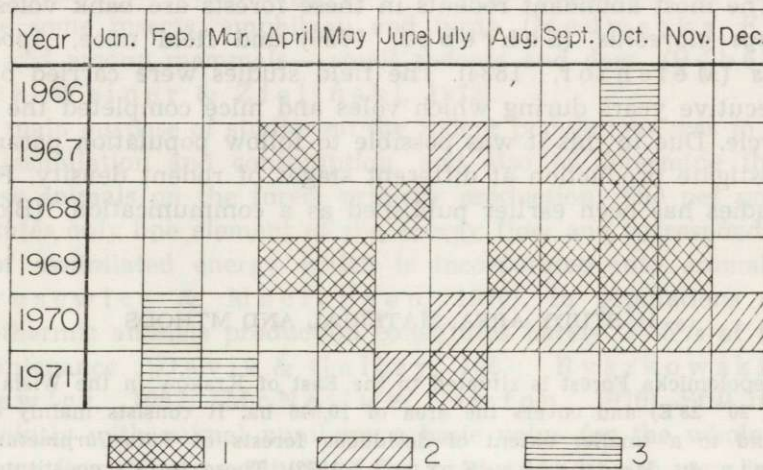


Fig. 1. Schedule of trappings in oak-hornbeam stands of the Niepolomicka Forest. 1 — »Standard Minimum« trappings on a 5.76 ha plot, 2 — trappings on 2.25 ha plots, 3 — trappings on trap-lines.

likelihood (Zippin, 1956; Janion, Ryszkowski & Wierzbowska, 1968) they were regarded as resident population. Due to migration the animals captured at a later time might not constitute a representative sample for the population age structure. The numbers from the trap-line were also estimated by means of a regression equation. The density was determined in relation to the area controlled by the trap-line, which was calculated by multiplying the length of the trap line by the radius of the home range (Golley *et al.*, 1965). The latter value was assumed as 20 m for the bank vole (Naumov, 1961), and 27 for the field mouse (Brown, 1956).

During five consecutive years 24 sections of age structure and estimates of animal numbers in particular age classes were obtained. On this basis (Bobek,

1969) the mortality was calculated, as well as life tables were constructed and survivorship curves were drawn (Deeves, 1947). For those months, in which no trappings were carried out, the animal numbers were extrapolated assuming that mortality in age classes between two consecutive samples occurs at the exponential rate. In the period of reproduction the number of newborn was estimated separately for each month (Bobek, 1969). Also the number of young animals staying in nests up to 18 day of life was estimated for this period. It was assumed that mortality in the age 0—1 month is also exponential. By adding this value to the number of trappable individuals (N_{tr}) it was possible to obtain the dynamics of all rodents (N_b), i.e. both trappable and staying in the nests. In effect, both the general numbers and the age structure of the population were obtained in month intervals for a few years period.

Table 1

Number of small rodents according to species, as trapped in oak-hornbeam stands of the Niepołomicka Forest in the years 1966—1971.

Year	<i>C. glareolus</i>	<i>A. flavicollis</i>	<i>A. agrarius</i>	<i>P. subterraneus</i>	<i>M. agrestis</i>	<i>M. avellanarius</i>	Total
1966	23	26	7	—	—	—	56
1967	1375	408	205	8	8	—	2204
1968	136	44	—	3	—	—	183
1969	350	296	12	1	—	3	662
1970	307	99	9	—	—	—	415
1971	75	48	2	—	—	—	125
N	2266	921	235	12	8	3	3445
%	65.9	26.7	6.8	0.3	0.2	0.1	100.0

All the calculations on the dynamics of numbers were made for two dominant species, i.e. bank vole and field mouse. The remaining rodents were added up on the basis of their percentage share in the total numbers of all rodents. The net production was estimated by means of Allen's method (1950) employing growth-survivorship curves.

III. RESULTS

1. Dynamics of Rodent Numbers

The dynamics of rodent numbers was investigated accurately on the basis of the data from the years 1967—1971 which included four full year cycles stretching from spring to the next year spring. During this period there occurred the mass appearance of rodents followed by three years of reduced numbers. These fluctuations were caused mainly by the population of bank voles dominating in respect of numbers. The year of mass occurrence 1967/68 was characterized not only by very high numbers but also by altered seasonal dynamics in comparison with the remaining years. The reproduction of voles began very early. In April

at the density of 60.5 rodents per ha as much as 67% of vole and mouse females were already pregnant or lactating. This caused a fast rise in the number of both populations which reached the maximum already on the turn of May and June (86.7 individuals/ha) — Fig. 2. Then the inhibition of reproduction occurred being associated with the increased mortality, and in July only 14.5% of females were reproducing while the density decreased to 65.4 rodents per ha (Babińska & Bock, 1969). In October the number of rodents was reduced to 34.5/ha, and in late spring of the next year it reached barely 5.5 individuals/ha. Hence the density was almost 16 times lower than in the corresponding period

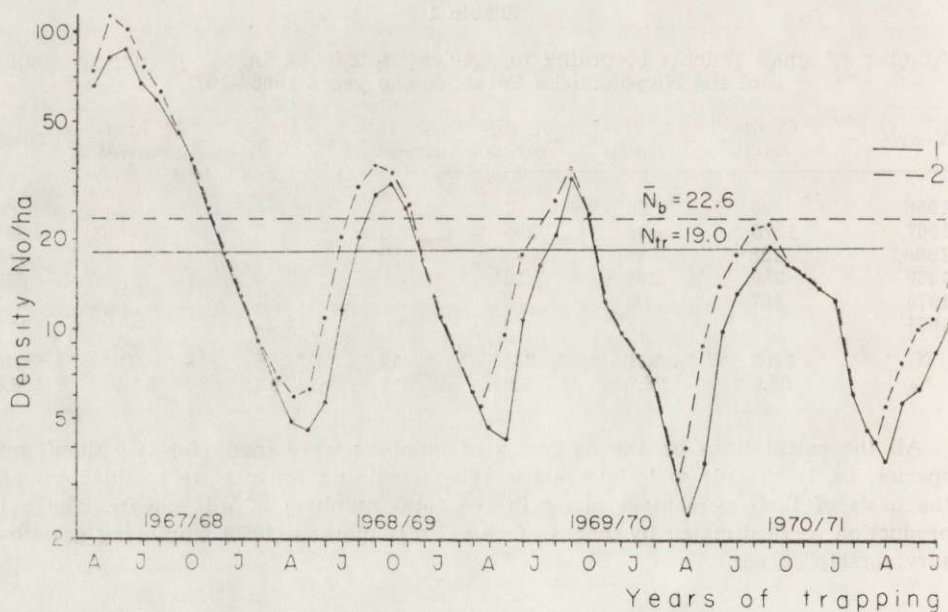


Fig. 2. Dynamics of numbers of small rodents in oak-hornbeam stands of the Niepołomicka Forest in the years 1967—1971.

1 — trappable rodents (N_{tr}), 2 — all rodents, *i.e.* trappable and staying in nests (N_b), horizontal lines show mean densities for the whole period.

of the previous year. In subsequent years (1968—71) it was found that the populations of both rodent species rebuilt their numbers reaching the average density level without such drastic changes of numbers in the year cycle. The lowest density in normal years was reached by these populations usually at the end of winter before breeding season. Later the density increased gradually to the maximum in September or October. Hence in these years the density peak corresponded to early autumn, whereas at the mass occurrence it was observed already in late spring.

For each year the mean density of trappable rodents (N_{tr}) was estimated as the weighted mean from April till April. This value was the highest in the first year of investigations and amounted to 39.8 individuals/ha. In subsequent years the dynamics of numbers showed a decreasing trend. The mean density in 1968/69 was reduced to 14.2 animals/ha, and in next year to 11.1 ha. The lowest value of 10.3 animals/ha was recorded in the last year. The amplitude of numbers change in four consecutive years was thus very high and the year of mass occurrence (1967—68) exceeded by four times the mean density in the last year of study (1970/71) (Fig. 2).

Such drastic changes in the density of all rodents were reflected in the fluctuation of numbers of the bank vole population. The mass occurrence in the first year of studies concerned mainly bank voles, the density of which amounted in this year to 32.1/ha (Table 2). In the subsequent years the numbers of voles decreased and was comprised within 7.2—10.2/ha (Table 2, Fig. 3).

Table 2

Mean year densities (No/ha) of the populations of small rodents in oak-hornbeam stands of the Niepołomicka Forest.

	Species	1967/68	1968/69	1969/70	1970/71	Avg 1967—71
\bar{N}_{tr}	<i>C. glareolus</i>	32.1	10.2	7.2	8.1	14.4
	<i>A. flavicollis</i>	5.9	3.7	4.3	2.0	4.0
	All rodents	39.8	14.2	11.8	10.3	19.0
\bar{N}_b	<i>C. glareolus</i>	37.0	12.8	8.8	9.8	17.1
	<i>A. flavicollis</i>	7.0	4.4	5.2	2.4	4.8
	All rodents	46.1	17.5	14.3	12.4	22.6

The mean density of trappable field mice was in all years lower (1.6—5.4 times) from the corresponding numbers of bank voles. In the first year of study the mean density of mice was estimated as 5.7 individuals/ha, in the next year as 3.7/ha (Table 2). Then the population of field mice again increased in numbers to 4.3 individuals/ha in 1969/70. In September of that year the numbers of field mice were the highest for the whole year cycle and reached 17.9/ha. These numbers were not only higher than voles in this month but also exceeded the highest density of mice in the first year of mass occurrence (Fig. 3).

During four years in the population of voles only one peak of density was observed followed by three years of normal (low) density. On the other hand, field mice showed two increases in their numbers, although less pronounced. However, the rise of the population of field mice in

1969 showed different features than in 1967 — without intensive reproduction in spring and with the maximum numbers in September. The mean density for the whole first year of studies was higher from the mean figure for 1969 (Table 2), and finally in spring 1968 the depression of numbers was deeper from the corresponding one in 1970. For this reason only the rise of mouse density in 1967 was assumed as typical for the mass appearance.

For the whole period of studies (1967—71) the mean density of all trappable rodents, estimated as the weighted mean for consecutive years,

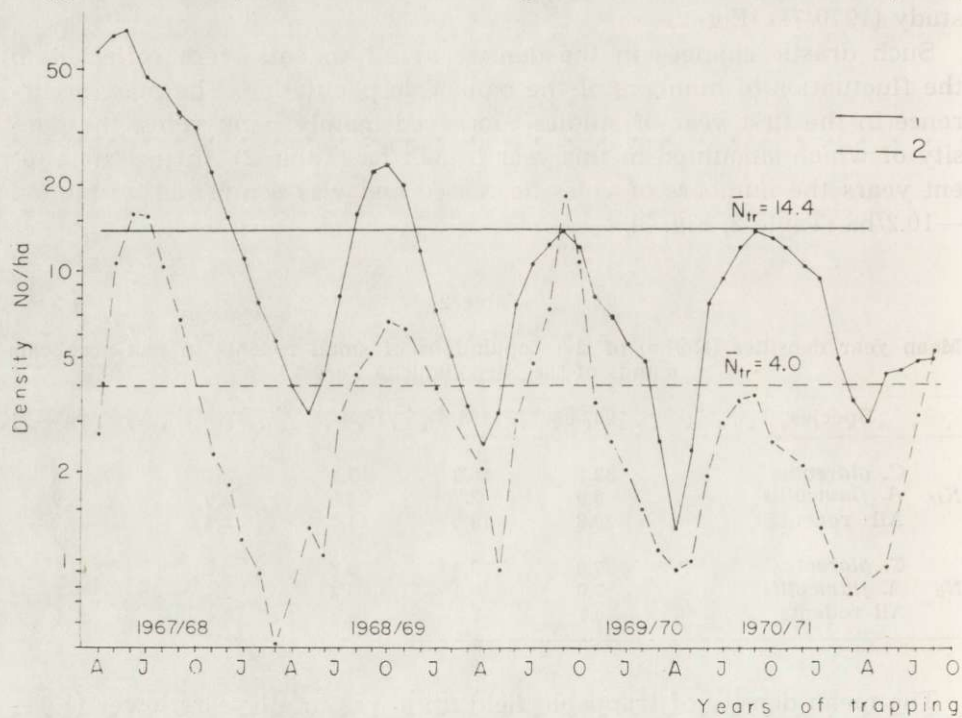


Fig. 3. Dynamics of numbers in the population of bank voles (1) and field mice (2) in oak-hornbeam stands of the Niepołomicka Forest. All values refer to trappable animals (semilogarithmic scale). Horizontal lines show mean densities of trappable rodents during the whole period of investigations.

amounts to 19.0 individuals/ha. This value includes 14.4/ha of voles and 4.0/ha of mice. The remaining 0.6/ha falls for striped field mice, pine voles, field voles and scarce common dormice. These data represent trappable animals without young staying in nests up to 18 days of life. After taking this into consideration (cf. part II) it was found that the mean density of all rodents ($N_b = \text{trappable} + \text{staying in nests}$) is equal to 22.6/ha. The corresponding figures for bank voles and field mice are

Table 3

Life tables for the population of bank voles and field mice.

 l_x — number of animals surviving to the beginning of a given age interval, d_x — number of animals dying in a given age,100 q_x — mortality rate in per cent, e_x — expected further length of life.

The data are grouped for the year of mass appearance 1967/68 (A) and for the years of low density 1968–71 (B).

Age, months	l_x		d_x		100 q_x		e_x	
	A	B	A	B	A	B	A	B
<i>C. glareolus</i>								
0— 1	100.0	100.0	49.5	47.1	49.5	47.1	2.2	2.6
1— 2	50.5	52.9	20.3	15.1	40.2	28.5	2.8	3.6
2— 3	30.2	37.8	8.5	7.4	28.3	19.7	3.3	3.8
3— 4	21.7	30.4	3.1	6.3	14.2	20.7	3.5	3.6
4— 5	18.6	24.1	2.4	2.7	13.0	11.1	2.9	3.4
5— 6	16.2	21.4	3.6	7.3	22.3	34.1	2.3	2.8
6— 7	12.6	14.1	4.2	4.9	33.3	35.0	1.8	3.0
7— 8	8.4	9.2	4.0	1.5	47.3	15.9	1.5	3.3
8— 9	4.4	7.7	2.4	2.4	55.6	30.7	1.5	2.8
9— 10	2.0	5.3	1.1	1.3	56.8	24.7	1.6	2.9
10— 11	0.9	4.0	0.4	1.1	43.8	29.4	1.9	2.7
11— 12	0.5	2.9	0.2	0.8	32.9	27.2	2.1	2.5
12— 13	0.3	2.1	0.1	0.4	30.3	19.3	2.2	2.3
13— 14	0.2	1.7	0.07	0.7	33.6	40.0	1.8	1.8
14— 15	0.13	1.0	0.05	0.3	38.4	33.0	1.6	1.7
15— 16	0.08	0.7	0.04	0.4	45.9	53.2	1.4	1.1
16— 17	0.04	0.3	0.02	0.15	48.8	50.0	1.2	1.0
17— 18	0.02	0.15	0.01	0.07	59.0	48.0	1.0	0.9
18— 19	0.02	0.08	0.01	0.08	100.0	100.0	0.5	0.5
<i>A. flavicollis</i>								
0— 1	100.0	100.0	36.7	38.4	36.7	38.4	2.4	3.3
1— 2	63.3	61.6	20.2	16.6	31.8	26.9	2.5	4.1
2— 3	43.1	45.0	14.1	3.6	32.7	8.0	2.4	4.4
3— 4	29.0	41.4	10.3	6.0	35.6	14.6	2.3	3.8
4— 5	18.7	35.4	7.5	13.5	40.3	38.3	2.3	3.3
5— 6	11.2	21.9	4.1	5.4	36.3	24.9	2.5	4.4
6— 7	7.1	16.5	1.9	1.7	26.2	10.4	2.7	4.2
7— 8	5.2	14.8	1.4	3.0	26.2	20.0	2.3	3.5
8— 9	3.8	11.8	1.2	2.4	30.8	20.4	2.3	3.5
9— 10	2.6	9.4	0.9	2.2	35.3	23.0	2.1	3.2
10— 11	1.7	7.2	0.3	1.9	20.8	27.2	1.9	3.1
11— 12	1.4	5.3	0.3	0.9	20.8	16.4	1.3	3.0
12— 13	1.1	4.4	1.1	0.6	100.0	14.3	0.5	2.5
13— 14		3.8		0.9		24.7		1.9
14— 15		2.9		1.7		58.6		1.3
15— 16		1.2		.05		38.7		1.5
16— 17		0.7		0.3		47.4		1.3
17— 18		0.4		0.2		48.0		1.0
18— 19		0.2		0.2		100.0		0.5

17.1 and 4.8 individuals/ha. This means that the numbers of all rodents exceeds by 18.9% the number of trappable rodents; the relevant figures for voles are 18.7% and for mice 20.0% (Table 2). The calculations presented above on the density estimates neglect the range of trapping plot and hence may be in fact slightly overestimated.

2. Survival

The curves deciding on the dynamics of numbers were drawn from life tables (Deevey, 1947) in which one month was assumed as the unit of time (Table 3). The survival of rodents depends considerably on the

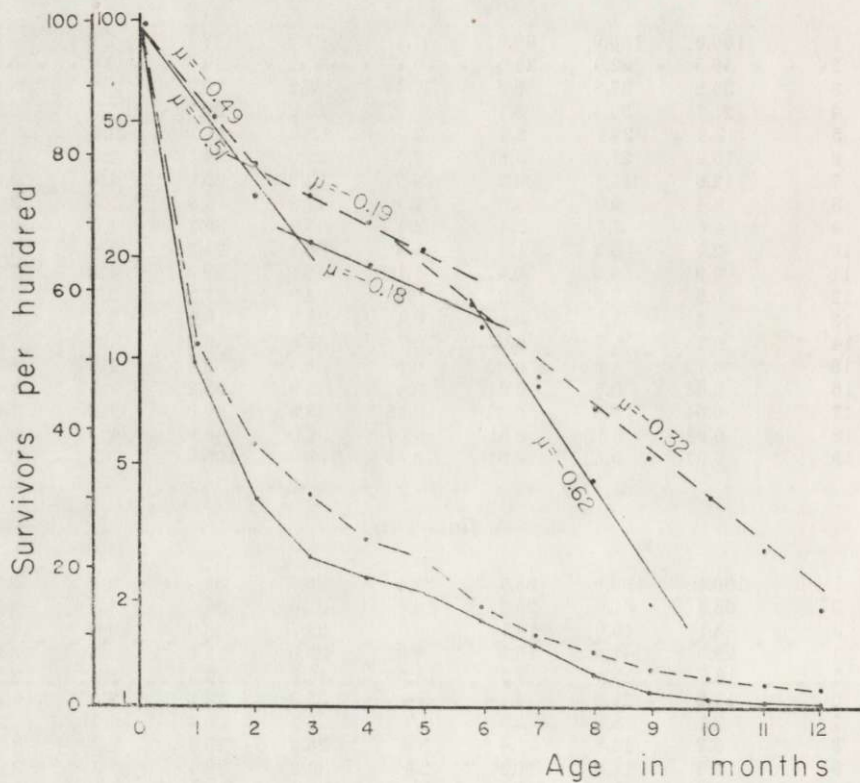


Fig. 4 A.

population density (Bobek, 1969; Tupikova & Konovalova, 1971), hence the whole material was divided into two parts. The first one (A) includes the data of the year of mass occurrence (1967/68), while the second one (B) contains the material of the three remaining years (1967—71). On this basis life tables were constructed treating separately the two dominating species, *i.e.* bank vole and field mouse.

Among 100 voles born in the year of mass occurrence 50.5 reached the age of one month (Table 3), 12.6 the age of six months, and only 3 survived for the whole year. In the same year field mouse showed a slightly better survival than vole. The age of one month reached 63.3 mice, six months — 7.2 mice, and one year — 1.6 animals (Table 3). However, a considerably better survival was shown by the two species in subsequent years at low densities of their populations. Almost 53 per cent of voles and 62 per cent of mice reached than the age of one month, while up to six months lived 14.1 voles and 16.5 mice, and up to one year nearly two voles and over four mice. Due to this the mean life span of

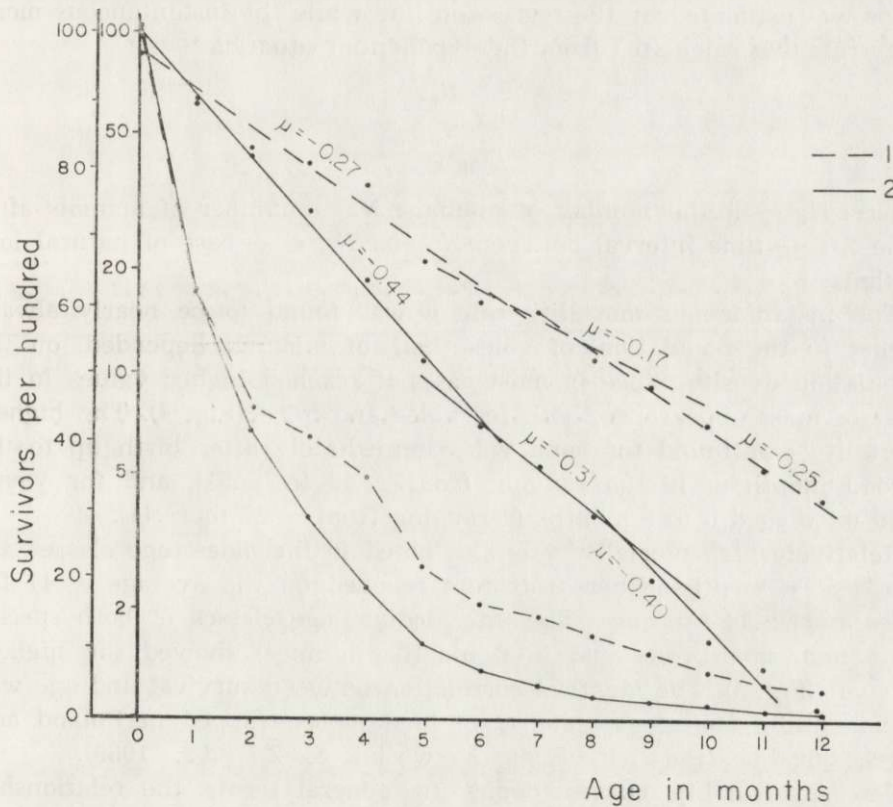


Fig. 4 B.

Fig. 4. Curves of survival of bank voles (A) and field mice (B) in the year of low density (1968—71) — (1), and in the year of mass appearance (1967/68) — (2). They are drawn in a linear scale with logarithmic values at one side (where the instantaneous mortality rate μ is given).

these species, read off from Table 3, was shorter in the year of mass appearance by 18—37%. In such year voles lived on the average 2.2

months and mice 2.4 months. On the other hand, in normal years the mean life span was longer and for voles amounted to 2.6 and for mice 3.3 months. Hence the survival in the years of low density was significantly better. Independently of population density field mice lived always longer than bank voles.

After plotting the values from column l_x of life tables (Table 3) the survivorship curves of bank voles and field mice are obtained (Fig. 4). They were drawn in linear scale, and additionally in semi-logarithmic scale, which shows better the relationship between survival and age. Each of these curves exhibits three segments differing in the slope. The slope was estimated by the regression line while the instantaneous mortality rate was calculated from the exponential equation:

$$\mu = - \frac{\log \frac{N_t}{N_o}}{t \log e} \quad (2)$$

where: N_o — initial number of animals, N_t — number of animals after time t , t — time interval between N_o and N_t , e — base of natural logarithms.

The instantaneous mortality rate μ was found to be nearly always higher in the population of voles than of mice. It depended on the population density, since in most cases it reached higher values in the year of mass appearance, both for voles and mice (Fig. 4). The highest mortality was found for bank voles immediately after birth up to the second month of life (μ ranging from $-.49$ to $-.51$), and for young field mice aged 0 to 5 months (μ ranging from $-.27$ to $-.44$).

Relatively high mortality was also noted in the oldest age classes, *i.e.* above 6–8 months, where this rate reached on the average $-.47$ for voles and $-.32$ for mice. The intermediate age classes of both species (2–6 months in voles and 5–8 months in mice) showed the highest survival (Fig. 4). The identical correlation between survival and age was found on the numerous material of bank voles trapped in Poland and Czechoslovakia (Pucek, Ryszkowski & Zejda, 1969).

The survivorship curves depict in general terms the relationship between age and survival. More information on this subject can be gained by analysing mortality rate ($100 q_x$) in consecutive age classes. Such relative rates for the populations of voles and mice in the years of low density (1968–1971) are drawn in Fig. 5. The curves are based on the large material of 868 voles and 487 mice and show a similar course for both species. They begin with a high mortality in the youngest age classes, which is especially related to the period when animals leave the nests. Immediately afterwards a conspicuous decrease of mortality

occurs, falling usually for the period of late summer and early autumn. A rise of mortality occurs again in the period when the rodents enter wintering. Then the mortality is rather high and constant. A drastic decrease of survival takes place in the age of 12—18 months and it corresponds to death of overwintered animals from early summer till the beginning of next winter. The life tables described here were elaborated jointly for all cohorts.

In the years of mean density the reproduction of voles and mice continues for 7—8 months, but in late spring and early summer (during 3—4 months) as many as 75—80% of all young are born (cf. part 4;

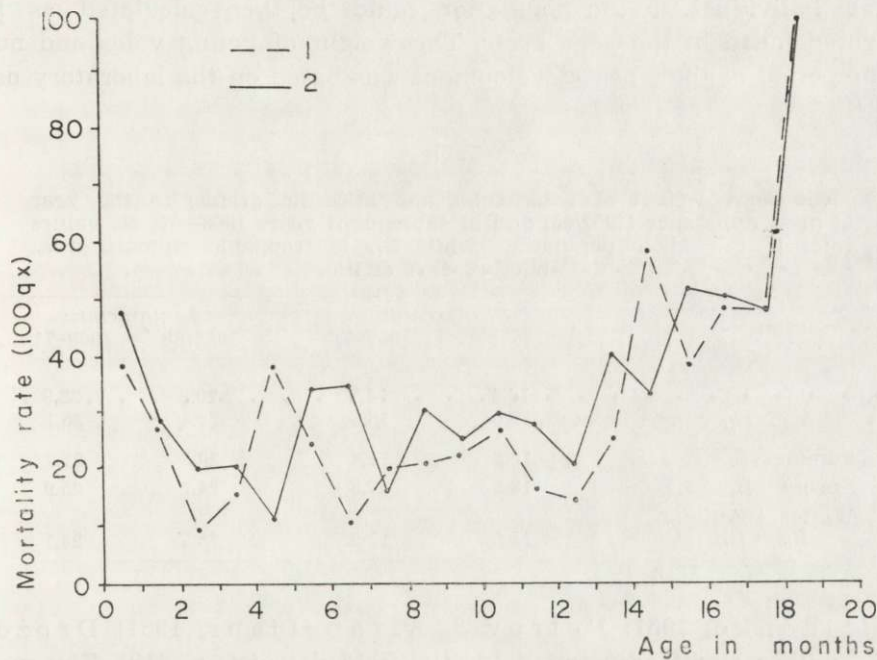


Fig. 5. Changes in the mortality rate $100 q_x$ with the age of field mice (1) and bank voles (2) in the years of low density in their populations (1968—71).

Table 6). Hence Fig. 5 depicts rather seasonal-age functions than age functions alone. On the example of the population of bank voles normal years 1968—71 also the survival of young animals (0—1 month) in consecutive cohorts was calculated. Among voles born in spring months (April—May) the mortality reaches 40% within the first month of life. The lowest mortality (32%) was found for summer litters (June, July and August), and the highest (69%) for rather scarce generations born in late summer and early autumn (September, October).

3. Mean Body Weight and Individual Growth Curves

Estimates of the mean body weight in a rodent population are usually slightly exaggerated since they do not include young animals staying in nests, and since the winter data are usually lacking, when most rodents decrease their body weight (Pokrovskij, 1966; Tanton, 1969).

In order to avoid this error the age structure for each month was calculated from 24 population sections, but separately for the year of mass appearance and for the remaining years. Then the number of individuals in each age class was multiplied by their body weight obtaining in this way a range of products for each month. The mean body weight of an individual in the population could be then calculated as the weighted mean in the year cycle. The weight of young voles and mice in the period of their nest development was based on the laboratory data

Table 4

Mean body weight of bank voles and mice (in grams) in the year of mass appearance (1967/68) and in subsequent years 1968—71. B_b values refer to the whole population, while B_{tr} to trappable animals, i. e., above 18 days of life.

Season	<i>C. glareolus</i>		<i>A. flavicollis</i>		
	1967/68	1968-71	1967/68	1968-71	
All year	B_b	16.4	14.7	20.8	22.9
	B_{tr}	18.0	16.6	24.4	25.1
Summer	B_b	16.5	14.4	20.3	21.1
Spring	B_{tr}	18.5	17.3	24.2	25.9
Winter + Autumn	$B_b = B_{tr}$	15.6	15.2	25.7	24.1

(Sviridenko, 1951; Petrov & Airapetjans, 1961; Drożdż, 1965), with a slight adjustment for the field data (cf. p. 419). The mean weights of voles and mice obtained in this way represent the whole population (B_b), or only its trappable part (B_{tr}). These values are presented as year means, average for period of spring-summer and autumn-winter (Table 4).

The mean body weight of all animals in the population is lower by 1.7—17.3% from the mean weight of trappable animals. From the analysis of mean values it may appear that in the year of mass occurrence the growth rate of rodents was better than at the low population density. However, when the material is separated for the animals born in a given year and for overwintered animals it appears that young voles were growing more slowly at a higher population density. The mean

body weight of voles born in 1967 reached 13.2 g, and those born in subsequent years — 14.5 g. The corresponding values for field mice in these periods are 17.8 and 20.6 g, respectively. It can be concluded that the mean weight in the year of mass occurrence was augmented by the presence of large overwintered animals, which were numerous in this year.

In normal years the mean weight of all voles and mice was the lowest in summer (Table 4). Young and small animals (some of them still staying in nests) prevail in the population, while heavy overwintered animals have already perished. Among trappable part of the population in normal years the mean body weight of an individual in summer is higher than in winter and than the year mean. This is caused mainly by a decrease of body weight in winter (Table 5). In different cohorts of animals born in a given year the process of body weight loss begins already in

Table 5

Winter depression of body weight of bank voles in different generations estimated on the basis of materials collected in the years 1968—1971. All values are given in grams, pregnant females are omitted.

Months	Month of generation birth		
	August	June — July	May
October	18.0	17.5	20.1
November	14.2	15.5	17.2
December	14.2	15.3	16.5
February	13.9	15.2	17.8
March	16.7	18.7	19.9
April	19.6	22.3	21.0

October and proceeds in subsequent months. In younger animals born in summer a significant body weight loss is observed till November, and later it becomes very small. In the animals from the spring cohort the body weight loss occurs from October till December, and the increase of weight begins already in February. Hence younger animals show smaller body weight loss than those from older cohorts. The voles born in August lose on the average 7.3% of body weight, while those born in June — July and May lose 12.0 and 17.9% of their autumn weight. In early spring (March, April) the animals in all cohorts rebuild and exceed their autumn body weight. Similar fluctuations in the body weight were also observed in field mice, but they were less distinct.

In effect of the described phenomena the mean body weight of voles and mice changed in the year cycle (Fig. 6). The trappable animals in both populations were the heaviest in early spring and in full spring.

The mean weight of all individuals in the population (B_0) differed from the trappable part (B_{tr}) in the period of reproduction (April—October) and reached the lowest values in late spring.

The collection of data on the body weight of voles and mice in different age permitted to draw the mean growth curves for these animals in the year of mass occurrence and in the remaining years. These curves represent weighted means summing up all generations (cohorts) and all

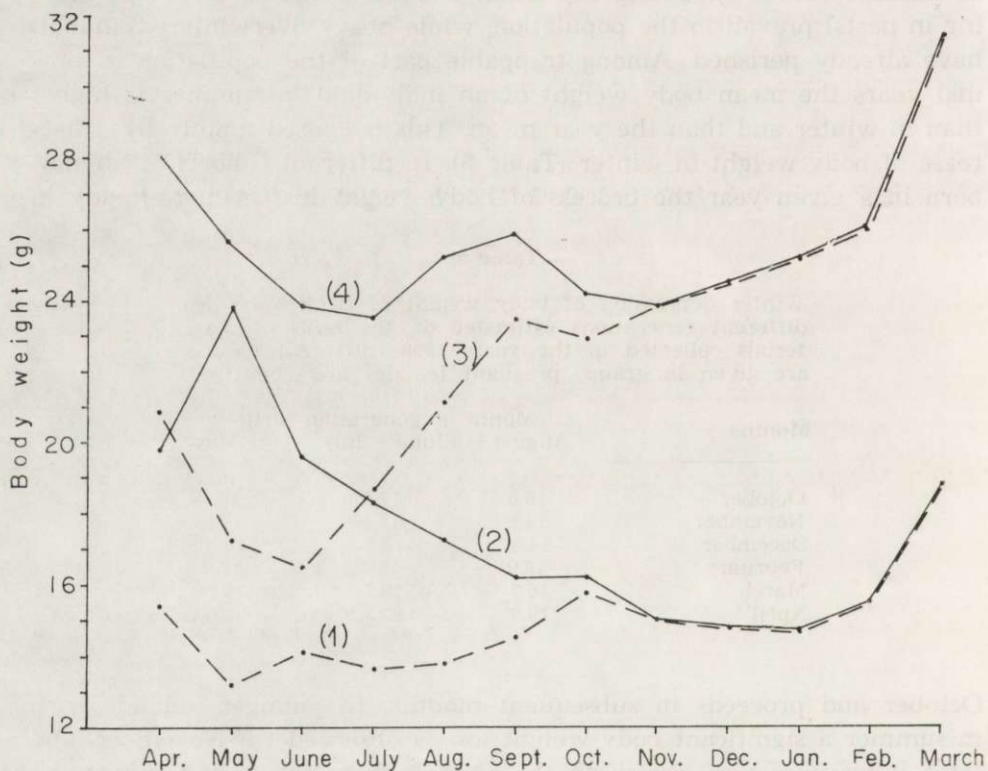


Fig. 6. Seasonal changes of the mean body weight in the populations of bank voles (1, 2) and field mice (3, 4) in the years of low density. Continuous lines concern trappable individuals, and broken ones — the whole population, *i.e.* trappable individuals and those staying in nests (full circles).

seasons. The growth rate of young animals depends on the period in which they were born. For example in a normal year the voles born in spring reach 18 g body weight in the age of one month, while those born in summer have less than 14 g in the same age, and those from September — only 12 g. The beginning of growth curves is based on the data obtained in the laboratory and in open-air pens, according to

which the newborn bank voles have 1.6—1.7 g (Petrov & Airapetjans, 1961; Drożdż, 1965; Sawicka-Kapusta, 1973), and field mice 2.3 g (Sviridenko, 1951). In the laboratory wild rodents grow usually faster than during nest development in the field. For this reason the weights of voles and mice till 18 days of life were taken from the laboratory data but after decreasing them by the per cent of difference between the weight of animals aged one month and

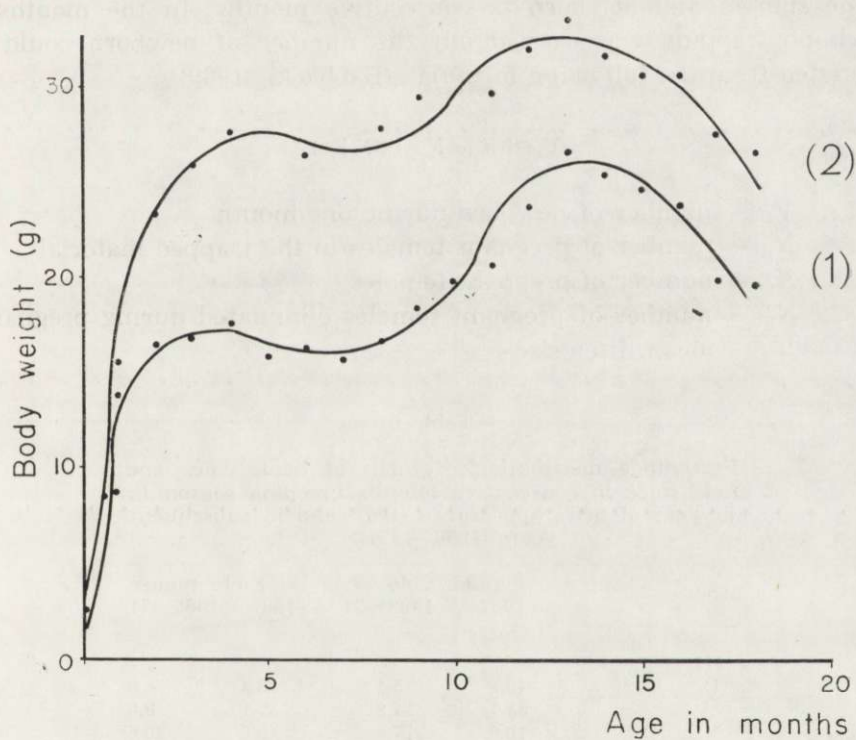


Fig. 7. Individual growth curves of bank voles (1) and field mice (2) based on the material from the years 1968—71.

growing in the laboratory in comparison with those from natural habitats. In the year of mass appearance at the moment of nest leaving (18 days) the weight of voles should be 7.3 g and mice 8.3 g, while that of one month old animals 12.1 and 14.8 g, respectively. Growth of both species was considerably better in normal years, because at the age of 18 days the weight of voles was 8.3 g and mice 9.1 g, while one month old animals reached 13.7 and 15.4 g. The growth curves analysed on the example of normal years (Fig. 7) show a biphasic character. On the average up to the fourth month the growth of voles and mice is fast.

During wintering growth is inhibited, the animals decrease their body weight. In early spring both voles and mice again grow fast until 13 months of life. Then the second considerable decrease of body weight is observed accompanied by a high mortality.

4. Reproduction

The total number of voles and mice born during a year was estimated as the sum of animals born in consecutive months. In the months in which no trapping was carried out the number of newborn could be calculated from the following formula (Bobek, 1969):

$$V_t = [(N_p - N_{pe}) + N_l] \times \bar{L} \quad (3)$$

where: V_t — number of newborn during one month
 N_p — number of pregnant females in the trapped material
 N_l — number of pregnant females
 N_{pe} — number of pregnant females eliminated during pregnancy
 \bar{L} — mean litter size

Table 6

Percentage distribution of birth of bank voles and field mice in consecutive months breeding season in the year of mass appearance (1967) and in subsequent years (1968—1971).

Month	Bank vole		Field mouse	
	1967	1968—71	1967	1968—71
III	—	—	—	1.1
IV	43.9	5.1	36.4	8.9
V	33.1	14.2	37.1	9.0
VI	10.6	17.3	15.6	20.6
VII	11.4	23.5	10.9	18.3
VIII	0.4	24.5	—	18.2
IX	0.5	12.3	—	18.3
X	—	3.1	—	5.5
Total	99.9	100.0	100.0	99.9

For the months without trappings V_t was estimated on the basis of age structure of adult animals and previously constructed life tables (cf. Results, part 2). According to such estimates in the year of mass occurrence 1030 voles and 193 mice should be born on the trapping plot (5.76 ha). Most of young voles and mice (87.6 and 89.1%) were born in the period April-June (Table 4). In the next years the number of

born rodents decreased considerably. In the population of bank vole the values were rather constant and equal to 314 in 1968, 222 in 1969 and 261 in 1970. In the population of field mice the corresponding values reached in these years 105, 99 and 54 young animals.

In normal years the reproduction of both populations began usually in April and stopped by the end of September, or exceptionally in early October (Table 6). In the year of mass appearance the first pregnant females were trapped already in early March, while the reproduction was arrested already in July.

The mean litter size for the whole period of investigations was estimated as $4.86 \pm .94$ embryos in the population of voles and $5.66 \pm .94$ in the population of field mice. In voles this mean includes low values in the year of mass appearance (4.59 ± 1.16 embryos) and considerably higher ones in the year of low density ($5.37 \pm .54$). The mean values from these two periods are significantly different ($t=3.75$, $p<.02$). Similarly in field mice the mean number of embryos was significantly lower ($p<.05$) in the year of mass occurrence ($5.44 \pm .72$) than in subsequent years ($5.76 \pm .99$). Hence the differences in the litter size in particular years were more pronounced in voles. In the year of mass occurrence the mean number of embryos was in voles lower by 17% while in field mice by only 5.8%.

IV. DISCUSSION

1. Estimation of the Net Production

The net production (P_n) in the populations of bank voles and field mice was estimated in four consecutive years by means of Allen's method (1950). For this purpose the growth-survivorship curves were employed jointly with the number of animals born in a given year (Petrusewicz & Macfadyen, 1970). Fig. 8 shows such estimates for the population of bank voles and field mice in the year of mass occurrence. Starting from the sum of voles and mice born on the trapping plot, and then drawing their number in relation to the mean body weight in consecutive months of life, two areas (ABD and $A'B'D'$) were obtained representing net production in the discussed populations.

The net production of all rodents was the highest in the year of mass appearance when it reached 2691 g of biomass/ha. This value consisted mainly of production of bank voles (1977 g/ha) and field mice (560 g/ha). In the next year (1968) these populations of small rodents produced jointly 1168 g/ha, out of this 771 g/ha falling for voles and 369 g/ha for mice. In further years the production decreased in parallel

with the fall of population density, reaching 825 g/ha in 1969 and 755 g/ha in 1970. In these two last years bank voles produced 477 and 562 g/ha and field mice only 327 and 177 g/ha (Fig. 9).

On the average for the whole four year period the net production amounted to 1360 g/ha year (bank voles 947 g, field mice 366 g, remaining species 47 g). The production of biomass was computed for the energy values, multiplying it by caloric equivalents of rodent body given by Górecki (1965). The caloric value of voles and mice bodies is very similar and amounts on the average to 1.454 and 1.450 kcal/g of biomass.

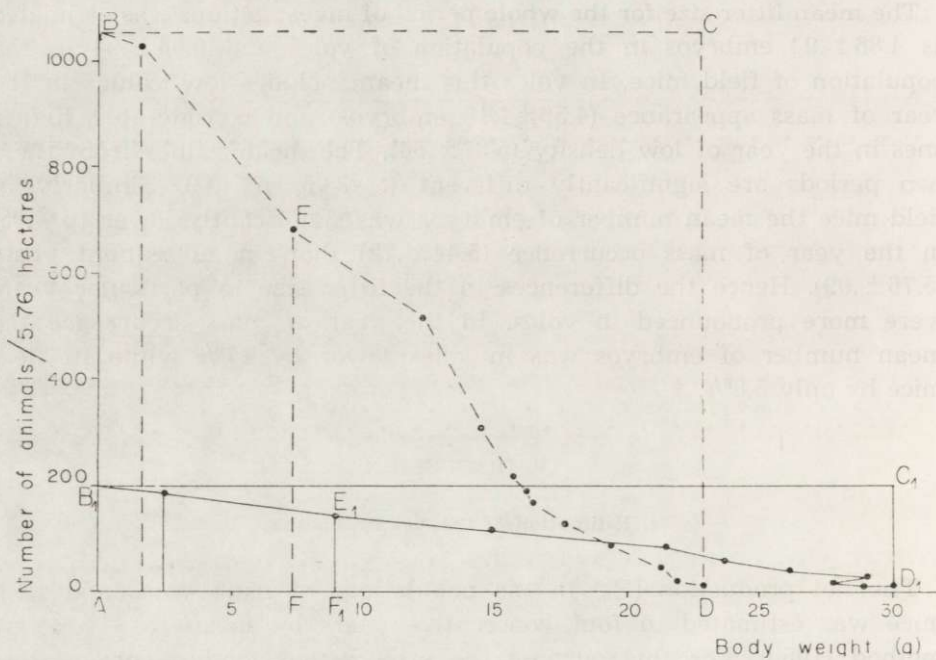


Fig. 8. Estimation of the net production in the population of bank voles (broken lines) and field mice (continuous line) in the year of mass appearance (1967/68). The curves of growth and survival were employed in the calculations, and all cohorts were cumulated. The areas of ABD and $A'B'C'$ represent total net production including production due to reproduction ($ABDF$ and $A'B'D'F'$) and production due to growth (EDF and $E'D'F'$). Two rectangles ($ABCD$ and $A'B'C'D'$) show the potential ability of production in these populations.

For the remaining rodents the caloric equivalent of striped field mouse was used: 1.636 kcal/g (Górecki, 1965). The production for the whole period of study computed in such way amounts on the average to 1983 kcal/ha year, including production of bank voles (1376 kcal/ha year), field mice (530 kcal/ha year), and the remaining rodent species 77 kcal/ha year).

Estimation of production by Allen's method permits to distinguish production due to reproduction (P_r) appearing during pregnancy and lactation, and production due to growth (P_g), which is realized during self-dependent life of individuals in the population (Petrušewicz & Walkowa, 1968) (Fig. 8). In consecutive years the proportions of these two parts changed only slightly. In the population of bank vole as much as 58% of production fell for P_r (13% correspond to production during pregnancy), and only 42% was formed during self-dependent growth of individuals. In the population of field mice production due to reproduction was slightly smaller and constituted 45%. Very similar

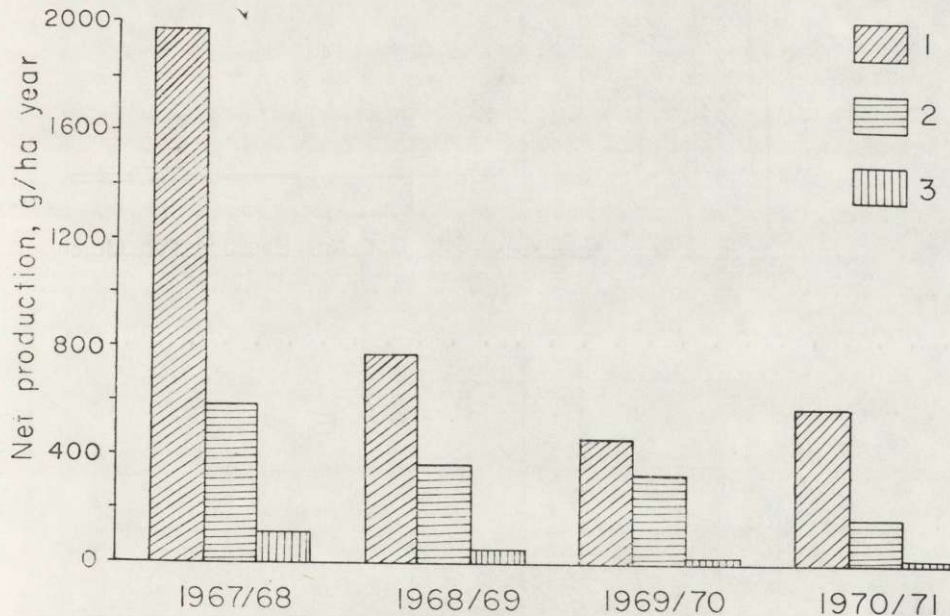


Fig. 9. The net production in the population of small rodents in a deciduous forest of *Tilio-Carpinetum* type during four consecutive years. 1 — bank voles, 2 — field mice, 3 — remaining species.

values were found previously for an open population of bank voles in beech forests (Bobek, 1969). A slightly modified proportion to the favour of growth ($P_g=49\%$) was reported for a population of voles isolated on an island (Petrušewicz *et al.*, 1968).

Estimation of production by the graphic method (Fig. 8) permits also for drawing the potential net production, which, however, is never realized totally. Due to considerable mortality only some rodents may

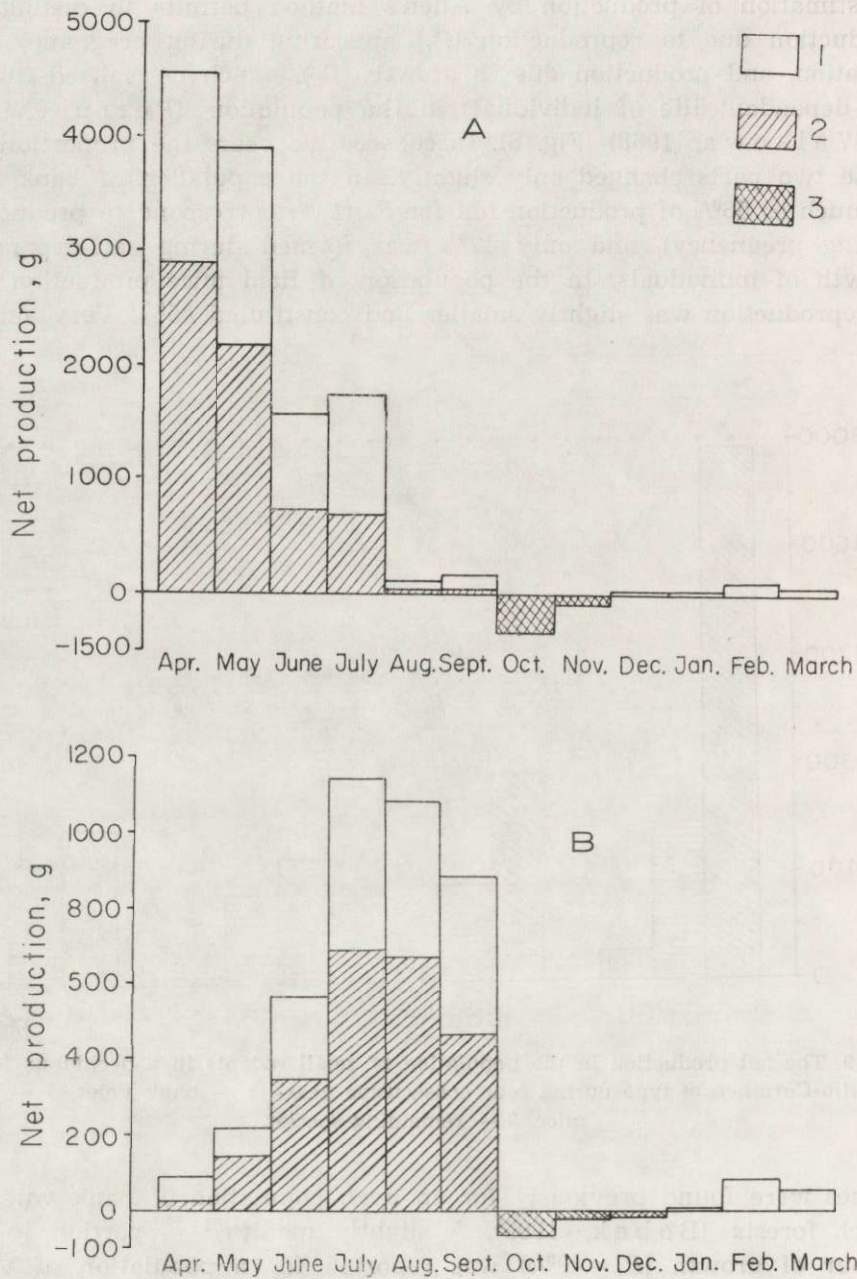


Fig. 10. Distribution of net production (g per 5.8 ha) in the populations of bank voles during the year of their mass appearance (1967/68) — A, and in the year of low density (1968/69) — B. 1 — production due to growth, 2 — production due to reproduction, 3 — negative production of growth.

reach maximum body weights during their life. For this reason the voles in the year of mass appearance realized only 44% of the potential production, and in years of low density — slightly more, *i.e.* 54.5% on the average. Also the population of field mice at a high density reached smaller percentage of such production (53.0%) in comparison with the years of low density (61.5%). This was because both growth and survival were worse in the year of mass appearance.

Intensive growth of young rodents in the period of pregnancy and lactation is responsible for the fact the period of reproduction in the population exerts a conspicuous effect on the distribution of production in consecutive months of the year. This has been presented on the example of bank vole population in the year of mass occurrence and in one year of a low density (Fig. 10). At the high density the reproduction of voles began in April and ended practically in July (*cf.* Results, part 4). In this period as much as 79.9% of the total annual production was formed, whereas in the corresponding period of the next year barely 49.8% of the total vole production was realized. In autumn and winter months the production of biomass is negligible, and in some periods is even negative due to body weight loss (Fig. 10).

2. Turnover

The value reached by production depends mainly on the turnover rate. Every population can be characterized by the turnover of individuals (Θ_N) and turnover of biomass (Θ_B). The latter is very difficult to empirical estimation and thus turnover of individuals is sometimes used for the calculation of the net production. The turnover of individuals depends on the mean life span in the population (\bar{t}) (Table 3):

$$\Theta_N = \frac{1}{\bar{t}} \quad (4)$$

where: \bar{t} corresponds to the mean life span, 1 is the unit of time in respect of which the mean life span is calculated. In the populations of both bank voles and field mice the turnover of individuals was found to be greatly dependent on density. At higher densities (year of mass appearance) the turnover was faster by 19.6—38.9% in comparison with the years of low density (Table 7). Independently of density the turnover was always higher in the population of bank vole.

A direct relationship between turnover of individuals and turnover of biomass is lacking (Petrušewicz, 1966; Petrušewicz & Macfadyan, 1970), hence the latter was calculated reciprocally from the

net production estimated by Allen's method:

$$\Theta_B = \frac{P_n}{\bar{B}} \quad (5)$$

where: P_n corresponds to net production, \bar{B} —mean biomass ($N_b \times B_b$) (Petrušewicz, 1967).

The relationship between turnover of biomass and population density is not as clear as in the case of turnover of individuals. In all cases the turnover of biomass is lower than turnover of individuals by 11 to 40% (Table 7). The data concerning turnover of individuals and

Table 7

Some parameters of estimation of the net production and efficiency of production in relation to respiration in populations of bank voles and field mice. All the data are given for the year of mass appearance (1967/68) and for subsequent years of low density (1968—1971).

Type of parameter	Bank vole		Field mouse	
	1967/68	1968-71	1967/68	1968-71
Density of all rodents	37.0	10.5	7.0	4.0
Turnover of individuals	5.5	4.6	5.0	3.6
Turnover of biomass	3.3	3.9	4.0	3.2
Net production kcal/ha year	2874	877	856	422
Net production Respiration $\times 100$	2.30	2.80	3.40	3.41

turnover of biomass are very similar to those found for the isolated population of bank voles on an island (Petrušewicz *et al.*, 1959) where they amounted to 4.73/year (Θ_N) and 3.76/year (Θ_B).

3. Production in Different Populations of Rodents

Production of rodents has been already investigated in a dozen or so forest and grassland ecosystems (Table 8). The studies concerned mainly populations of voles (*Microtus*, *Clethrionomys*) but also various mice (*Apodemus*, *Peromyscus*). The available data from the literature are listed in Table 8 in grams and in kilocalories.

The mean year net production of rodents in various types of forests (deciduous, coniferous, mixed) ranges from 1.1 to 2.2 kg of biomass/ha (Grodziński *et al.*, 1970; Pachinger, 1970; Grodziński, 1971; Petrušewicz *et al.*, 1972). The mean value for the oak-hornbeam stands of the Niepołomska Forest (1.4 kg) fits well into this range. The only described exception among forest ecosystems is re-

Table 8

Comparison of net production of small rodents in different ecosystems.

Ecosystem	Dominating rodent species	g/ha year	kcal/ha year	Authority
<i>Tilio-Carpinetum</i>	<i>C. glareolus</i>	1360	1983	This paper
Niepotomska Forest, Poland	<i>A. flavicollis</i>	(755—2691)	(1096—3910)	
<i>Tilio-Carpinetum</i>	<i>C. glareolus</i>	3017	4387 ¹	Petrusewicz et al., 1971
Masurian Lake Region, Poland		(2857—3265)	(4154—4747)	
<i>Quercus-Carpinetum</i>	<i>A. flavicollis</i>	2224 ²	3225 ¹	Pachinger, 1970
Bab. Czechoslovakia	<i>A. sylvaticus</i>			
<i>Fagetum carpaticum</i>	<i>C. glareolus</i>	1111	1670	Grodziński et al., 1970
Ojców, Poland	<i>A. flavicollis</i>	(469—2083)	(681—3024)	
Taiga forest	<i>C. rutilus</i>			
College, Alaska	<i>Tamiasciurus hudsonicus</i>	1667 ³	2500	Grodziński, 1971
	<i>M. oeconomus</i>	(400—5200)	(600—7800)	
<i>Piceetum myrtillosum</i>		825	1199 ¹	
Vitosha Mountain, Bulgaria	<i>C. glareolus</i>	(729—1338)	(1060—1338)	Petrusewicz et al., 1972
<i>Picea abies</i> plantation	<i>M. agrestis</i>	3147 ³	4720	
Bjornstorp, Sweden	<i>C. glareolus</i>	(2320—3973)	(3480—5960)	Hansson, 1971
Desert bushes (<i>Larrea tridentata</i>), San Simon Valley, Arizona	<i>Dipodomys merriami</i>	3959 ³	5740	Chew & Chew, 1970
Old field community (<i>Poa compressa</i>) Okemos, Michigan.	<i>Lepus californicus</i>	3774 ³	5170	Golley, 1960
Old field community Savannah River, S. Carolina	<i>M. pennsylvanicus</i>	600 ³	1200	Odum, Connell & Daveport, 1962
Alpine meadows (<i>Calamagrostis arundinacea</i> , <i>Poeta-Deschampsietum</i>) Bieszczady, Poland	<i>Peromyscus polionotus</i>	650	955	Grodziński et al., 1966
Cultivated field Turew, Poland	<i>P. subterraneus</i>			
	<i>M. agrestis</i>			
	<i>M. arvalis</i>	22752 ³	33427	Trojan, 1969

C. — *Clethrionomys*, A. — *Apodemus*, P. — *Pitymys*, M. — *Microtus*.¹ Computed for kcal utilizing the values reported by Górecki (1965), ² Data computed from the mean »standing crop«, ³ Computed reciprocally from caloric values.

presented by the population of bank voles isolated on an island, which produced twice as much (Petrušewicz *et al.*, 1971). A significantly higher production is reached by rodent populations in some grassland ecosystems, especially those with the secondary succession of plants. On the old or afforested fields (Golley, 1960; Hansson, 1971), as well as in desert bushes (Chew & Chew, 1970) the populations of rodents produce 3.1 to 4.0 kg/ha year. Considerably lower production of rodents (.6 to .7 kg/ha year) was noted only on dry old field and meadows in mountains (Odum, Connell & Davenport, 1962; Grodziński *et al.*, 1966).

Production in the population of field vole (*M. arvalis*) deviates considerably from all the reported data since in the cultivated field it can reach 22.8 kg/ha year (Trojan, 1969). This occurred, however, in the year of mass appearance of voles, and moreover, the production was estimated in a slightly different way.

Some of the discussed rodents consume mainly green plants (*Microtus*) while others prefer seeds (*Apodemus*, *Peromyscus*, *Tamiasciurus*) or utilize mixed food (*Clethrionomys*). It appears that populations of »grazing« rodents can reach higher production than those consuming seeds. In all rodents, however, the efficiency of net production from one ha is several times lower than for example in cattle.

Table 8 gives not only the mean year production but also fluctuations in a few year cycle for some populations of rodents. It is clear that these fluctuations are considerable. In the deciduous forest studied here the production in consecutive years differed by a factor of 3.6. In a mixed forest the observed difference was 4.5 times (Grodziński *et al.*, 1970), and in a coniferous forest as much as 13 times (Grodziński, 1971). This is possible due to marked fluctuations in the rodents numbers, such as observed in the present study. The increase in the number of voles and mice in a forest is often related to the tree-seeds crop, which constitute favourite food for these animals (Grodziński & Sawicka-Kapusta, 1970). The abundant fall of acorns may stimulate winter reproduction of voles and mice (Smyth, 1966), and additional food accelerates their reproduction in spring, and may prolong it as well (Watts, 1970). In the studied oak-hornbeam forest an abundant crop of acorns was observed in autumn 1966 amounting to 1305.3 kg of dry mass/ha (Bandoła, unpubl. data). This fact can explain very early reproduction of voles and mice in the next spring and their high density in 1967 (Fig. 3). The decrease of this mass appearance cannot be related, however, to the lack of food available for rodents, since food is always in a great excess (Grodziński, 1963; Drożdż, 1966).

The net production constitutes only a small proportion in the balance

of energy flow through a population of rodents (Ryszowski & Petruszewicz, 1967; Grodziński *et al.*, 1970). Its estimation, even at known population numbers, is very difficult and time consuming, as witnessed by the present study. Utilizing daily functions of energy budgets of the bank vole and field mouse (Grodziński *et al.*, 1970)

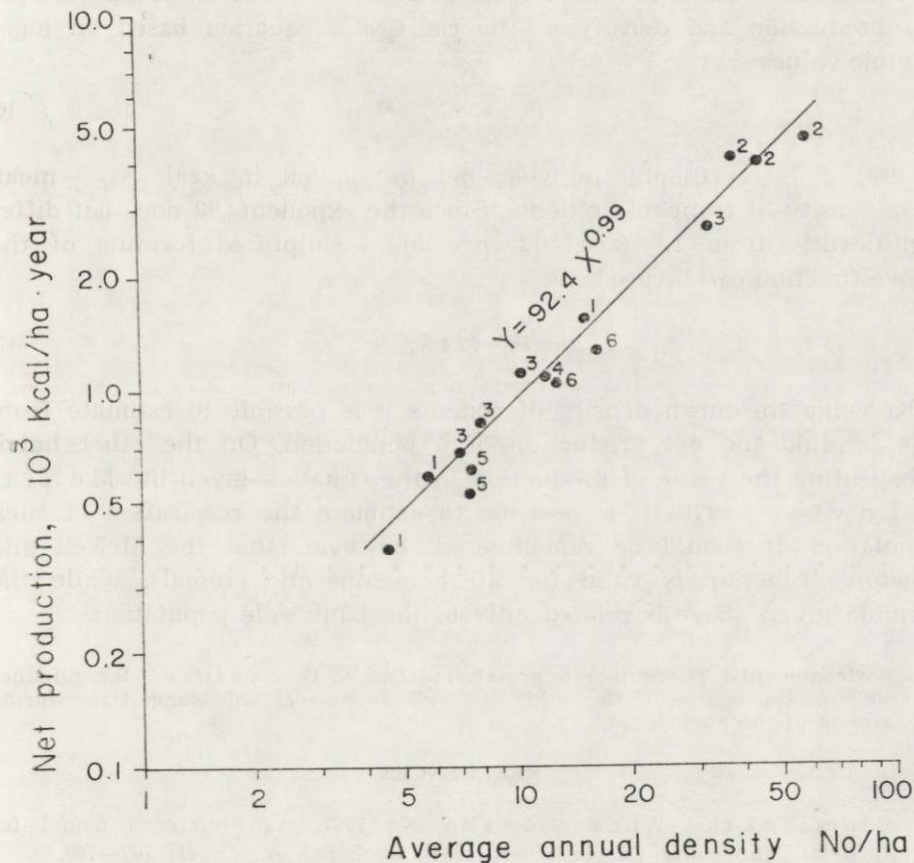


Fig. 11. Relationship between net production of bank voles and their density in different types of forests (double logarithmic scale).

The graphs contains the data from beech forests of Southern Poland (1) Grodziński *et al.*, 1970, oak-hornbeam forests of Northern Poland — (2), Petruszewicz *et al.*, 1971, oak-hornbeam forests of Southern Poland (3), the present study, and from the Alaska taiga forest, USA — (4), Grodziński, 1971, and spruce forests in Bulgaria — (6), Petruszewicz *et al.*, 1972.

the daily costs of maintenance (respiration) were estimated for the populations of these rodents in the Niepołomicka Forest. The efficiency of net production in relation to total respiration amounted to barely 2.3—2.8% in voles and 3.4% in mice (Table 7). An attempt was made

to correlate the net production and population density of forest rodents. The mean year population densities and corresponding values of the net production were plotted on the double logarithmic scale (Fig. 11). The data for the populations of voles (*Clethrionomys*) were used, since jointly 15 values were available. All the points in Fig. 11 lie along a straight line, hence it was possible to describe the relationship between net production and density as the regression equation based on logarithmic values:

$$P_n = 92.4 \bar{N}_{tr}^{0.99} \quad (6)$$

where: P_n —represents the year net production in kcal, \bar{N}_{tr} —mean year density of trappable rodents. Since the exponent .99 does not differ significantly from 1.0 ($t=.1562$, $p<.05$), a simplified formula of the above function can be used:

$$P_n = 92.4 \bar{N}_{tr} \quad (7)$$

Knowing the mean density of rodents it is possible to estimate from this formula the net production of a population. On the other hand, substituting the value of production to the equation given by McNeil & Lawton (1970) it is possible to estimate the respiration of such population. It should be remembered, however, that the McNeil and Lawton's function is valid for all homeothermic animals, while the formula given above is related only to the bank vole population.

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PRODUKCJA NETTO POPULACJI GRYZONI W GRĄDACH PUSZCZY
NIEPOŁOMICKIEJ

Streszczenie

W lasach grądowych (*Tilio-Carpinetum*) Puszczy Niepołomickiej w ciągu czterech kolejnych lat oceniano liczebność gryzoni posługując się metodą zanęcania i intensywnego wyłowu (Ryc. 1). Nornice rude (*Clethrionomys glareolus*) i myszy leśne (*Apodemus flavicollis*) stanowią 92,5% wszystkich gryzoni w tym lesie (Tabela 1). Drobne gryzonie przeszły w tym czasie cykl populacyjny od zagęszczenia wysokiego (32,1 nornic i 5,9 myszy na ha, średnio w ciągu roku) do niskiego (odpowiednio 8,1 i 2,0). Średnia liczebność dla cyklu czteroletniego wynosi 19,0 gryzoni/ha. Wszystkie te wartości reprezentują zwierzęta łowne, jeśli uwzględnić młode znajdujące się jeszcze w gniazdach to średnie liczebności wzrastają o około 20% (Tabela 2, Ryc. 2, 3).

Określono wiek nornic i myszy, skonstruowano ich tabele życia oraz wykreślono krzywe wzrostu osobniczego. Przeżywalność nornic i myszy zależy od liczebności populacji, przy wysokim zagęszczeniu średnia ich długość życia wynosi 2,2 i 2,4 miesiąca a przy niskim odpowiednio 2,6 i 3,3 miesiąca (Ryc. 4—5). Tempo wzrostu ciężaru ciała było gorsze w roku masowego pojawu. W wieku jednego miesiąca nornice osiągały wtedy 12,1 g a myszy 14,8 g, podczas gdy w latach niskiego zagęszczenia odpowiednio 13,7 i 15,4 g (Tabele 4, 5, Ryc. 6, 7). Rotacja osobników była związana także z zagęszczeniem, w populacji nornic osiągała ona od 5,5 do 4,6/rok, a w populacji myszy 5,0 — 4,0/rok. Rotacja biomasy wynosiła średnio 3,6/rok w obu tych populacjach (Tabela 7).

Oceniono liczbę gryzoni urodzonych w ciągu roku oraz ich procentowy rozkład urodzeń (Tabela 6), a z ich krzywych wzrostu i przeżywania oceniono produkcję netto (Ryc. 8). W kolejnych latach wahała się ona od 755 do 2691 g/ha rok, w czym produkcja nornic stanowiła 562 — 1977, a myszy 177 — 755 g/ha rok (Ryc. 9). Na produkcję rozrodu przypadało 58% (nornice) i 45% (myszy). Średnia roczna produkcja wszystkich gryzoni wynosiła 1360 g co odpowiada 1983 kcal./ha rok. Porównano produkcję netto gryzoni w kilkunastu ekosystemach leśnych i trawiastych (Tabela 8). Na przykładzie populacji nornic rudych obliczono funkcję logarytmiczną, która opisuje zależność produkcji populacji od ich średniego rocznego zagęszczenia.