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**Survival, Turnover and Production of Small Rodents  
in a Beech Forest\***

[With 5 Tables &amp; 5 Figs.]

The number of small rodents in a mixed beech forest (in Southern Poland) was determined by the method of prebaiting and intensive removal during 3 years. Bank voles (*Clethrionomys glareolus*) and field mice (*Apodemus flavicollis*) showed in this period the population cycle from a higher density (the mean number 16 + 11 animals/ha/year) to a lower one (4 + 4 per ha). The age of all the voles and mice (N = 819) was determined with the accuracy of approximately 1 month. From the age structure and mortality in the cohorts the life tables were constructed. The life span of voles was 2.4 months on the average, and that of mice — 3.1. The survival in both populations depends on the density; during the years of lower density the mean life span was longer (3.2 and 3.6 months, respectively). The number of new born per year as well as individual growth curves in field conditions for both rodents were determined. Within the average life span the voles reach only 13.2 of body weight and mice 19.1 g while the corresponding figures for trappable animals are 17.3 and 22.7 g.

The net production was computed from the growth-survivorship curves. In the high density population of voles the net production reached 1.142 g or 1.666 kcal/ha/year. As much as 58 per cent of this value was provided by the production due to reproduction. The turnover of individuals exceeded the turnover of biomass by 10 to 31 per cent. Other methods of estimation of the production based on the turnover of individuals were also compared and discussed.

## I. INTRODUCTION

Mixed beech forests (*Fagetum carpaticum*) in the Ojców National Park became the object of extensive studies on the primary and secondary productivity (Medwecka-Kornaś & Łomnicki, 1967). The energy flow through the population of rodents in such forest requires the determination of the population size and its net production, as well as various bioenergetic parameters. The numbers of rodents, however, represents a basic value for calculation of the production as well as costs of maintenance (Grodziński, 1968).

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The mixed beech forest in Ojców has a simple community of small rodents among which the red bank vole, *Clethrionomys glareolus* (Schreber, 1780) and the yellow-necked field mouse, *Apodemus flavicollis* (Melchior, 1834) are the most numerous. During three years the voles and mice of this forest went through the population cycle, from a high density in 1965 to a low one in 1967/68. In the first year (1965) the mean number of voles reached 15.6/ha while that of mice 10.9/ha. In the consecutive years (1966, 1967) the number of voles decreased to 5.8/ha and 4.5/ha while the density of mice was reduced to the level of 3.9/ha and 4.4/ha (Grodziński, Pucek & Ryszkowski, 1966; Bobek, 1967; Grodziński *et al.* 1968).

The purpose of the present study was to find the best method of estimation of the net production in the above-mentioned populations of voles and mice. Starting from the dynamic changes in the population size the age structure of voles and mice was studied and the results were used for construction of the life tables as well as for computation of the mean life span and turnover of individuals. It was also possible to investigate the effect of population density on the survival. From the survivorship-growth curves the production in the population of voles was calculated and the results used to verify the credibility of other simpler estimations.

## II. MATERIALS AND METHODS

The total number of 959 rodents derived from the Ojców National Park near Kraków (50°13' N, 19°40' E) where the animals were captured in the beech forests during three consecutive years (1965—1967). The trapping procedure was repeated every spring (April) and autumn (October) by the method of prebaiting and intensive removal on a permanent plot of the area equal to 5.76 ha (Grodziński *et al.* 1966). In summer (July) 1965 and 1967 some additional trapping was carried out on a smaller (2 ha) removal plot or by using 25 trap-lines (Bobek, unpublished). On the whole eight samples of material were available to estimate the age structure in the populations of bank voles and field mice. These two species represented as much as 98.5% all the captured rodents.

The age structure determination was based on animals captured during the first 3—4 days of trapping and these rodents were considered as a resident population (Zippin, 1956; Janion, Ryszkowski & Wierzbowska, 1968). Animals captured in subsequent days might immigrate to the trapping plot and thus were not included into the sample representing the population. Hence the age was determined in 503 bank voles and 316 field mice (total 819 rodents among 959 captured).

The age of mice was estimated on the basis of upper molars wear (Adamczewska-Andrzejewska, 1967), while that of voles on the basis of length of  $M_1$  roots (Pucek & Zejda, 1968). The applied methods allow to estimate the age of both species of rodents with the accuracy of approximately 1 month although in mice it was not possible to distinguish between 9 months old specimens and older.

The mean life span in populations of bank voles and field mice was determined from the life curves by means of: (1) construction of life tables (Deevy, 1947), and (2) application of the formula proposed by Ryszkowski (1967). The survivorship curves were prepared in the following order using certain additional assumptions:

1. The population density of rodents was related to the whole area of the standard removal plot, *i.e.* 5.76 ha, in spite of the fact that such a plot corresponds probably to a slightly larger area. The number of rodents estimated in summer on the smaller plot or in the trap-lines was suitably transformed to obtain values corresponding to the standard plot.

2. First the age structure was estimated in the material obtained during 3 or 4 days of trapping. According to these values the number of animals determined by the function of maximum likelihood was again distributed between various age classes in the studied area of 5.76 ha.

3. Finally 8 cross-sections of the age structure, separated by periods of 3–5 months, were prepared. By comparison of these sections the fate of particular cohorts was studied and the obtained material cumulated in the corresponding age intervals for further calculations.

4. It was assumed that animals are lost with the exponential rate in the period between two measurements in the cumulated cohorts. The relative mortality rate  $q_x$  was calculated for every month of life of cumulated cohorts according to the formula:

$$q_x = \frac{d_x}{l_x}$$

where:  $d_x$  — number of animals lost during a given month,

$l_x$  — number of survivors till the beginning of the age interval (1 month).

### III. RESULTS

#### 1. Analysis of the Age Distribution

The method of analysis will be demonstrated on the field mouse populations (Tables 1 & 2). After chronological comparison of eight cross-sections of the mice population age structure fragments of history of 26 cohorts were found. Since trapping was carried out in 3–5 months intervals the mortality within a cohort could be investigated in most cases between two subsequent cross-sections, and only in 4 cases between 3 sections of the age structure. Sometimes no loss of animals from the cohort was observed. Among 26 studied fragments it occurred in 6 cases and only in less numerous groups. In order to avoid these accidental disturbances all the cohorts were cumulated in eight corresponding each other 3–4 months age intervals (Table 1). The estimation of the number of new born animals (interval 0–3 months) will be discussed in detail in the next section. The last interval (8.4–12 months) is based on a very limited material. This group of animals started at the age of 7–9 months (the weighted average equal to 8.4 months) and

**Table 1.**

Cohorts of field mice cumulated in 3 months intervals and the calculated corresponding monthly mortality rates ( $100q_x$ ).

Age intervals of the cumulative cohort (in months)	The initial number of animals in cohorts	Animal number in cohorts after three months	Monthly mortality rate ( $100q_x$ )
0-3	171.7	66.0	27.3
1-4	66.0	33.0	20.6
2-5	52.0	17.0	31.1
3-6	79.0	25.3	31.5
4-7	45.0	15.6	29.8
5-8	18.1	7.0	27.7
6-9	35.8	9.0	36.9
8.4-12	9.0	3.0	24.0

**Table 2.**

Calculation of monthly mortality rates ( $100q_x$ ) for all cohorts of the field mouse.

	Age interval in months											
	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12
Mortality rates of the cumulative cohorts	27.3	27.3 20.6	27.3 20.6 31.1	20.6 31.1 31.5	31.1 31.5 29.8	31.5 29.8 27.7	29.8 27.7 36.9	27.7 36.9	36.9 24.0	24.0	24.0	24.0
Avg.	27.3	23.9	26.3	27.7	30.8	29.7	31.5	32.3	30.5	24.0	24.0	24.0

later was found at the age of approximately one year, or certainly older than 9 months.

The mortality in various age intervals of the cohorts varied from 21 to 37 per cent per month (Table 1). All these values were segregated in monthly intervals according to the increasing age (Table 2). By adding the values of consecutive months the mean mortality rates, varying between 24 and 32%, were obtained. Such average mortality rates ( $100q_x$ ) in populations of the field mice and bank voles were used for construction of survival curves and life tables.

### 2. Estimation of the Number of New Born During the Trapping Period

Efforts were made to estimate the number of born animals in relation to the whole month when the trapping period took place. It was assumed that evidently females lactating during trapping periods produced the litter a few days earlier while pregnant females were expected to do so in a short time. Hence the number of new born was calculated by multiplying the number of pregnant or lactating females by the

**Table 3.**

Estimation of the number of bank voles and field mice born during months of trapping (spring and summer).

	Bank vole			Field mouse		
	April '65	July '65	July '67	April '65	July '65	July '65
Number of pregnant females	28.0	8.0	2.9	14.0	8.0	2.9
Number of lactating females	10.0	3.0	—	6.0	4.0	—
Average age of pregnant females (in months)	8.1	6.8	4.0	6.5	6.8	3.0
Monthly mortality rate of pregnant females (in per cents)	32.0	18.9	19.9	31.5	31.5	27.7
Number of females eliminated during pregnancy	9.0	1.5	—	4.4	2.5	—
Number of reproducing females corrected for elimination	29.0	9.5	2.9	15.6	9.5	2.9
Mean litter size (number of embryos)	6.0	4.2	6.0	6.3	5.9	6.0
Number of actually born	174.0	39.9	17.4	98.3	56.0	17.4

mean litter size and corrected for elimination. The elimination of pregnant females was estimated from their mean age and from the mortality rate of this age interval (Tables 4). The presented method of reasoning may be summarized in a simple formula:

$$V_t = [(N_p - N_{pe}) + N_l] \cdot L,$$

where:  $V_t$  number of born during 1 month  
 $N_p$  number of pregnant females  
 $N_{pe}$  number of pregnant eliminated females  
 $N_l$  number of lactating females  
 $L$  mean litter size

It is impossible to apply here a more accurate formula for the number of new born (Petrušewicz, 1968) because the trapping period was very short and any pregnant female was encountered only once, when killed in a snap-trap.

Table 4. Life tables for bank voles and field mice.

Age in months	$l_x$			$d_x$			$100q_x$			$e_x$		
	A	B	C	A	B	C	A	B	C	A	B	C
<i>C. glareolus</i>												
0-1	100.0	100.0	100.0	38.5	38.5	38.5	38.5	38.5	38.5	3.2	2.2	2.4
1-2	61.5	61.5	61.5	11.8	26.5	24.5	19.2	43.1	39.8	4.0	2.2	2.5
2-3	49.7	35.0	37.0	9.5	12.7	12.1	19.2	36.4	32.6	3.8	2.6	2.9
3-4	40.2	22.3	24.9	10.6	8.0	8.4	26.5	35.9	33.6	3.6	2.3	3.0
4-5	29.6	14.3	16.5	5.8	3.0	3.3	19.5	20.9	19.9	3.7	3.1	3.3
5-6	23.8	11.3	13.2	7.5	2.6	3.1	31.6	22.7	23.6	3.5	2.8	3.0
6-7	16.3	8.7	10.1	3.0	1.9	1.9	18.6	21.5	18.9	3.8	2.5	2.8
7-8	13.3	6.8	8.2	3.1	2.3	2.5	23.5	33.4	30.6	3.6	2.0	2.3
8-9	10.2	4.5	5.7	1.5	1.8	1.8	14.8	40.0	32.0	3.5	1.8	2.2
9-10	8.7	2.7	3.9	0.9	1.1	1.2	10.1	41.8	32.0	3.0	1.6	2.1
10-11	7.9	1.6	2.7	0.6	0.7	0.8	7.1	43.7	30.4	2.3	1.4	1.8
11-12	7.2	0.9	1.9	0.3	0.3	0.4	3.7	35.6	19.8	1.5	1.1	1.3
12-	6.9	0.6	1.5	6.9	0.6	1.5	100.0	100.0	100.0	0.5	0.5	0.5
<i>A. flavicollis</i>												
0-1	100.0	100.0	100.0	27.3	27.3	27.3	27.3	27.3	27.3	3.6	2.9	3.1
1-2	72.7	72.7	72.7	16.4	17.5	17.4	22.6	24.1	23.9	3.8	2.7	3.0
2-3	56.3	55.2	55.3	9.4	15.8	14.5	16.7	28.6	26.3	3.8	2.5	2.8
3-4	46.9	39.4	40.8	5.3	13.3	11.3	11.4	33.8	27.7	3.4	2.2	2.7
4-5	41.6	26.1	29.5	4.7	10.3	9.1	11.4	39.5	30.8	2.3	2.1	2.5
5-6	36.9	15.8	20.4	5.4	4.8	6.1	14.7	30.5	29.7	2.1	2.2	2.4
6-7	31.5	11.0	14.3	14.6	3.3	4.5	46.2	30.0	31.5	1.4	2.0	2.2
7-8	16.9	7.7	9.8	12.6	2.4	3.2	74.5	31.0	32.4	1.1	1.6	2.0
8-9	4.3	5.3	6.6	2.1	2.2	2.0	49.2	41.3	30.5	2.0	1.1	1.7
9-10	2.2	3.1	4.6	0.5	3.1	1.1	24.0	100.0	24.0	2.4	0.5	2.3
10-11	1.8	3.5	3.5	0.4	0.8	0.8	24.0	24.0	24.0	1.9	1.8	1.8
11-12	1.4	2.7	2.7	0.3	0.6	0.6	24.0	24.0	24.0	1.3	1.2	1.2
12-	1.1	2.1	2.1	1.1	2.1	2.1	100.0	100.0	100.0	0.5	0.5	0.5

$l_x$  — the number of animals surviving at the beginning of age interval for 100 born;  $d_x$  — number of dying within the age interval for 100 born;  $100q_x$  — mortality rate in per cent;  $e_x$  — life expectation for individuals of the age  $x$ ; A — low population density in 1966/67; B — high population density in 1965/66; C — average for the whole period 1965-67.

The Standard Minimum trapping was carried out in early spring before reproduction period starts in the voles and mice populations, and late autumn, *i.e.* after this period was finished. For this reason the whole material of reproducing females derived mainly from summer 1965 and 67, and additionally from spring 1965 when due to the high population density the reproduction started much earlier. During these three periods only 87 reproducing females ( $N_p + N_i$ ) of voles and mice were trapped and from this number 17 should be still eliminated ( $N_{pe}$ ) before parturition (Table 3). These females should produce 231 young voles and 172 mice during one month. From the new born animals only 54 voles and 66 field mice reached the age of 3 months, hence the mortality rate in this initial period was as high as 77% in voles and 62% in mice (Table 3).

The values given in Table 3 for various seasons were cumulated and used for calculation of the mortality rate  $q_x$  in each month out of the first three months of life. The mean mortality rate in the age 0—1 month was equal to 38.5% in voles and 27.3% in mice. In subsequent months these values were superimposed on the mortality rates of older age groups (Table 2).

### 3. Tables of Survival of Voles and Mice

Computation of the average mortality rates in the first and successive months of life constituted a basis for the life tables construction (Table 4). The number of surviving ( $l_x$ ) voles and mice is also presented as the survivorship curves (Figs 1 & 2). From the comparison of these two figures it appears that the survival in the mice population is better than in voles, because the mortality was higher in voles in any month of the life (see also Table 4). The survivorship curves for both species are close to the exponentials (Figs 1 & 2, curves denoted — 1). In the years of rather low population density of voles and mice the survivorship curves deviate from the exponential model. They show an apparent plateau in the period between 2 or 3 and 6 months because the mortality rate is then significantly lower (Figs 1, 2 & 3, curves — 2; Table 4). The survivorship curves for the whole material stand between the curves representing either low or high state of the population density. In Figs 1 & 2 such curves are plotted on a semi-log scale and presented under the form of the regression line.

The value of mortality rate ( $100 q_x$ ) (see Table 4) corresponds better to the actual mortality in particular age intervals than the shape of curves. Graphical presentation of this rate in voles indicates that it resembles the letter »U«. The mortality was highest in the new born

voles, decreased during the intermediate months of life, and again increased in older age (Fig. 3). The pattern of this rate is also related to the population density. During the year of a low population density the voles showed a high mortality rate in the first age classes. The between the second and fifth months the mortality decreased to approximately 19%, but again increased up to nearly 32% at 5—6 months. Older classes exhibited slightly lower mortality and due to this

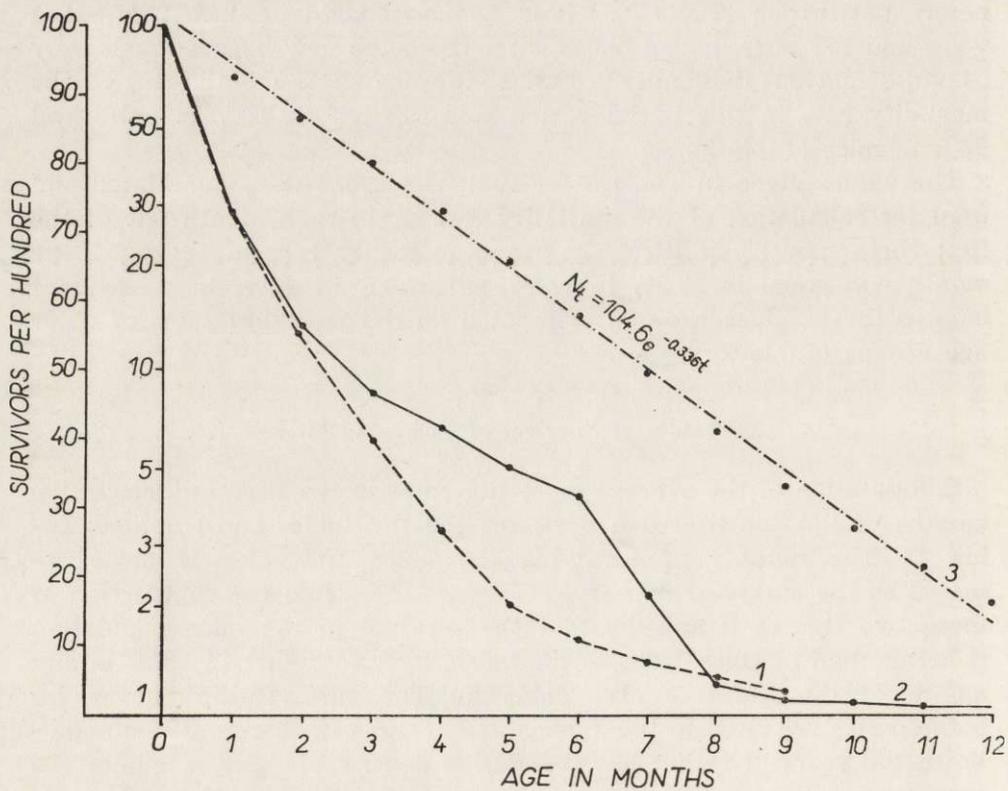


Fig. 1. Survivorship curves for mice. Curves for the high (1) and low (2) population densities are plotted on a linear scale while the regression line for the whole material (3) on a semi-log scale.

fact approximately 7% of voles lived longer than 12 months in a population of not too high density. On the other hand during the year of a high population density the great mortality was observed at the age 1—3 months (36—43%) with a marked decrease between 4 and 7 months. At the age 7—12 months the mortality rate rose steeply and in three consecutive age classes exceeded 40%. In the case of field mice the relationship between the age and mortality rate showed a less regular

pattern. For the mice population of a normal density the graphical presentation of the  $q_x$  resembled the widely open letter »U«, while with high density the mortality rate was slightly higher in younger classes but always oscillated around the level of 30%.

Analogue life tables were constructed separately for the period of summer and winter in populations of both rodents. With such division the material of some cohorts is very limited, and moreover in winter

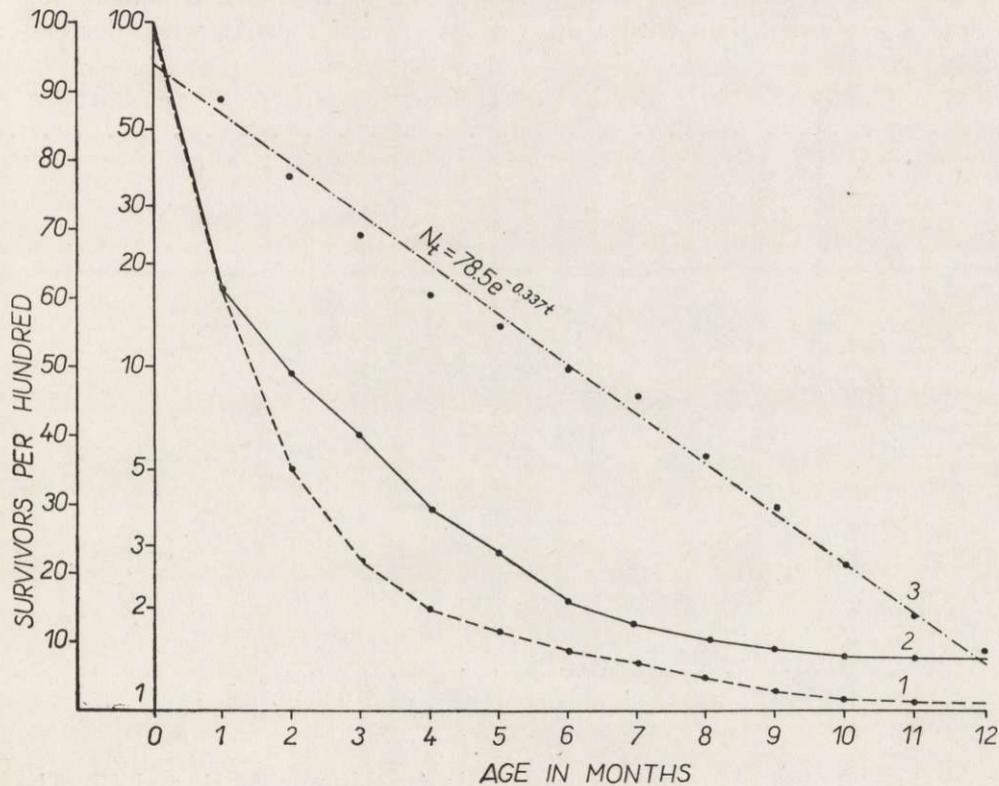


Fig. 2. Survivorship curves for voles. For explanations see Fig. 1.

the youngest age classes are absent (the rodents do not reproduce in this period). For this reason these tables are omitted here and only some conclusions arising from them are given. In most age classes the mortality rate was significantly higher in winter than in summer. It occurred both in the voles and mice populations, but the winter mortality was always higher in voles than in mice. Thus among rodents living during the winter a higher percentage of mice survived till the next spring.

#### 4. Estimation of the Mean Life Span

The mean life span may be read off directly from the life tables where is given as the first position in the column  $e_x$  (Table 4). In the whole studied material this average value approached 2.4 months in the bank voles and 3.1 months in field mice. The mean life span, however, varied in relation to the population density. Both in voles and mice it was markedly higher during years of the normal density (3.2 and 3.6 months) than with a mass occurrence of rodents, when deca-

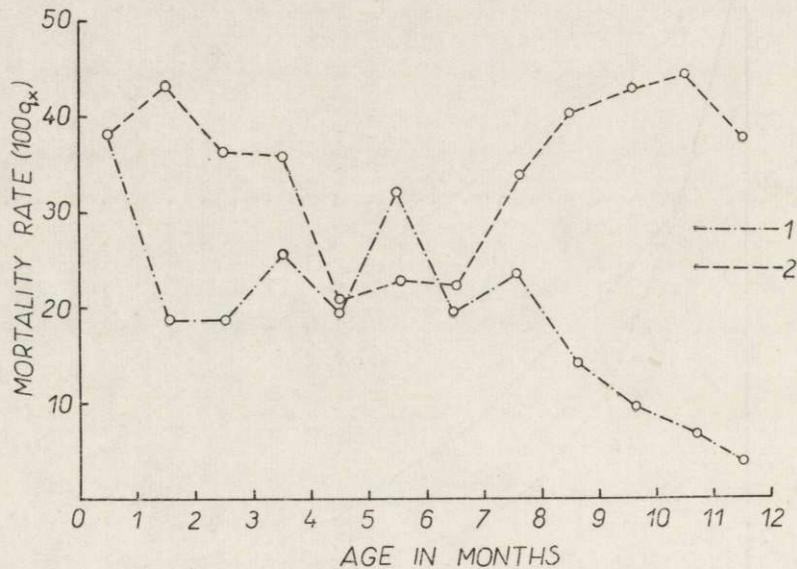


Fig. 3. Mortality rate in bank voles (100  $q_x$ ).  
(1) — low density population; (2) — high density population.

ed to 2.2 and 2.9 months (see Table 4, columns A, B, and C). The mean values for the 3 year period given earlier are of course intermediate between two various densities, but they correspond more closely to the period of mass occurrence. It is caused by the numerical superiority of cohorts from this year over the material from normal years.

The mean life span for the whole material was calculated by using the formula proposed by Ryszowski (1967):

$$\bar{t} = \frac{1}{\mu},$$

where:  $\bar{t}$  mean life span  
 $\mu$  instantaneous mortality rate

This formula may be also subjected to the following transformation:

$$\mu = -\frac{\log \frac{N_t}{N_0}}{t \log e}, \quad \text{or } \mu = -\frac{\ln \frac{N_t}{N_0}}{t},$$

where:  $N_0$  initial numbers in the cohort

$N_t$  numbers after time "t"

$t$  interval of time between numbers  $N_0$  and  $N_t$

$e$  basis of natural logarithms (2.71)

The credibility of results obtained by means of this formula is higher with the constant mortality rate ( $q_x$ ) in particular age intervals. In such case the survivorship curves become similar to exponentials and form straight lines on a semi-log scale. When these lines are described by the regression equation it is possible to find the instantaneous mortality rate » $\mu$ « which in voles is equal to 0.337 and in mice 0.336. Hence the mean life span is calculated:

$$\bar{t} \text{ (for voles)} = \frac{1}{0.337} = 2.97 \text{ months,}$$

$$\bar{t} \text{ (for mice)} = \frac{1}{0.336} = 2.98 \text{ months.}$$

Both values are almost identical and very close to three months. In mice the life span computed from the instantaneous mortality rate  $\mu$  (3.0 months) is quite similar to the values obtained from life tables (3.1 months). On the other hand in voles both values are divergent (the difference amounts to 0.6 month). This is caused by the fact that the mortality rates  $q_x$  are more constant in mice than in voles (compare Table 4).

Due to the differences in the survival of voles and mice (compare section 3) the two species show various average life spans. The mice live always longer than voles: in years of the normal population density the difference is equal to 12% and increases to 32% in years of the high density. But even in the years of high density the mice were never so numerous as the voles.

##### 5. Individual Growth Curves

The age of the all captured voles and mice was determined with the accuracy of approximately 1 month. Since the animals were also weighted it was possible to draw the growth curves of voles and mice under field conditions (Fig. 4). For obvious reasons the early part of these curves is based on the laboratory data (Sviridenko, 1951, 1959; Petrov & Airapetyans, 1961; Mazàk, 1962; Drożdż, 1965). It was found, however, that during 3 weeks of growth in the nest

young voles and mice gain more weight in the laboratory than under field conditions (Table 5). The youngest voles and mice trapped in the beech forest (age slightly below 1 month) reached a lower body weight than 3 weeks old animals reared in the laboratory. Hence these lower field data were included into the growth curves.

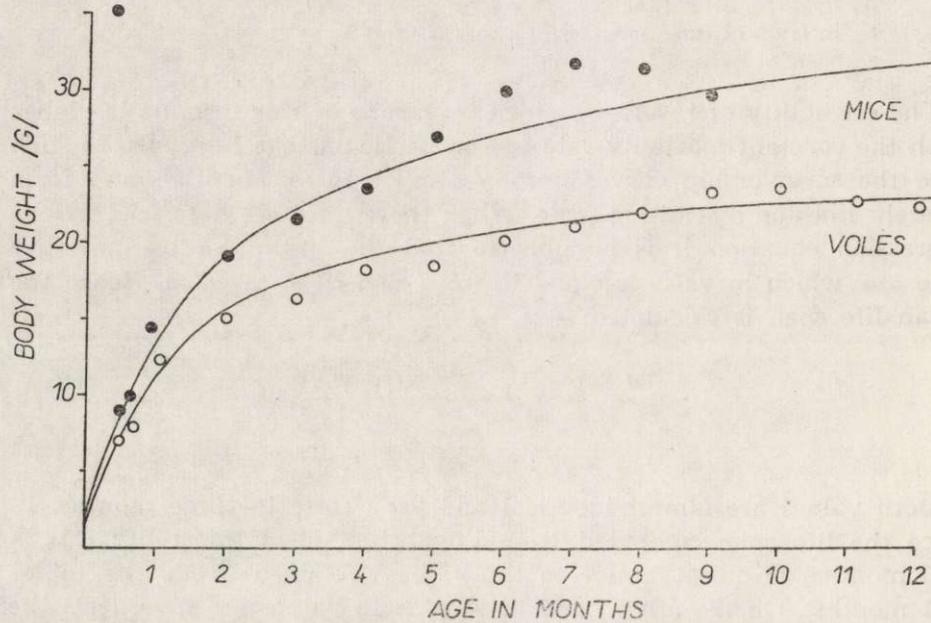


Fig. 4. Individual growth curves of bank voles and field mice under field conditions. Pregnant females are omitted.

Table 5.

Average body weight (in grams) of voles and mice at different age. Laboratory data for young voles based on Sviridenko (1959), Petrov & Airapetyans (1961), Mazák (1962) and Drożdż (1965) whereas those for mice from Sviridenko (1951). See also Fig. 4.

Age in months	Laboratory data		Field data (beech forest)			
	0	0.7	< 1	3	6	9
Bank voles	1.6—1.7	10—13	8.1	16.6	20.6	23.0
Field mice	2.3	11.8	9.8	21.8	30.0	31.2

During the mean life span voles reached only 13.2 g body weight of trappable voles was as much as 17.3 g. Corresponding figures of the mean body weight of mice were 19.1 and 22.7 g.

The average growth curves presented here do not take into account possible differences in the growth rate between various generations or

the effect of the population density on the body weight. From the analysed material it appears, however, that in the high density year rodents had smaller weight than in subsequent years.

#### IV. DISCUSSION

The purpose of the present study was to find parameters essential for computation of the net production in rodents populations from data obtained by the »Standard-Minimum« trapping (Grodziński, *et al.* 1966). This method has been generally accepted in the International Biological Programme studies on the productivity of rodents (Golley, Pelikan & Ryszkowski, 1968).

However, the »Standard-Minimum« trapping provides samples of material obtained every few months, sometimes not enough numerous, and deriving from the open population. For this reason the life tables calculated for animals obtained by this method cannot be as accurate as tables based on the large material of rodents from the laboratory or closed populations (Leslie & Ranson, 1940; French, Maza & Aschwanden, 1967).

The various ways of estimation of the net production will be discussed by using, as an example, the bank vole population in 1965/66. This species showed in these years the highest density in the four year cycle in the beech forest of the Ojców National Park. The number of voles ( $N$ ) is of course the basic value. One should distinguish, however, two different measures: numbers of trappable animals ( $\bar{N}_{tr}$ ), *i.e.* at the age of 1 month or older, and numbers of born ( $\bar{N}_b$ ), representing higher figure, which includes both trappable animals and those staying in nests (juvenile).

The numbers of trappable voles on the whole Standard-Minimum trapping plot reached the value of 120.1 in April 1965, 184.0 in July, and 73.0 in October. A remarkable drop occurred during the winter and the corresponding figure for the next spring was 7.1 animals (Grodziński *et al.* 1966; Bobek, 1967). The weighted mean of the number calculated for such dynamic annual changes is equal to 90.1 voles on the whole plot, or 15.6 voles per 1 ha.

The number of new born voles ( $\bar{N}_b$ ) in the same one year period was computed from the age structure of trappable animals and increased by the corresponding mortality values in cohorts according to the life tables. The total sum of new born voles during the year was estimated as 526 animals, while the average number of trappable and juvenile voles ( $\bar{N}_b$ ) was 125.5 per plot or 21.8 per 1 ha. These last figures markedly exceed the mean number of trappable voles ( $\bar{N}_{tr}$ ) by almost 40%.

The reproduction period in bank voles in 1965 started in March and continued till the end of July. The number of pregnant females during this interval varied between 43.1 and 9.2% and the mean litter size was equal to 5.1 embryos. If the information concerning the number of reproducing females is substituted into the formula on the number of new born (Bujalska, Andrzejewski & Petruszewicz, 1968)

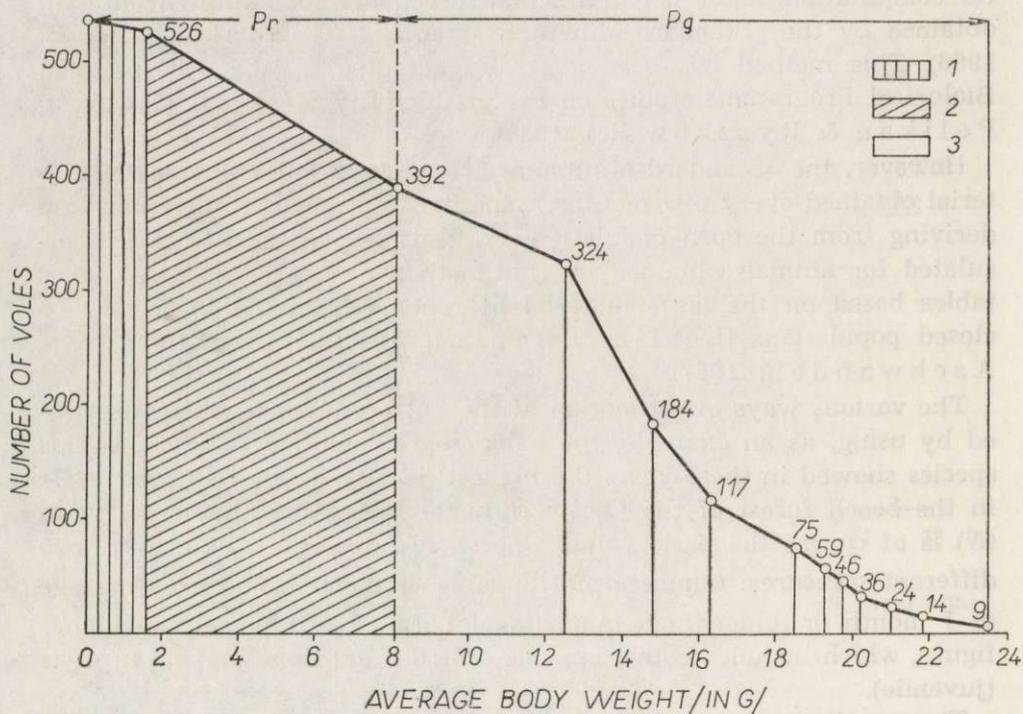


Fig. 5. Estimation of the net production in the population of bank voles based on their growth-survivorship curves.

All the cohorts were cumulated to the same starting point. Production due to reproduction ( $P_r$ ) — hatched area: 1 — during pregnancy, 2 — during nursing by the mother; production due to growth ( $P_g$ ) — open area: 3 — during independent life. The area of the first trapezium represents the production of new born, the areas of other trapeziums separated by continuous lines — production in consecutive months of life. Numbers refer to specimens surviving till the beginning of next month.

the figure of 670 born voles is obtained. This value is higher by 27% compared with the estimation presented above, but the agreement would be much better provided a correction is applied for the elimination of reproducing females according to the formula given by Petruszewicz (1968).

Starting from the total number of new born ( $N_b$ ) and using the life tables (see Results, section 5) it is possible to calculate the net production by the graphical method suggested by Allen (1950) (see also Chapman, 1958; Macfayden & Petruszewicz in litt.). For this reason the growth-survivorship curve was drawn by plotting the total number of bank voles in successive months against the mean individual body weight in this age (Fig. 5). The net annual production in the bank vole population reached 1.142 g or 1.666 kcal/ha/year assuming after Górecki (1965) the caloric value of the vole equal to 1.454 kcal/g of biomass.

The total net production in the population is equal to the sum of area of trapeziums. The increase in the body weight per unit of time constitutes the base of the trapezium while its sides correspond to the number of voles at the beginning and the end of the unit of time (usually one month) (Fig. 5). From this figure it is also possible to estimate the production due to reproduction ( $P_r$ ) and production due to growth ( $P_g$ ) (Petruszewicz & Walkowa, 1968). The former, ( $P_r$ ), consists of the development of embryos in the mother's body (approximately 848.8 g) and of growth of young voles in the nest during 3 weeks of nursing them by the mother (2,980 g). Hence the total production due to reproduction approaches 3,829 g while further production due to growth ( $P_g$ ) amounts to 2,747 g. The ratio  $P_r/P_g$  is equal to 1.4. As much as 58% of production is obtained at the expense of the mother: pregnancy covers 12.9% and lactation 45.3%. A similar proportion was found in a closed population of bank voles living on an island (Petruszewicz *et al.* 1968).

Fidelity of the described evaluation of net production depends to a great extent on the accuracy of estimation of the number of new born. The determination of net production from the growth-survivorship curve is the most accurate method which at present may be used for the population of rodents. The value of annual production — 9,562 kcal/plot/year should correspond to the product of the mean number of all animals ( $\bar{N}_b$ ) (*i.e.* trappable and staying in the nest), the mean body weight ( $B_b$ ), and the turnover of biomass ( $\theta_B$ ). There is no simple relationship between the turnover of biomass ( $\theta_B$ ) and turnover of individuals ( $\theta_N$ ) (Petruszewicz, 1966; Macfayden & Petruszewicz, in litt.). Thus the graphical method described above may constitute the only basis for verification of other ways of computation of the net production which employ the turnover of individuals ( $\theta_N$ ). Three such formulas evaluating the net production in the same population of voles are compared below with the Allen's method (1).

	Formula	kcal/plot/year	in % of (1)
(1)	Allen method $P_n = N_b B_b \Theta_B$	9,562	100.0
(2)	$P_n = N_b B_b \Theta_{Nb}$	12,445	130.1
(3)	$P_n = N_{tr} B_{tr} \Theta_{Ntr}$	8,014	83.8
(4)	$P_n = N_{tr} B_b \Theta_{Nb}$	8,933	93.5

The meaning of symbols:

$P_n$ net production	$\Theta$ turnover rate
$\bar{N}$ mean number	$b$ of all animals (since birth)
$B$ mean body weight	$tr$ of trappable animals

In the formula (2) the substituted values represent the mean for all animals in the population ( $N_b$ ). The calculated production is by 30% too high because the turnover of individuals, used in the formula, always exceeds the turnover of biomass. In the formula (3) the turnover of individuals also appears, but all the values refer to the trappable animals neglecting the juvenile voles staying in nests. In this case the number of trappable animals is apparently too low, but the body weight of these animals ( $B_{tr}$ ) is obviously higher than the mean body weight of all animals in the population ( $B_b$ ). The turnover of trappable animals ( $\Theta_{Ntr} = 3.75/\text{year}$ ) is lower than the turnover of all specimens ( $\Theta_{Nb} = 5.5/\text{year}$ ), although in some cases it may be similar to the turnover of biomass. In effect the formula (3) always gives lower estimate of production in the discussed year the difference was approximately 16% but in other years it was as much as 32.5%

Finally the formula (4) derives from the studies by Grodziński *et al.* (1968) and Grodziński (1966) where it was used to obtain the estimate of the energy flow through the population of rodents. In this formula the values for trappable animals ( $N_{tr}$ ) and parameters calculated for all the animals ( $B_b$  and  $\Theta_{Nb}$ ) are mixed up on purpose and the final result is very close to the true one. This is possible due to the fact that in all cases  $\bar{N}_{tr} < \bar{N}_b$  and at the same time  $\Theta_{Nb} > \Theta_B$ . These values seem to be slightly correlated together.

The errors of estimation by the formulas (2), (3), and (4) are mainly due to using the turnover of individuals instead of biomass. In populations of voles and mice the turnover of individuals should be always greater than the turnover of biomass. The former is described by a simple formula:

$$\Theta_N = \frac{1}{t}$$

where  $t$  is the mean life span (in months), and 1 is the unit of time, in this case 12 months.

When the mean life spans of the studied population of voles (see Results, section 4) are substituted into the formula, the calculated turnover of individuals ( $\theta_{Nb}$ ) in the year of mass occurrence amounts to 5.5/year while at a low population density is equal to 3.8/year. On the other hand the turnover of individuals calculated reciprocally according to the formula (1) from the graphical evaluation amounts to 4.2/year in 1965/66 and 3.4/year in 1966/67. Hence in this two cases  $\theta_{Nb}$  exceeded  $\theta_B$  by 31 and 10%, respectively.

The most accurate evaluation of the net production for the materials obtained by the »Standard Minimum« method is probably based on the growth-survivorship curves. This procedure, however, requires detailed and time consuming estimation of the age structure, construction of life tables and determination of individual growth. Moreover the estimation of the number of new born is often associated with a significant error. Thus in certain cases employment of the formula (4) seems to be justified.

In the Standard Minimum trapping one might recommend three series of trapping during the year (spring, summer, late autumn) instead of the two carried out at present (usually late spring and autumn). This would significantly improve the accuracy of calculation of both the survival itself and the net production. For studies on the productivity of rodents the improvement in the accuracy of estimation of the animal numbers ( $N$ ) remains a basic problem. One should remember that both estimates of the net production and respiration, which constitutes usually over 97% in the balance of energy flow through the rodent population, are based on the estimate of ( $N$ ) animal number (Grodziński, 1968; Ryszkowski & Petruszewicz, 1967).

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PRZEŻYwalNOŚĆ, ROTACJA I PRODUKCJA NETTO DROBNYCH GRYZONI  
W LESIE BUKOWYM

Streszczenie

W mieszanym lesie bukowym Ojcowskiego Parku Narodowego w ciągu trzech lat (1965—67) oceniano liczebność drobnych gryzoni, posługując się metodą zanęcania i intensywnego wyłowu (Standard-Minimum). Nornice rude, *Clethrionomys glareolus* (Schreber) i myszy leśne, *Apodemus flavicollis* (Melch.) przeszły w tym czasie cykl populacyjny od wysokiego zagęszczenia (średnia roczna: 16 + 11 zwierząt/ha) do niższego (4 + 4/ha).

Wiek wszystkich nornic i myszy określono według zębów z dokładnością do około jednego miesiąca. Ze struktury wiekowej i śmiertelności w kohortach (Tabele 1, 2 i 3) wykreślono krzywe przeżywania (Ryc. 1, 2) i zbudowano tabele życiowe dla obu badanych gryzoni (Tabele 4, 5). Tabele te są nieco odmienne dla całego okresu oraz dla lat o wysokim i niskim zagęszczeniu w populacjach.

1. Średnia długość życia nornic wynosiła 2,4, a myszy 3,1 miesiąca. Przeżywalność w obu populacjach zmieniała się wraz z zagęszczeniem, dlatego w latach

niskiej liczebności długość życia była większa (3,2 i 3,6 miesięcy), podczas gdy przy wysokim zagęszczeniu znacznie się skracala (2,2 i 2,9), (por. Tabela 4). Wskaźnik śmiertelności ( $100 q_x$ ) miał nieco inny przebieg w populacji nornic i myszy, w obu jednak zależał od zagęszczenia (Ryc. 3).

2. Wykreślono osobnicze krzywe wzrostu obu gryzoni w warunkach terenowych (Ryc. 4, Tabela 5). Przy średniej długości życia nornice osiągają zaledwie 13,2 g, a myszy 19,1 g. Przeciętny ciężar zwierząt łowiących się w pułapki jest wyraźnie wyższy i wynosi 17,3 oraz 22,7 g.

3. Kojarząc krzywe przeżywania z krzywymi wzrostu, na przykładzie populacji nornic, oceniono produkcję netto — graficzną metodą Allen'a. W populacji tej przy wysokim zagęszczeniu produkcja osiągnęła 1,142 kg lub 1.666 kcal/ha/rok. W tej liczbie na produkcję rozrodu ( $P_r$ ) przypada aż 58%, z czego w okresie ciąży powstaje 13%, a w okresie karmienia przez matkę dalszych 45%. Zatem stosunek produkcji wzrostu ( $P_g$ ) do produkcji rozrodu wynosi 1:1,4. Na tym przykładzie zweryfikowano także sposoby oceny produkcji netto oparte na rotacji osobników.

4. Rotacja osobników ( $\theta_N$ ) w populacji nornic przy wysokim zagęszczeniu sięgała 5,5/rok, a przy niskim tylko 3,8/rok. Natomiast rotacja biomasy ( $\theta_B$ ) wynosiła analogicznie 4,2 i 3,4/rok. W tych dwóch przypadkach rotacja osobników przewyższała więc rotację biomasy o 10 i 31%.