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

VOL. 18, 8: 167—190 BIAŁOWIEŻA August, 1973

Władysław AULAK

Production and Energy Requirements in a Population of the Bank Vole, in a Deciduous Forest of Circaeo-alnetum Type*)

[With 19 Tables & 6 Figs.]

During the period of one year (February 1967 — January 1968) production in population of red bank voles, *Clethrionomys glareolus* (Schreber, 1730), was studied in the Białowieża National Park, in a deciduous forest of *Circaeo-Alnetum* Oberd., 1953 type periodically flooded with flowing waters. The trappings were carried out by a modified method of prebaiting and intensive removal. Nine cohorts differing by 2-month birth intervals were distinguished. The annual flow of energy through the population of bank voles (=110,000 kcal/ha), as well as corresponding consumption (= 138,000 Kcal/ha), were estimated. The daily energy requirement in winter amounted to 302.5 Kcal/ha, and in summer to 456.3 Kcal/ha. Very low efficiency of production in relation to costs of maintenance was ascertained (1.92%). A relation between the amount of food available in the herb layer plants and energy requirements in the population of bank voles was estimated for winter and summer periods. In summer the energy requirement of the bank vole population is approximately 0.4%, and in winter to approximately 13.5%, of the available food. Annual consumption by the population of red bank vole constitutes 2.19% of the total primary production of herb layer plants.

---

*) This study was carried out under the Small Mammal Project of the International Biological Programme in Poland, and project No. 09.1.7, coordinated by the Institute of Ecology, Polish Academy of Sciences.

1. INTRODUCTION

Investigations of energy flow and food requirements in herbivorous are important for evaluating a relationship between the energy intake from the environment and food carrying capacity of the ecosystem. Scarcity of food or difficulties in obtaining it may represent factors limiting the numbers of small rodents.

From the investigations carried out on the relation between energy requirement and food carrying capacity of the habitat (Górecki & Gębczyński, 1962; Drożdż, 1966; Grodziński *et al.*, 1966; Bobek, 1969; Grodziński, 1971, and others) it arises that the total primary production during a year in various habitats exceeds by ten — to twentyfold the year food requirements of rodents. This might indicate that regarding food scarcity as a factor limiting numbers of rodents is not justified. However, this would be true only when changes in the plant biomass in the year cycle occurs in parallel to changes in the food intake. In fact, a majority of plant production constituting the main food for rodents corresponds of herbaceous plants that undergo a full production cycle in the vegetative period and die over winter. Hence, in the periods of winter and early spring after disappearance of snow cover, the forest may not provide sufficient food. According to preliminary data (Aulak, in preparation) the biomass of herb layer plants in the oak-horn-beam forest (*Tilio-Carpinetum* Tracz., 1962) in the Białowieża National Park in winter (under snow) is $^1/_8$ that of the maximum stage. Even after the disappearance of of snow, this value remains approximately six times lower than the maximum. The differences in the food availability between summer and winter are probably even higher than the ratio of total plant biomasses in these periods. Hence it seems not justified to deny the importance of the amount of plant biomass in the biotope as a limiting factor of the rodent population only on the basis of a relation between primary production and energy requirement of herbivorous animals in the scale of the whole year. Scarce or inaccessible herbaceous plants are supplemented by a considerable share of other foods, such as seeds, insects, *etc.* in the winter and spring diet of the bank vole (Holišova, 1971).

In the present study the production and energy requirement of one herbivorous species, the red bank vole, *Clethrionomys glareolus* (Schreber, 1780) were analysed over one annual cycle. At the same time an attempt was made to estimate differences in the daily energy requirement between particular seasons in order to determine the existence (or its lack) of parallelism in the dynamics of energy requirements and food carrying capacity of the studied forest. Particularly it was intended to establish the size of differences between energy requirements in winter and in summer.

2. STUDY AREA AND METHODS OF INVESTIGATION

The investigations were carried out in the Białowieża National Park in a deciduous forest (*Circaeo-Alnetum* Oberd., 1953) from August 1966 to June 1968. The small mammals were trapped by a modified Standard-Minimum method (SM) with additional employment of trapping cylinders besides two snaptraps at each trapping point (Aulak, 1967). The number of voles were estimated by the regression method (Hayne, 1949; De Lury, 1947; Grodziński *et al.*, 1966). The »border effect« (Aulak, 1967; Chełkowska & Ryszkowski, 1967; Hansson, 1969) was not taken into consideration since, despite numerous studies, a relationship between real density on a given area and probable overestimated density with the use of the SM method, has not been accurately determined to date. In the present considerations, this problem is important only in those cases when the values of various parameters were calculated per ha. For comparison made between periods (relative indices) absolute density is not important.

Suitable periods of time were left between particular trappings to ensure repopulation of the area, according to the data of Andrzejewski & Wrocławek (1962).

The collected material was elaborated in the laboratory of the Mammals Research Institute, Polish Academy of Sciences. The following parameters were determined for each individual: age, body weight, sex, *etc.* The method of Pucek & Zejda (1968) was employed for estimating age.

In the trapping periods, the estimated density corresponds to the number of animals collected, while in other periods it derives from the interpolation between neighbouring censuses assuming rectilinear changes of numbers. This assumption was supported by the distribution of numbers in particular cohorts along the time axis. In the majority of cohorts (except youngest animals) the points describing density fell in the vicinity of the line between extreme points. In a few cases intermediate points were found above this line. The assumption of uniform mortality simplifies to a certain degree the course of natural losses, but nevertheless the differences between interpolated numbers according to rectilinear and exponential elimination are small, particularly in winter periods.

All the analyses described here concern the period between 1 February 1967 and 31 January 1968. The states in August 1966 and June 1968 were used only to estimate numbers of particular cohorts in winter periods when no trappings were carried out. The 1st of February was chosen as the beginning of investigations for two reasons: (1) After subtracting from the first census in 1967 two-month periods (according to the accuracy of age determination) it was found that the first cohort derives from the period of February—March. Hence starting the period of investigation as 1st February simplified all calculations. (2) In the first census of 1967 no trace of cohorts born before February was found.

The analysed year was divided into intervals depending on trapping periods. Additionally, the period of February—June was divided into two 2-month intervals to record differences in various population parameters during winter-spring period.

Nine cohorts were distinguished in the collected material (Table 1). All calculations in particular periods were carried out separately for each cohort.

3. RESULTS

3.1. Population Density

Estimated numbers of age class II were always higher than would been expected from the trappings of age class I two months earlier (Table 2). This is because individuals of this class stay in the nest up to 20—21 days of life and they consitute the untrappable part of the population. The numbers of the age class II were taken as real values while the numbers of the class I were calculated from the number of births in a given two-month period assuming uniform mortality from birth up to the age class II.

Table 1

Origin of cohorts of the red bank vole according to the month of birth.

Cohort	Time of birth		Category
1	Oct. — Nov.	1965	Over-wintered individuals
2	Febr. — March	1966	
3	April. — May	1966	
4	June — July	1966	
5	Aug. — Sept.	1966	
6	Febr. — March	1967	This year individuals
7	April — May	1967	
8	June — July	1967	
9	Aug. — Sept.	1967	

Table 2

Population numbers of the bank vole.

Time	Number of voles caught on		Number of overwintered individuals per 1 ha	
	SM area	N/1 ha	N	%%
Aug. 1966	246	36.1	3.1	8.6
Febr. 1967	—	23.1 *	23.1	100.0
Apr. 1967	—	23.9 *	16.3	68.2
June 1967	190	36.6	9.5	26.0
Aug. 1967	195	53.8	4.6	8.6
Oct. 1967	239	44.6	0.5	1.1
Jan. 1968	—	29.8 *	0.0	0.0
June 1968	338	51.8	8.0	15.4

* Number of voles estimated from the interpolation between neighbouring censuses.

Mean density amounted to N=37.6 individuals/ha in the analysed year (Fig. 1). The annual cycle shows the highest density at the beginning of August, *i.e.* at the end of the period of maximum reproduction. At this time the density exceeds by approximately 50% the mean yearly value and is almost double the winter density. A rather high mortality in young voles and decreased reproduction in autumn period lead to a considerably reduced density at the beginning of winter.

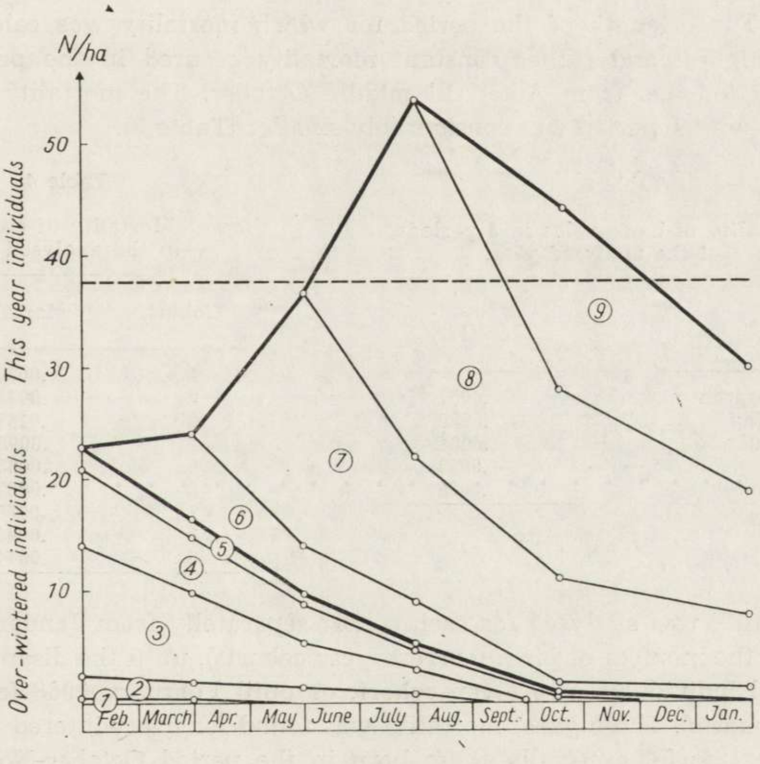

Fig. 1. Population density of red bank vole (N/ha) taking into account cohorts in the annual cycle. Horizontal broken line indicates the mean annual density. Numbers in circles correspond to cohorts (according to Table 1). Points surrounded by circles represent data obtained by interpolation.

The proportion of overwintered animals in the population (Table 2) shows a systematic decline from spring till autumn. In 1967 none of the overwintered (1966) animals started the second wintering. Already before culmination of reproduction (June) the number of voles produced in 1967 is almost three times higher than overwintered ones. The first cohort of 1967 was not too numerous and entered the wintering period in small numbers. On the other hand, the cohorts born in next months constituted the reproductive basis of population and represent 97.3% of the wintering population of 1967.

The mortality (μ) was analysed for each period of the year according to formula given by Gliwicz *et al.* (1968):

$$\mu=(N_o-N_t):\left(T\frac{N_o+N_t}{2}\right)$$

where: N_o — numbers at the beginning of the period
N_t — numbers at the end of the period
T — length of the period for which mortality was calculated.

The highest and rather constant mortality occured in the period of reproduction, *i.e.* from April till middle October. The mortality in the autumn-winter period was considerably smaller (Table 3).

Table 3

Mortality of bank voles in 5 periods of the analysed year.

Period	Mortal ity
Febr. — March	.0057
Apr. — May	.0089
June — July	.0084
Aug. — Oct.	.0083
Oct. — Jan.	.0038

Table 4

Mortality of cohorts in the analysed year.

Cohort	Mortality
1	.0050
2	.0045
3	.0167
4	.0095
5	.0083
6	.0067
7	.0056
8	.0048
9	.0044

Mortality was analysed for each cohort separatelly from January 1967, or from the moment of birth (current-year cohorts), until the disappearance of all individuals of a given cohort, or until February 1968 (current-year cohorts). The highest mortality was found for overwintered animals (cohorts 1 to 5), especially those born in the period October-November 1969 (Table 4). The mortality of current-year individuals was similar in all cohorts (cohorts 6 to 9).

3.2. Intensity of Reproduction

To calculate reproduction the formula given by Petrusewicz *et al.* (1968) was employed:

$$R=(\bar{N}\cdot T\cdot L):t_p$$

where: R — number of born in a given period
$\bar{N}$ — mean number of reproducing females (according to the state at the beginning and end of the period)

L — mean litter size in a given period
T — length of the period in days
t_p — length of pregnancy in days

The length of pregnancy was assumed to be 20 days, as based on laboratory data (Buchalczyk, 1970), but also corresponding in approximation to the data from natural environment (Bujalska & Ryszkowski, 1966; Bujalska *et al.*, 1968).

Table 5

Reproduction of red bank voles in particular periods of the analysed year (per ha).

Period	Febr. – May	June – July	Aug. – Oct.
Avg. litter size	5.5	4.8	4.3
N born	43.8	43.8	26.0
Reproduction rate N born/day	0.4	0.7	0.3

Table 6

Number of newborn bank voles (*N*) in the annual cycle (per ha).

Period	Febr. — March	Apr. — May	June — July	Aug. — Oct.
N	11.0	32.8	43.8	26.0
%%	9.6	28.9	38.6	22.9

Table 7

Proportion of current-year females and overwintered bank voles in the reproduction on the SM area.

Month		June	August	October
This year individuals	N	3	14	1
Over-winter individuals	N	18	6	—
	%%	85.7	30.0	0.0

In 1967 654 individuals should have been born on the SM area (*i.e.* 113.6 per ha). Reproduction began, in February-March, as indicated by the presence in subsequent censuses of individuals born in particular periods of the year was varied (Table 5).

Since the period of February-June was additionally divided into two intervals, the young voles born in that period were divided correspondingly. It was assumed that reproduction increased in a linear manner from the minimum in February till maximum in June and that the number of young voles in the population similarly increased. Consequently it was estimated that 1/4 of voles were born in the period of February—March, and the remaining 3/4 in the period of April—May. The number of young voles per ha, constituting the initial state of 1967 cohorts, is given in Table 6.

The proportion of reproducing females (pregnant and lactating) shows in the year cycle (Table 7) a constant decrease of overwintered animals in comparison with this year females. Of course this results from general reduction of number of overwintered voles. In October only minimum reproduction occurred (a single female of the current year).

Table 8

Proportion of different age classes of bank voles in the reproduction according to the number of young animals.

Cohort	Per cent of young	Avg. litter size
1	6.3	4.0
2	9.4	3.8
3	19.3	3.7
4	—	—
5	3.1	6.0
6	17.2	5.5
7	27.2	5.2
8	17.5	4.8
9	—	—

Table 9

Percentage of reproducing and pregnant females in relation to all females of red bank vole.

Month		Reproducing	Gravid
August	1966	25.7	9.7
June	1967	26.4	19.8
August	1967	25.0	20.4
October	1967	0.8	0.0
June	1968	35.1	19.9

Litter size was larger in older age classes. The share of these age classes in general reproduction was considerably higher than young classes (Table 8). Despite the decreasing proportion of overwintered animals participating in reproduction (from spring till autumn) as many as 62.7% of newhorn voles derive from them, and only 37.3% from this year females. Hence the magnitude of reproduction in a given year depends on overwintered animals.

The percentage of reproducing or pregnant females in a given census was also calculated (Table 9). It was found that in spring and summer approximately 1/4 of females are engaged in reproduction. In 1968 a higher percentage of reproducing females was found in comparison with the analogous census of 1967.

3.3. Production and Costs of Maintenance

3.3.1. Individual Growth

To analyse production, each cohort was treated separately. The estimated numbers in each cohort in a given time and the mean body weight of individuals in this cohort consituted the basis for calculating costs of growth and maintenance.

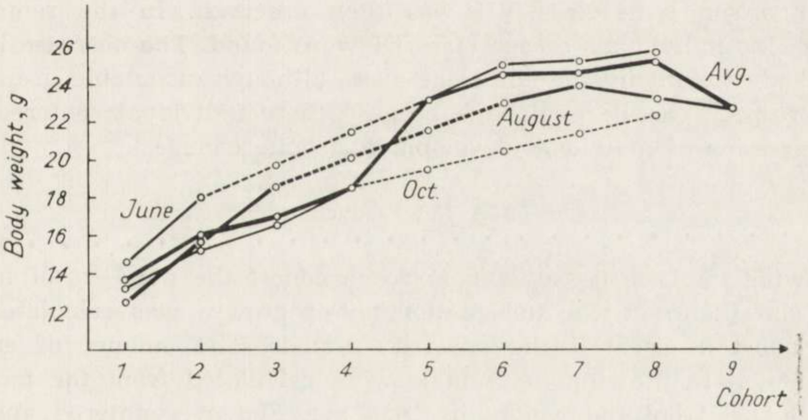

Fig. 2. Weight of bank vole individuals in particular age classes (1—9).

The curve of individual growth in particular age classes was estimated according to the mean weight of an individual of this class in different censuses (Fig. 2). Also the mean values for each age class were calculated taking into account all individuals trapped in a given year. In some places curves are drawn as broken lines since censuses lacked these age classes corresponding to voles born in the period from autumn 1966 till February 1967. In that period either reproduction was absent, or newhorn individuals died and were not shown in the first census in 1967.

The analysis of individual weights in age classes indicates that mean body weight decreased from summer till autumn in corresponding age classes. The curve for the whole year does not show a regular course but the values corresponding to it were taken for calculations since in a given year this curve gives the mean body weight of an individual in in a definite age class.

The diagram shows the mean body weight of an individual in the Ist age class according to trapped individuals. For the calculations a different value was employed. Since trapped individuals included a group which already left the nest, their age was between 21 and 61 days. Hence their mean age was around 41 days, whereas the mean age of class I was around 30 days. For this reason the mean body weight in this age class was interpolated between the body weight of a newborn (1,650 mg) and body weight of the vole 41 days old.

In the remaining age classes body weights were obtained from trapping data excluding pregnant females.

The mean body weight of individuals in age class IX is lower than in class VIII (Fig. 2). The data for the latter value were obtained only in the census in August 1967, nevertheless a distinct fall in body weight in comparison with class VII was then observed. In the remaining censuses no individuals of age class IX were found. The decrease in the mean body weight in the oldest age class, although disputable in quantitative respect, can be explained, because these individuals entered into the regression of individual development (senile changes).

3.3.2. Net Production

Knowing for each census and for each cohort the numbers of individuals and their age the net production of growth was calculated for each cohort in each of the analysed periods. The amount of energy accumulated in growing individuals were calculated from the moment of birth, *i.e.* from the weight of 1650 mg. For overwintered animals, January 1967 constituted the initial period.

The following formula (Petrusewicz *et al.*, 1968) was used in the calculations:

$$P = (N_T \times \Delta W + \Delta N_T + \Delta W_{T/2}) \cdot C$$

where: P — net production
N_T — number of individuals by the end of census
ΔW — body weight gain in the period T
ΔN_T — number of individuals eliminated in the period T
$W_{T/2}$ — body weight gain during half of the period T
C — caloric value of the red bank vole body (=1.454 Kcal/g according to Górecki, 1965).

The net production in 1967 amounted to 2,044.7 Kcal/ha. At the same time elimination amounted to 421.4 Kcal/ha, *i.e.* approximately 20.6%.

The highest intensity of production in the population of bank vole occurred between June and August (Table 10).

The costs of reproduction in the population were calculated separately since it was important to estimate their share in general costs of population maintenance. Moreover, for the nest period of young voles the calculations were made by methods other than generally employed.

From the empirical data it arises that the number of reproducing females in a given year amounted to 23.1 per ha, number of newhorn to 113.6, mean number of embryos per female to 4.9. Elimination was also taken into consideration in the calculations.

Table 10

Net production of bank vole growth in the annual cycle.

Period	Kcal/ha	%%	Kcal/day
Febr. — March	188.6	9.2	3.1
Apr. — May	433.4	21.2	7.2
June — July	647.8	31.7	10.8
Aug.—Oct.	548.3	26.8	7.3
Oct.—Jan.	226.6	11.1	2.2
Total/Avg.	2 044.7	100.0	5.7

Table 11

Intensity of production in the population of bank voles.

Period	Kcal/day/ha
February — March	2.2
April — May	8.5
June — July	3.6
August — October	8.6
October — January	12.6
Average	8.2

After taking into account the mean weight of a female, and after employing a factor for additional costs of maintenance of reproducing females (Kaczmarski, 1966), the costs of reproduction amounted to:

Period of pregnancy	1473.3 Kcal/ha
Period of lactation	5647.5 Kcal/ha
Total	7120.8 Kcal/ha

In further considerations only costs of pregnancy were taken into accout because costs of newborn voles were calculated as it they were self-supporting individuals. Additional costs for lactating females were incorporated in the production and respiration of newborn voles during their nest life.

Total net production was analysed during all 5 periods of the year because it varied over the annual cycle. Since not all periods were equally long the mean daily production per ha was calculated (Table 11).

The highest production occurred between June and August. At the same time in the period from February till October the production associated with growth is augmented by the production of embryos (up to the weight of 1650 mg). Finally, the last period includes only the production associated with growth because in winter no reproduction was observed. The daily production in particular periods of time increased from winter till summer in parallel with the rise of population biomass (Fig. 3) and with augmented reproduction.

Table 12

Net production in the bank vole population per unit of population biomass during the year.

Period	Avg. biomas	cal/g/day
February — March	481.22	7.49
April — May	509.17	16.90
June — July	643.86	19.66
August — October	506.34	11.59
October — January	624.48	3.46
Average	601.700	10.764

Table 13

Proportion of overwintered and current — year animals in the population of red bank vole in assimilation, production and reproduction.

	Over-wintered individuals	This year individuals
Assymilation %%	27.7	72.3
Production %%	11.5	88.5
Production of young %%	62.7	37.3

The mean daily production in particular periods was computed per g of biomass of the population living in a given period (Table 12). The maximum value occurs at the same period as total production per ha/day. Moreover, particularly in the period of reproduction (up to winter) variations of these values are smaller than in the case of total production. This variation in due to higher proportion of younger age classes during intensive reproduction, and hence related to the distribution of production between smaller biomass of population in a given period.

The role of overwintered and current-year animals was compared in respect of total production and assimilation during the year (Table 13). Maintenance of overwintered voles is expensive in relation to production

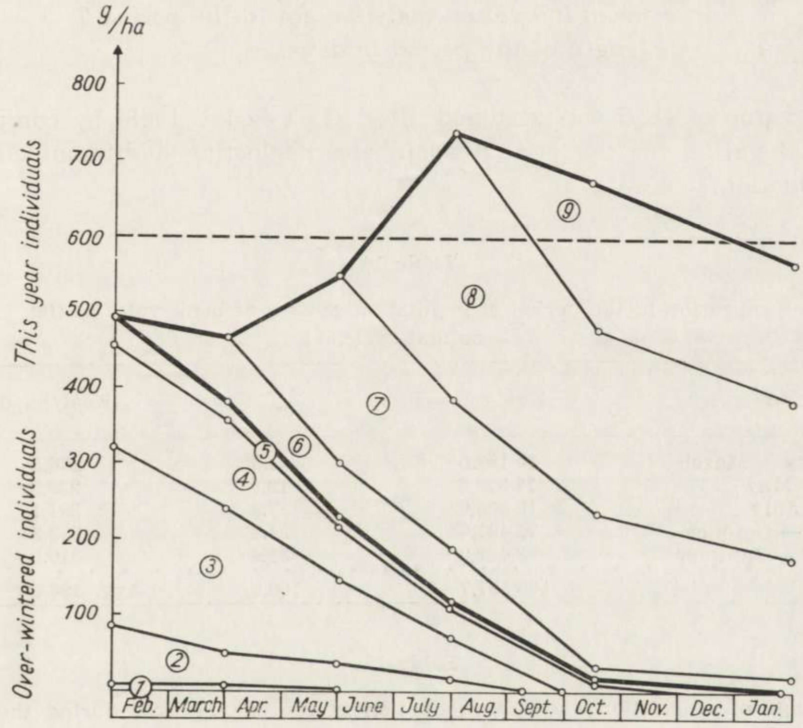

Fig. 3. State of biomass in the red bank vole population (per ha), taking into account cohorts in the annual cycle. Horizontal broken line indicates the mean annual state of population biomass. Numbers in circles correspond to cohorts (according to Table 1). Points labelled with circles represent data obtained by interpolation.

yielded by them, however, overwintered voles produce almost $^2/_3$ of the annual young and hence are important for the population. Despite considerable costs of maintenance they constitute the basis of reproduction for the population.

3.3.3. Costs of Maintenance

Respiration in the period of growth, as well as production due to growth, were calculated for each cohort and each period separately. The following formula was used:

$$R = DEB \times (\bar{N} \times S) \times T$$

where: R — respiration (costs of maintenance)
DEB — daily energy budget (=0.50 Kcal/g/day)
$\bar{N}$ — mean number of individuals in a given period (according to the state at the beginning and at the end)
S — mean individual body weight in the period T
T — length of the period in days.

The value of *DEB* was assumed after Górecki 1968) by computing seasonal values for the annual mean and neglecting additional costs of reproduction.

Table 14

Respiration in the period of population growth of bank voles in the annual cycle.

Period	Kcal/ha	%%	Kcal/ha/day
February — March	14 191.6	13.3	236.5
April — May	14 355.6	13.5	239.3
June — July	18 066.6	17.0	301.1
August — October	26 491.0	24.8	353.2
October — January	33 492.9	31.4	319.0
Total	106 597.7	100.0	Avg. 296.1

Table 15

Percentage of respiration and net production in the energy flow during the year.

Period	Production	Respiration	Costs of pregnancy
Febr. — March	1.32	98.68	.97
Apr. — May	2.89	97.11	2.80
June — July	3.42	96.58	2.95
Aug.—Oct.	2.02	97.98	1.23
Oct.—Jan.	.67	99.33	.00
Average	1.88	98.12	1.34

Total respiration in the period of krowth for the whole year amouted to 106,597.7 Kcal/ha, and elimination to 25,311.7 Kcal per ha, *i.e.* approximately 23.7%. The costs of maintenance of current-year cohorts in the above calculations include individuals from the moment of birth. The highest daily costs of populatoin maintenance occurred in the period from August till October (Table 14).

3.3.4. Assimilation

Analysis of production due to growth, costs of maintenance and pregnancy in the population of red bank voles carried out in particular periods for each cohort gave jointly the following value of energy flow:

Net Production (*P*)	2072.5 Kcal/ha
Respiration (*R*)	108043.2 Kcal/ha
Total	110115.7 Kcal/ha

The annual ratio of *P*/*R* was 1.92%. The structure of costs of maintenance in particular periods (Table 15) shows small differences in distinction to the share of costs of pregnancy and growth. At the some time additional costs of pregnant females were divided proportionally to the number of individuals born in particular periods.

Table 16

Percentage of energy eliminated in the vole population during the year (production + respiration).

Period	%%
February — March	17.23
April — May	24.89
June — July	24.67
August — October	31.04
October — January	19.50
Average	23.69

The costs of pregnancy increase from February to August but later they fall. In winter reproduction is absent. Similarly the costs of growth increase from winter till summer and decrease in autumn period reaching the minimum in winter. To a certain degree these changes are parallel to costs of pregnancy — it is obvious that young individuals (from birth to age class II) show the highest growth rate. On the average, production constitutes approximately 2% of the energy flow through the population of the red bank vole.

A part of elimination, including individuals, already born was subjected to a separate analysis (Table 16). The highest percentage of elimination was observed after culmination of reproduction until autumn. This period includes death of overwintered voles and rather high mortality rate among young animals born at a high population density. Perhaps the deterioration of life conditions in autumn is also responsible for this phenomenon.

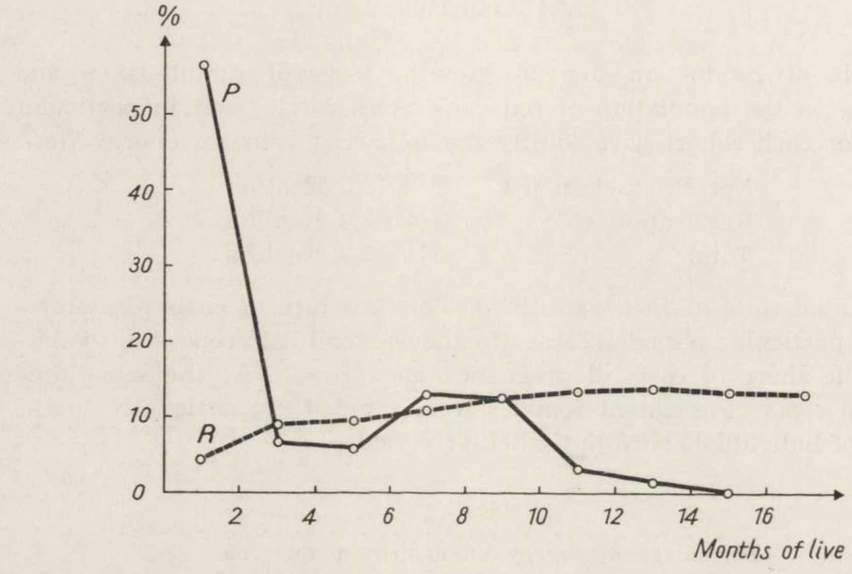

Fig. 4. Percentage distribution of energy in particular life periods of the individual: energy utilized for growth (P) and respiration (R). The total energy consumed for growth or respiration in the life cycle = 100%.

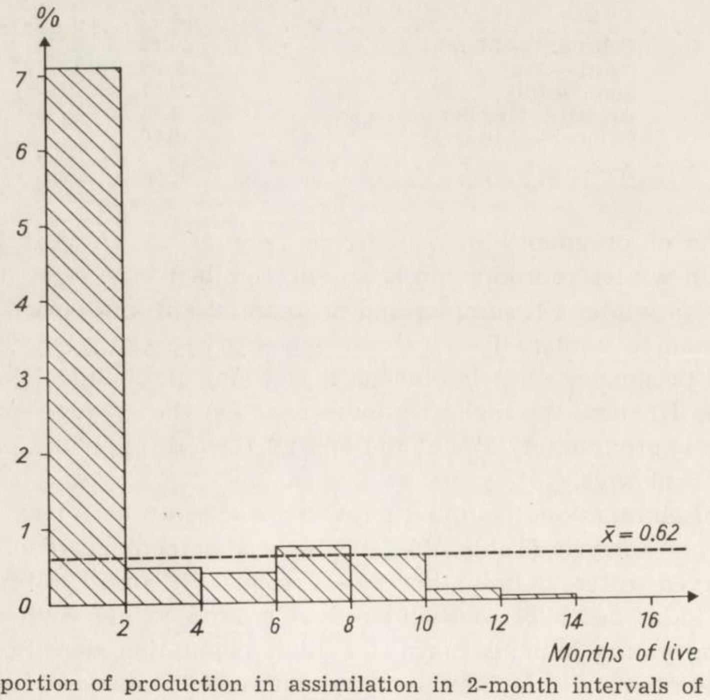

Fig. 5. Proportion of production in assimilation in 2-month intervals of life of the individual = P/A × 100.

The analysis of production and respiration in the life cycle of an individual (Fig. 4) clearly indicates that over half of the total energy utilized for growth is accumulated during the first two months of life. The consumption of energy for respiration is more uniform with the minimum falling for the first two months of life. In the last four months of life the total amount of consumed energy is utilized as costs of maintenance.

The comparison of production efficiency and assimilation (Fig. 5) indicates the occurrence of a maximum in the first two months of life, (around 7%). In the next two-month periods the proportion of assimilated energy incorporated into the body does not exceed oven 1%.

Table 17

The share of cohorts in the energy flow through the population of bank vole and the ratio of production to respiration (*P*/*R*) in %.

Cohort	Per cent of energy flow	*P*/*R*
1	0.1	0.1
2	3.3	0.1
3	13.5	0.2
4	8.5	0.5
5	2.3	0.6
1—5	27.7	—
6	7.9	2.2
7	24.2	2.4
8	27.1	2.6
9	13.1	3.1
6—9	72.3	—

The share of particular cohorts in the total assimilation was investigated (Table 17). Cohorts 7, 8 and 9 (of current-year animals) and cohort 3 of overwintered animals are the most important. The share of the remaining cohorts was small. The proportion of assimilated energy utilized for growth is higher in younger cohorts; this appears from the curve of individual growth.

3.4. Energy Requirements of the Population in the Annual Cycle

The population of bank voles living in a given area takes the energy for production and maintenance from the environment which offers an abundance of plant food during the year (Aulak, 1970; Aulak — in prep.). From the consumed food only 80% of the energy is assimilated by voles (Drożdż, 1968) while 20% is eliminated with feaces and with urine.

The total consumption per ha (at the coefficient of assimilation = 80%) and at the energy flow of 110,115.7 Kcal amounts to 137,644.5 Kcal.

The mean daily energy intake for the whole year amounts to 382.3 Kcal/ha (Fig. 6). The highest daily intake occurs after culmination of reproduction and persists until autumn. The distribution of this value during the annual cycle is rather characteristic, the oscillations around the mean year value being rather small. Particularly striking is the relatively high consumption in the winter period, when plant food is scarce in the habitat. The mean maximum daily consumption exceeds the minimum value by 50.8% only, whereas the biomass of the ground layer plants — the main food for this species — is several times higher in summer than in winter.

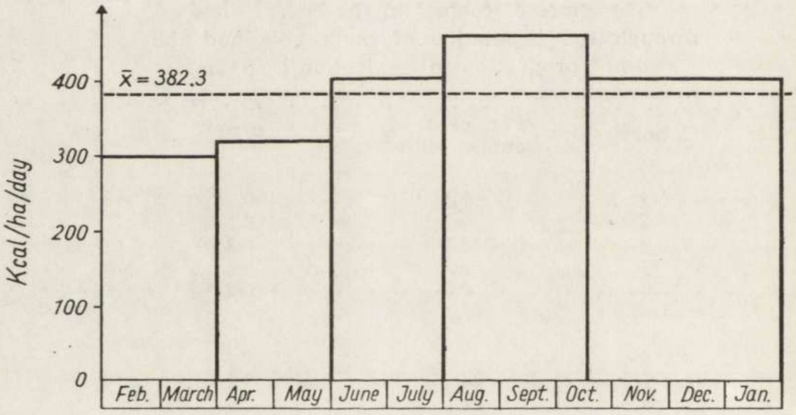

Fig. 6. Daily consumption by a red bank vole population during an annual cycle.

Comparison of the data for the whole year indicates a rather low relation between consumption and primary production of herb layer plants. The bank vole population can at most consume 2.19% of the annual production of herb layer plants.

4. DISCUSSION

Anaylsis of energy flow through a population of bank voles living in a deciduous forest of *Circaeo—Alnetum* type showed small variations in daily consumption between two extreme (in respect of food supply) periods of the year, *i.e.* winter and summer. To estimate the importance of food supply in the dynamics of population of herbivorous animals, the mean daily food carrying capacity of the biotope should be compared with daily food requirements of consumers.

In the analysed biotope only the annual production of the herb layer plants was determined (Aulak, 1970; Aulak — in preparation), according to the method of Traczyk (1967). The state of herb layer biomass in winter was not investigated.

The area of almost 6 ha used for trapping of small mammals was differentiated in floristic composition and primary production. A typical part, consituting 46.5% of the whole SM area, was characterized by the annual primary production of 1,074,573 g per ha. The remaining part (53.5%) with a thinned out tree stand, was wetter and more productive. The annual production of herb layer plants amounted there to 1,760,757 g per ha. The mean production of herb layer plants per ha of the whole SM area amounted to 1,441,682 g or 6,271,316 Kcal/year. The percentage of dominant species, which constituted 86.27% of production, is given in Table 18.

Production calculated by the method of Traczyk is, in this community similar to the maximum state of biomass, since most samples for the estimation of density and individual weight of paricular plant species are taken in a narrow interval of time during summer. The maximum state, with some oscillations, persists for approximately 2 months (July—August). Hence the mean daily capacity of food supply amounts during these two months to 102,808 Kcal, assuming uniform distribution of the biomass in this period.

The daily food carrying capacity in winter was estimated indirectly. It was assumed that the biomass of herb layer plants in winter constitutes 5% of the maximum state. This value is based on the analysis of the state of biomass in the oak-hornbean forest (Aulak — in prep.) where in winter the state of biomass amounts to ca 12% of the maximum state from summer. In that forest association, however, plant species preserving considerable proportion of green parts in winter (mainly *Hepatica nobilis* and *Galeobdolon luteum*) consitute approximately 70% of winter biomass. They are absent in the deciduous forest of *Circaeo-Alnetum* type. The herb layer plant species occuring in this forest may survive winter only in a small degree and they do not constitute valuable food for herbivorous animals. Hence it appears that the assumed index of biomass = 5% of the maximum state is not underestimated and provides a large margin of safety.

The snow cover persists in the Białowieża National Park for approximately 4 months (December—March). The estimated daily food carrying capacity of herb layer plants in this biotope amounts to approximately 2613 Kcal/ha. This constitutes 2.54% of the daily food supply at the summer maximum of the biomass (July—August).

Comparison of these data with the mean daily energy requirement in the population of bank voles (Table 19) clearly indicates that in summer the biotope might feed a population almost 2 than actually existed, and in winter — only a few times larger.

From the relation between winter food supply of herb layer plants in the studied forest and food requirement of the red bank vole population it may appear that even in winter the food is not lacking. However, some additional factors should be also taken into consideration:

Table 18

Proportion of dominant species of herb layer plants in general primary production on the studied area.

Species	%%
Urtica dioica	59.8
Impatiens noli tangere	7.4
Chaerophyllum hirsutum	5.7
Cirsium oleraceum	4.8
Cyperacea	2.2
Graminae	2.2
Chrysosplenium alternifolium	2.1
Geum urbanum	2.0
Total	86.2

Table 19

Relations between daily food supply of the forest (herb layer plants only) and consumption in the red bank vole population.

Season	Summer	Winter
(B) Biomas/day, Kcal	102 808	2 613
(C) Consumption/day, Kcal	429	352
C/B, %%	0.42	13.47

1. Not all species of herb layer plants are consumed by voles. The dominant species in this biotope, *i.e. Urtica dioica,* giving over one half of the total annual production is not attractive for bank voles. Moreover, the majority of dominant species green parts consumed by voles during winter. Hence it seems that the estimate of the biomass under snow as 5% of the maximum state is exaggerated.

2. The Red bank vole is not the only consumer of plants in this biotope; other include some rodents and hoofed mammals.

3. For the winter period red bank voles migrate to the area less frequently flooded with water but also less productive in respect of primary production (by $^1/_3$). Hence a part of the winter biomass is not utilized at all while the pressure of consumers on the remaining part is increased. According to the distribution of trapped voles in summer 50—60% of individuals inhabited the upper, less flooded part of the forest. In autumn this proportion increased already to 70%.

4. The caloric value of plant parts under snow (often with washed out nutritive components) is lower than that of living plants.

5. The most difficult to estimate, and at the same time probably the most important factor in the relation of food-consumer, is food availability. The snow cover is often frozen and renders access to food impossible making the index of winter consumption (13.5%) rather unreal.

After taking into consideration all these factors it becomes clear that the assumption of a constant excess of highly caloric plant food in the annual cycle is doubtful. Any factor changing the relation of food-consumer to the disfavour of consumer (*e.g.* prolonged winter, repeated freezing of the snow cover, *etc.*) may lead to scarcity of food and, in effect cause an increased mortality among rodents.

Analyses of food requirements in populations of small rodents have been conducted by several authors (Górecki & Gębczyńska, 1962; Drożdż, 1966; Grodziński *et al.*, 1966; Holišova, 1966; Watts, 1968; Bobek, 1969; Gębczyńska, 1970; Ryszkowski, 1969; Grodziński, 1971; Holišova, 1971; and others). It was found that the ration of consumption to primary production amounts to merely a few per cent. These relative indices include in principle relations between the annual consumption and production of food. In the deciduous forest of *Circaeo-Alentum* type analysed here the value of this index amounts to 2.19%. In the papers cited above the possibilities of seasonal shortage of food were also considered. However, these were either assumptions or comparisons of the state of food in one selected period with energy requirements of rodents without taking into consideration the factor of food availability, which is difficult to establish.

The study of Holišova (1971) indicates the occurrence of distinct seasonal changes in the diet of bank vole. In early spring the herb layer plants constitute the principal food; in summer the compoistion of the diet is varied. On the other hand, in autumn seeds of trees and shrubs dominate in the stomach content of voles. The analysis of stomach content in the most critical period of winter, when the forest floor is covered with snow, is unfortunately lacking. The fall of seeds occurs mainly in autumn and by then they are in abundance. On the other hand, seed fall in winter is very small, especially in *Circaeo-Alnetum* type of forest. Other food components (fungi, bark, invertebrates, etc.) constitute according to Holišova (*l.c.*) only a small percentage of the diet in spring and late autumn.

Hence it appears that the problem of food scarcity is still an open question. Nevertheless, among factors limiting rodent populations, the lack of one of the basic components of the diet, *e.g.* herb layer plants, may exert significant influence.

Acknowledgements: The author wishes to express cordial thanks to Professor Z. Pucek for enabling these investigations to be carried out, for providing technical and material support, and for critical evaluation of the manuscript. Thanks are due to Dr. K. R. Barbehenn, Washington University, St. Louis, U.S.A., for revising the English text. The help of technical staff of the Mammals Research Institute in the collection and laboratory analysis of the material is also gratefully acknowledged.

REFERENCES

1. Andrzejewski R. & Wrocławek H., 1962: Settling by small rodents a terrain in which catching out had been performed. Acta theriol. *6*, 9: 257—274.
2. Aulak W., 967: Estimation of small mammals density in three forrest biotopes. Ekol. pol. A *15*, 39: 7555—778.
3. Aulak W,. 1970: Studies on herb layer production in the *Circaeo-Alnetum* Oberd., 1953 association. Ekol. pol. A *18*, 19: 411—427.
4. Bobek B., 1969: Survival, turnover and production of small rodents in a beach forest, Acta theriol. *14*, 15: 191—210.
5. Buchalczyk A., 1970: Reproduction, mortality and longevity of the bank vole under laboratory condition. Acta theriol. *15*, 10: 153—176.
6. Bujalska G., Andrzejewski R. & Petrusewicz K., 1968: Productivity investigation of an island population of *Clethrionomys glareolus* (Schreber, 1780). II Natality. Acta theriol. *13*, 24: 415—425.
7. Bujalska G. & Ryszkowski L., 1966: Estimation of the reproduction of the bank vole under field conditions. Acta theriol. *11*, 14: 531—361.
8. Chełkowska H. & Ryszkowski L., 1967: Causes of higher abundance estimates of small rodents of the edges of sampling areas in forest ecosystems. Ekol. pol. A *15*, 37: 737—746.
9. De Lury D. B., 1947: On the estimation of biological populations. Biometrics *3:* 145—167.
10. Dróżdż A., 1966: Food habits and food supply of rodents in the beech forest. Acta theriol. *11*, 15: 363—384.
11. Dróżdż A., 1968: Digestibility and assimilation of natural foods in small rodents. Acta theriol. *13*, 21: 367—389.
12. Gębczyńska Z., 1970: Bioenergetic of a root vole population. Acta theriol. *15*, 3: 33—66.
13. Gliwicz J., Andrzejewski R., Bujalska G. & Petrusewicz K., 1968: Productivity investigation of an island population of *Clethrionomys glareolus* (Schreber, 1780). I. Dynamics of cohorts. Acta theriol. 13, 23: 401—413.
14. Górecki A., 1965: Energy values of body in small mammals. Acta theriol. *10*, 23: 333—352.

15. Górecki A., 1968: Metabolic rate and energy budget in the bank vole. Acta theriol. *13*, 20: 341—365.
16. Górecki A. & Gębczyńska Z., 1962: Food conditions for small rodents in a deciduous forest. Acta theriol. *6*, 10: 275—295.
17. Grodziński W., 1971: Energy flow throught populations of small mammals in Alaskan Taiga Forest. Acta theriol. *16*, 17: 231—275.
18. Grodziński W., Bobek B., Drożdż A. & Górecki A., 1969: Energy flow throught small rodents in a beech forest [in: »Energy flow through small mammal populations«, Eds. Petrusewicz K. & Ryszkowski L.]. Polish Sci. Publ.: 291—298. Warszawa.
19. Grodziński W., Górecki A., Janas K. & Migula P., 1966: Effect of rodents on the primary productivity of alpine meadows in Bieszczady Mountains. Acta theriol. *11*, 20: 419—431.
20. Grodziński W., Pucek Z. & Ryszkowski L., 1966: Estimation of rodent numbers by means of prebaiting and intensive removal. Acta theriol. *11*, 10: 297—314.
21. Hansson L., 1969: Home range, population structure and density estimation of removal catches with edge effect. Acta theriol. *14*, 11: 153—160.
22. Hayne D. W., 1949: Two methods for estimating population from trapping records. J. Mammal. *30:* 399—411.
23. Holišova V., 1966: Food of an overcrowded population of the bank vole, *Clethrionomys glareolus* Schreb., in a lowland forest. Zool. listy *15*, 3: 207--224.
24. Holišova V., 1971: The food of *Clethrionomys glareolus* at different population densites. Acta Sc N.at. Ac. Sci. Boh. *5*, 11: 1—33.
25. Kaczmarski F., 1966: Bioenergetics of pregnancy and lactation in the bank vole. Acta theriol. *11*, 19: 409—417.
26. Petrusewicz K., Andrzejewski R., Bujalska G. & Gliwicz J., 1968: Productivity investigation of an island population of *Clethrionomys glareolus* (Schreber, 1780). IV Production. Acta theriol. *13*, 26: 435—445.
27. Pucek Z. & Zejda J., 1968: Technique for determining age in the red-back vole, *Clethrionomys glareolus* (Schreber, 1780). Small Mammal Newsletter *2:* 51—60.
28. Ryszkowski L., 1969: Estimates of consumption of rodent population in different pine forest ecosystems [In: »Energy flow through small mammal populations«, Eds. Petruszewicz K. & Ryszkowski L.]. Polish Sci. Publ.: 281—289. Warszawa.
29. Traczyk T., 1967: Propozycja nowego sposobu oceny produkcji runa. Ekol. pol. B *13*, 3: 241—247.
30. Watts C. H. S., 1968: The foods by wood mice (*Apodemus sylvaticus*) and bank vole (*Clethrionomys glareolus*) in Wytham Woods, Berkshire. J. Anim. Ecol. *37:* 25—41.

Accepted, January 30, 1973

Institute of Forest and Wood Protection,
Agricultural Academy,
Rakowiecka 26/30, 02-528 Warszawa,

and

Mammals Research Institute,
Polish Academy of Sciences,
17-230 Białowieża, Poland.

Władysław AULAK

PRODUKCJA I ZAPOTRZEBOWANIE ENERGETYCZNE POPULACJI NORNICY RUDEJ, *CLETHRIONOMYS GLAREOLUS* (SCHREBER, 1780) W LESIE ŁĘGOWYM

Streszczenie

W Białowieskim Parku Narodowym w zespole *Circaeo-Alnetum* Oberd., 1953 prowadzono odłowy drobnych ssaków zmodyfikowaną metodą SM (Aulak, 1967) w latach 1966—1968.

Dla okresu jednego roku przeanalizowano przepływ energii i zapotrzebowanie pokarmowe populacji *Clethrionomys glareolus*. Wyliczenia prowadzono dla 5 okresów roku w wyróżnionych 9 kohortach różniących się interwałem wiekowym równym 2 miesiące.

Liczebność populacji w każdym cenzusie oszacowano według prostej regresji dodając w każdym wypadku ilość osobników niełownych (młodych w gniazdach). Przeciętne zagęszczenie populacji w analizowanym roku wyniosło 37,6 osobników na 1 ha (Ryc. 1).

Wielkość asymilacji określono na 110.115,7 Kcal/ha.

Określono produkcję przeciętną dzienną w różnych okresach roku. Maksimum przypada na okres intensywnej reprodukcji (Tab. 10).

Stwierdzono duży udział przezimków w przepływie energii przy małej ich produkcji netto. Uznano, że mimo zbyt kosztownego dla populacji utrzymania przezimków, stanowią one bazę rozrodczą w danym roku, dając ponad 60% młodzieży.

Określono wielkość rocznej konsumpcji = 137.644,5 Kcal/ha. Stwierdzono, że wahania dobowego zapotrzebowania energii przez populację nornicy między okresami niewiele się różnią (Ryc. 6).

Zbadano relacje między dobowymi możliwościami wyżywieniowymi warstwy runa badanego biotopu a dobową konsumpcją w okresie maksimum i minimum żeru (Tab. 19). Wykazano bardzo dużą nadwyżkę żeru w okresie lata (ponad 200 krotna) i tylko kilkukrotną nadwyżkę stanu karmy w okresie zimowym w porównaniu z zapotrzebowaniem populacji nornicy.

Stosunek konsumpcji całorocznej do rocznej produkcji pierwotnej runa wyniósł 2,19%.