

Bioenergetics and total impact of vole populations

W. Grodziński, M. Makomaska, R. Tertil, J. Weiner

Department of Animal Ecology, Jagiellonian University, Kraków

Grodziński, W., Makomaska, M., Tertil, R. and Weiner, J. 1977. Bioenergetics and total impact of vole populations. - *Oikos* 29: 494-510.

The objective of this study has been to estimate the consumption of common vole *Microtus arvalis* (Pall.) populations in the field and to compare it with total impact, e.g. destruction of plants, suppression of growth, and crop deterioration. Respirometric investigations have shown that the average daily metabolic rate (ADMR) of voles is correlated with body weight, ambient temperature, season, and number of individuals living in a group. The equations have been fitted to predict energy requirements of voles of various age and sex categories. Starting from energy budgets a simulation model of energy balance for the whole population has been constructed. The choice of population parameters (numbers, age and sex structure) was rather arbitrary, but based on values obtained from the literature. Estimations were done for four variants: alfalfa and wheat fields in a year of normal and outbreaking density of voles. Total energy consumption estimated in this way ranged from 219.3 to 1765.7 Mcal ha⁻¹ yr⁻¹ in the year of normal density and from 1765.7 to 24321.8 Mcal ha⁻¹ yr⁻¹ in the year of outbreak for wheat and alfalfa fields, respectively. The highest consumption was observed in mid-summer, the lowest in early spring. Total impact on alfalfa fields was determined for a period of 42 d in late summer. The maximum daily consumption of alfalfa was 27.2 kg ha⁻¹ d⁻¹, while the total impact as much as 365.2 kg ha⁻¹ d⁻¹. In wheat fields the impact was estimated for a period of 80 d (April-July) in terms of influence on grain quantity and quality. In the year of outbreak, consumption of the population reduced the grain crop by 0.5 kg ha⁻¹ d⁻¹, and total impact by 2.25 kg ha⁻¹ d⁻¹. The total impact on both crops studied was 4 to 13 times greater than the consumption as computed from energy requirements. Thus, extraenergetic effects of rodents on vegetation markedly exceed the effects of consumption alone.

W. Grodziński, M. Makomaska, R. Tertil and J. Weiner, Dept of Animal Ecology, Jagiellonian University, Krupnicza 50, 30-060 Kraków, Poland.

Предмет данного исследования - измерение потребления пищи популяциями *Microtus arvalis* (Pall.) в природных условиях в сравнении с общим влиянием, т.е. повреждением растений, подавлением роста и детериоризацией урожая. Измерение дыхания показало, что средне-суточная метаболическая активность коррелирует с весом тела полевок, окружающей температурой, сезоном и числом животных в группе. Предложены уравнения для выражения энергетических потребностей полевок различного пола и возраста. На основании энергетического бюджета создана энергетическая модель всей популяции. Выбор параметров (численность, возрастная структура, соотношение полов) несколько произволен, но базируется на литературных данных. Измерения сделаны для 4-х вариантов: поля люцерны и пшеницы в годы нормальной численности и вспышки массового размножения. Общее потребление энергии составляло 219,3-1765,7 мкал.га⁻¹.год⁻¹ - в год нормальной численности и 1765,7-24321,8 мкал.га⁻¹.год⁻¹ - в год массового размножения для полей пшеницы и люцерны соответственно. Наибольшее потребление наблюдалось в середине лета, минимальное - ранней весной. Общее влияние на полях люцерны составляло период в 42 дня поздним летом. Максимум суточного потребления люцерны составлял 27,2 кг.га⁻¹.д⁻¹, а общее влияние на растительность - 365,2 кг.сут.⁻¹. На полях пшеницы влияние измерялось 80 дней (апрель-июль), что выражается в количестве и качестве зерна. В год массового размножения потребление популяции снижает урожай зерна на 0,5 кг.га⁻¹.день⁻¹, а общее влияние - 2,25 кг.га⁻¹.день⁻¹. Общее влияние на растительность на обоих исследованных полях в 4-13 раз больше, чем потребление пищи, рассчитанное на основании энергетических потребностей. Таким образом, экстраэнергетическое влияние грызунов на растительность значительно превосходит результаты одного лишь потребления пищи.

1. Introduction

In a bibliography for voles of the genus *Microtus* Golley (1963) listed 900 references of which only three refer directly to the metabolism and nutrition of these rodents. Over the last decade of IBP the knowledge of bioenergetics of voles increased greatly (Grodziński and Wunder 1975).

In Europe, two vole species (*Microtus arvalis* and *Microtus agrestis*) have become the primary subjects of studies of metabolism, energetics of growth and reproduction and utilization of food energy. Consequently, we are able to construct refined energy budgets for both species.

Energy processing is important, but the ecological and economic role in various ecosystems is usually far greater than may be inferred from simple energy estimates of consumption. This study deals with populations of the common vole *M. arvalis* (Pall.), which is a serious crop-pest in continental Europe. However, the work is relevant to the field vole *Microtus agrestis* (L.), which is a similar nuisance in Scandinavian countries and also on the British Isles.

The aim of this work has been to compare estimates of energy utilization with estimates of total impact in the case of populations of the common vole. Sophisticated bioenergetic modelling has been applied to estimate total consumption by populations, but population parameters of an "artificial" vole population have been considerably simplified.

This paper reports on research carried out during five years in the Dept of Animal Ecology, Jagiellonian University, and mainly includes unpublished material. The following studies have contributed to this work: metabolic investigations on the common vole (Grodziński unpubl.); studies of metabolic rate of vole groups (Makomaska 1973), and research concerning vole impact upon cultivated fields (Tertil 1976, 1977). All efforts with modelling are due to J. Weiner. There are a few monographs on the common vole (e.g., Kratochvil 1959, Bashenina 1962, Straka 1967) from which we have extracted many data, but not the idea for our team effort.

Energy budgets for *Microtus* voles have previously been constructed. Golley (1960) first used the double fasting metabolic rate (FMR) to determine energy requirements of the meadow vole *Microtus pennsylvanicus* under field conditions. Later, the resting metabolic rate (RMR) was applied to the estimation of energetics of this vole (Wiegert 1961) and the field vole, *Microtus agrestis* (Grodziński 1961). Trojan and Wojciechowska (1969) followed the RMR approach in constructing a more complex ecological model of energy budget for *Microtus arvalis*.

2. Material and methods

Almost 320 common voles were used in the studies

extending over a period of 5 yr (1971-75). All the voles were taken from southern Poland. The animals were held in captivity for a short time; only a few reproduced in captivity. Metabolic investigations were carried out in the laboratory, while field studies were conducted at the Experimental Farm of the Jagiellonian University in Polanka-Haller.

Average daily metabolic rate (ADMR) and resting metabolic rate (RMR) were measured by oxygen consumption. Two types of close circuit-system respirometer were used - an automatic, continuously recording Morrison respirometer (Morrison and Grodziński 1975), and a modified Kalabukhov-Skvortzov respirometer (Górecki 1975). With larger groups of voles, measurements were taken in an open flow respirometer "Spirolyt", with paramagnetic analyser for oxygen and diapherometric one for carbon dioxide.

The procedure for ADMR and RMR measurements has been described in detail previously (Morrison and Grodziński 1975, Górecki 1975). The two measurements differ mainly in the duration of run and size of animal chamber. The ADMR runs lasted from 25 to 28 h, while the RMR runs only about one hour, including an adaptation time. During ADMR measurements the voles were kept in large 9-l chambers with food, nest and activity treadmill. In contrast, during RMR measurements the animals remained in small (100 cm³) wire cages which limited their activity. In the large chambers, animal activity out of the nest box was recorded from switching gates and treadmills.

Series of standard ADMR measurements, i.e. taken at ambient temperature of 20°C, were completed in three seasons: late spring to early summer, autumn and winter. Additional ADMR measurements were taken in winter at different ambient temperatures (0°, 10°, 20° and 30°C) with or without nest, with or without treadmill, and in groups of 2 to 4 individuals. The resting metabolic rate (RMR) was measured in winter and summer at four ambient temperatures: 0°, 10°, 20° and 30°C.

The influence of social effects in a group of voles on their metabolism was investigated separately by measuring the metabolism of natural "families" consisting of from 3 to 15 voles. During measurements the voles remained in the same cages in which they were reared (surface area of about 850 cm²), provided with food and nest, ambient temperature being 20°C. The measurements lasting from 2 to 4 h included periods of both activity of the animals and of their sleep in the nest. All the conditions of these measurements, except their duration, meet the requirements of an ADMR measurement.

A method of impact estimation has been described by Tertil (1974, 1976, 1977). It consists in exposing the above-ground parts of plants under controllable circumstances to the grazing of common voles. Framed wire screens of 0.5 m² were used. The screens were placed on the wheat crops in early spring, while on

alfalfa immediately after cutting. The screens with crop plants growing through, were then shielded with portable metal small enclosures to prevent voles from burrowing and escaping. The crop growing through the screen was exposed to grazing by one adult male, about 20 g in weight, for a period of one week. The impact was not estimated immediately after exposure but at harvest time. In the case of alfalfa, the green and dry mass and the stems/leaves ratio were estimated as well as the amount of weeds.

In wheat crop estimates were made of the number and weight of ears, and the weight of grain and straw. In addition, grain quality was estimated by determining the share of grain size fractions. The wheat grain was divided into four size fractions, depending on the minor diameter: 2.8, 2.5, 2.2 and below 2.2 mm (grain waste). In addition the weight of 1000 grains was estimated. Both these measures of yield quality are commonly adopted in agricultural practice. All results were related to the control plots which were not exposed to vole grazing, however covered by the same screens.

Significance of differences between means, regression slope coefficients and intercepts were estimated by t-test.

3. Results

3.1. Metabolic rates

The average daily metabolic rate (ADMR) has been adopted as a fundamental measure of metabolic rate. This ecological measure contains energy for basal metabolism, thermoregulation, locomotor activity and specific dynamic action (Gessaman 1973, Grodziński and Wunder 1975).

The values of ADMR for single adult common voles kept in large chambers with nest and food at 20°C, are given in Tab. 1. Mean body weights of the voles studied during these seasons varied only slightly, ranging from 19.0 to 22.2 g. Despite this, the average value of ADMR showed distinct seasonal changes, being highest in the late spring and summer, lowest in winter, and intermediate in autumn (Tab. 1). The differences in ADMR level were highly significant between winter and summer ($p < 0.01$) and between winter and autumn ($p < 0.05$), but not significant between summer and autumn ($0.1 < p < 0.2$).

Seasonal changes in the vole metabolic acclimatiza-

tion are well known (Smirnov 1968, Kalabukhov 1969) and the seasonal correction factors in Tab. 1 were employed for calculating annual energy budgets.

There was a strong correlation between the ADMR and vole body size. The relationship was additionally analysed for the autumn series, which was the most numerous ($N = 45$) and extended in the range of body weight (from 12 to 42 g). Relation between the ADMR and body weight may be expressed by the following power function (Grodziński 1969):

$$\text{ADMR} = 19.5 W^{-0.48} \quad (1)$$

where ADMR is measured in $\text{ccm O}_2 \text{ g}^{-1} \text{ h}^{-1}$, W in grams. Parametric values were determined by least squares regression of logarithmically transformed data.

The exponent of this function ($b = -0.48$) is statistically indistinguishable from that of a recently reported interspecific function ADMR - body weight for rodents ranging between 7 g and 370 g (Grodziński and Wunder 1975). The slope of the autumn regression ($b = -0.48$) has been used in all further computations. The intercept value (19.5) was modified by seasonal correction factors (Tab. 1) for the other seasons.

RMR is temperature-dependent (Fig. 1). The relationship being linear in winter as well as in summer up to thermoneutral zone, which for the common vole falls around 30°C (Bashenina 1966). These relationships may be expressed by the following linear regression equations:

$$\text{Winter: RMR} = 9.688 - 0.2183 t \quad (2)$$

$$\text{Summer: RMR} = 10.476 - 0.2174 t \quad (3)$$

where RMR is measured in $\text{ccm O}_2 \text{ g}^{-1} \text{ h}^{-1}$, t in °C.

The winter and summer regressions are almost identical as to their slope, but they differ significantly in the intercept ($p < 0.001$), the summer line situated well above the winter line. This may indicate that thermoregulation in winter is less intensive at the same temperature.

Our study was the first attempt to determine ADMR at various temperatures other than 20°C and has proved both instructive and useful for the modelling of energy budgets. The relationship was studied only in winter when it is crucial for the energetics of vole. It has a curvilinear character (Fig. 1) and, therefore, is best described by a polynomial of the second or third order:

$$\text{ADMR} = 7.315 - 0.2169 t + 0.00303 t^2 \quad (4)$$

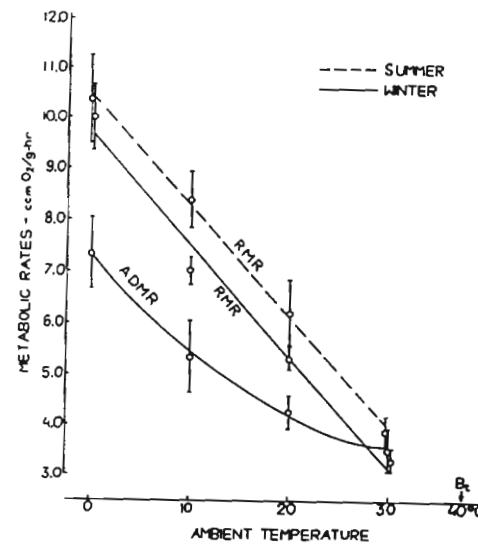


Fig. 1. Resting metabolic rates (RMR) and average daily metabolic rate (ADMR) of common voles at different ambient temperatures. RMR - linear regressions, ADMR - second order polynomial regression (Eqs 2, 3 and 4). Solid lines represent winter animals, broken line represents summer animals. Mean values (points) ± 2 S.E. are shown. B_t - body temperature.

where ADMR is measured in $\text{ccm O}_2 \text{ g}^{-1} \text{ h}^{-1}$, t in °C.

Regression analysis showed that a polynomial of 3rd order fits only slightly better than that of 2nd order, and, therefore, a quadratic equation has been applied to all further computations.

The curvilinear relationship between ADMR and ambient temperature suggests that we are dealing here with a function of several independent variables, including chemical thermoregulation, which varies depending on whether the animal is in or outside the nest, as well as various means of behavioral thermoregulation, e.g. adaptation to the duration and level of activity

outside the nest, insulation of nest etc. It was noted, for example, that at lower temperatures the voles utilized more materials for nest building. The curve ADMR - ambient temperature lies below analogous winter curve for the RMR - temperature relationship. This is possible due both to nest insulation in ADMR chambers and to some behavioural stress during the short runs in RMR cages. The two curves overlap only in the thermoneutral zone at 30°C. The credibility of this comparison is enhanced by the fact that the both metabolisms were measured in the same animals ($N = 21$).

The ADMR - ambient temperature function has been incorporated into the model of energy budget by solving for the temperatures recorded under natural conditions in cultivated fields.

To estimate the effect of nest insulation alone on the vole metabolism, the ADMR was measured for 14 individuals kept in respirometers with/or without nests at 20°C. The measurements carried out in winter gave an average ADMR value of $4.0744 \text{ ccm O}_2 \text{ g}^{-1} \text{ h}^{-1}$, with nests, as compared with $5.0815 \text{ ccm O}_2 \text{ g}^{-1} \text{ h}^{-1}$ without nests. The difference between these two values (24.7%) is highly significant ($p < 0.005$).

3.2. Social effect

A social effect, which decreases the metabolic rate, has been observed in all measurements obtained from groups of voles (Tab. 2). This decrease in metabolic rate may be expressed in relation to the anticipated metabolism of a group computed solely on the basis of body weight. An appropriate regression equation was calculated using data from measurements of single individuals under the same experimental conditions as for a group (Makomaska 1973). The level of metabolic rate for single animals has been assumed as 1.0. The coefficients of metabolic rate decrease show a significant difference between families of from 3 to 7 individuals, but they do not differ statistically between families of more than 7 individuals and those of 7 individuals. The decrease in metabolic rate can be described by the following equation (Fig. 2):

Tab. 2. Influence of social effects on the metabolic rate of common voles.

Number of animals in a group	2*	3	4	4*	5	6	7	9	10	12	15
Number of measurements	4	10	20	2	11	10	10	10	10	10	4
Mean \pm S.D. Metabolic rate $\text{ccm O}_2 \text{ animal}^{-1} \text{ h}^{-1}$	96.44 ± 6.68	113.28 ± 15.86	100.35 ± 9.89	87.24 ± 6.25	97.31 ± 11.11	86.63 ± 12.85	76.30 ± 11.09	78.56 ± 10.68	81.77 ± 11.11	78.38 ± 16.05	76.39 ± 13.45
Coefficient of metabolic decrease	0.958	0.864	0.797	0.836	0.784	0.744	0.657	0.705	0.731	0.718	0.680

* ADMR measured in Morrison's respirometer.

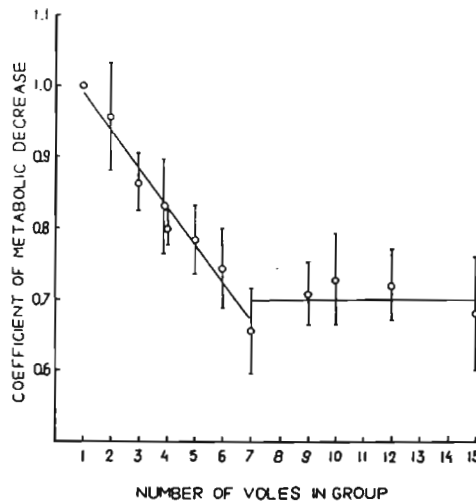


Fig. 2. Decrease in metabolic rate in groups of common voles consisting of 2-15 animals kept together. The coefficient 1.0 represents the metabolic level predicted for single animals studied separately.

$$h = \begin{cases} 1.0344 - 0.0509 N & \text{for } N < 7 \\ 0.701 & \text{for } 7 \leq N \leq 15 \end{cases} \quad (5)$$

where h is the decrease in metabolic rate relative to the single individuals, and N is number of voles in a group.

The social effect determined from ADMR measurements in Morrison's respirometer for groups of 2 and 4 voles did not differ from the result obtained with a flow respirometer. In groups of 2 and 4 individuals, the coefficients of metabolic rate decrease were 0.958 and 0.836, respectively. These figures fit well the regression computed solely from data obtained with a flow respirometer (Fig. 2).

Under natural conditions voles spend most of the 24-h period clustered in burrows (Frank 1953), mainly sleeping, although they also show some activity such as grooming or feeding on food reserves (Bashenina 1968).

The measurements of group metabolism carried out under conditions described in this paper take into account natural patterns of activity as well as the influence of social relations created in a group. Several attempts to estimate the influence of huddling on the metabolic rate decrease in voles have not dealt with social factors, and thus the effect of huddling may have been underestimated (Ponugaeva 1960, Trojan and Wojciechowska 1969).

3.3. Circadian activity

The activity of voles was recorded during all 24-h runs of ADMR, which made it possible to determine both the

duration of activity outside the nest and the daily pattern of activity. Total activity of the common voles outside the nests showed seasonal changes. At 20°C it averaged 6^h58' (28%) during late spring and summer, and 5^h55' (25%) in autumn, but only 4^h29' (18%) in winter.

Additional ADMR and daily activity measurements were completed in winter at various ambient temperatures. At 0, 10, 20 and 30°C the daily duration of activity averaged, 5^h43', 5^h30', 4^h35' and 10^h42' respectively. Activity showed great individual variability: the coefficient of variation ranged from 12 to 39%. Also the daily pattern of activity varied depending on season and ambient temperature, but was always polycyclic with most activity in darkness.

Many laboratory studies on the common vole and the field vole indicate that both voles are very active, their activity being of the polycyclic type and season-dependent (Davis 1933, Durup 1956, Erkinaro 1961, Grodziński 1963, Smirnov 1968, Hansson and Grodziński 1970). Only recently, however, has it become feasible to determine the daily activity of both vole species under natural conditions by means of continuous tracking of animals labelled with radio-cobalt (Nikitina et al. 1972) or by monitoring the temperature difference between the inside and outside the nest (Flowerdew 1973). On a July day the adult common vole may stay outside the nest for an average of 9^h43' (Nikitina et al. 1972) whereas a male field vole in March can be outside for almost 11 h. In winter the activity outside the nest is probably far more limited.

It seems that the activity, and at any rate its duration, recorded in this study on the common vole is not far below that found under natural conditions. The spontaneous daily activity of voles is regulated mainly by natural daylight. Therefore, it has been assumed in all further computations that an ADMR measurement includes the energy costs of locomotor activity, which is about the same as in the field conditions.

3.4. Nutrition: digestibility and assimilation of foods

Many observations exist on the diet of the common vole under field conditions and its seasonal changes (cf. Bashenina 1962). These data mainly come from the analysis of stomach contents (Holišova 1959) and lead to two general conclusions: the vole diet contains chiefly greens, at least 60-70% of the stomach contents, and seasonal changes in diet are much less than changes in the crops in the cultivated fields.

The utilization of natural and laboratory foods by the common vole has been studied in detail by Drożdż (1968) and Sawicka-Kapusta et al. (1975) using a technique of metabolic cages. Digestibility and assimilation is relatively low (Tab. 3). The assimilation of all greens and rape ranges from 59 to 68%, and only for oats grain it is definitely higher (90%). The utilization of alfalfa, clover and grass changes with season, because the plants have a different crude-fibre content in various

Tab. 3. Digestibility and assimilation of natural foods in common voles (as percentage of consumption i.e. of gross energy) (After Drożdż 1968, Sawicka-Kapusta et al. 1975).

Diets	Crude fibre content (% of dry matter)	Digestibility Av.	± S.D.	Assimilation Av.	± S.D.
Oats	1.6	92.3	1.4	89.7	0.9
Green wheat	27.5	70.4	1.6	65.2	1.1
Alfalfa - summer	15.1	71.2	5.6	66.5	5.9
- autumn	19.1	62.4	1.8	59.1	2.5
Clover - summer	29.2	74.9	9.6	68.3	10.8
- autumn	12.2	78.6	0.4	75.3	4.4
Grass - summer	19.3	65.9	1.3	60.7	1.0
- autumn	12.8	76.2	2.2	73.2	2.1
Rape - autumn	12.5	78.1	5.5	68.4	5.5

seasons or even harvests (Tab. 3). As is well known, the level of digestibility and assimilation depends on chemical composition of the food, mainly on the content of poorly digestible fibre, which is found in the cell-wall constituents, s.c. CWC (Keys and Van Soest 1970). The mean value of assimilation was about 65% for the foods studied in summer, while it reached 69% for the autumn foods (Tab. 3). It is very likely that foods available in winter, except grain, have an even lower nutritive value. It may be assumed that a mean annual coefficient of assimilation in the common vole is 60%, or even less. Such a level of assimilation, regardless of seasonal variations, has been applied to the model.

Voies are typical grazing herbivores and are characterized by the lowest level of digestibility and assimilation among small mammals (Grodziński and Wunder 1975). In several vole species (*Microtus agrestis*, *M. pennsylvanicus*, *M. oeconomus*) fed on natural foods, the digestibility and assimilation of energy and/or organic matter has been found to range from 50% to 74% (Gębczyńska 1970, Johnson and Groepper 1970, Keys and Van Soest 1970, Hansson 1971).

3.5. Impact

Energetic estimation of consumption by herbivorous rodents made it possible to evaluate their impact on a given kind of vegetation. However, (Spitz 1968, Ryszkowski et al. 1973, Abaturon et al. 1975, Zlotin 1975) the consequences of animal feeding may considerably exceed the amount of consumption of primary production itself. The difference between these values is of particular importance when estimating the impact on cultivated plants.

Crops that are affected by rodents may be divided into two main categories: (1) those utilized by man in the same form that is devoured by rodents in the field (fodder crops cultivated as green forage, e.g. alfalfa, clover and mixed grasses), and (2) those exploited by man in a form other than that on which the rodents feed during most of vegetative season (e.g. cereals and root crops). In both crop types, voles utilize mainly the

green, above-ground parts of plants (Bashenina 1962, Ružić 1971).

Estimation of the total impact on alfalfa requires consideration of: (1) the level of consumption, (2) biomass wasted but not consumed, (3) losses due to unrealized growth of the crop's green mass, (4) changes in the botanical composition of the crop (succession by weeds, especially some monocotyledons), and (5) changes in the characteristics of individual plants resulting from grazing (stem/leave ratio).

Effects (1) and (2) are the easiest to determine; however, reduction of the rodent impact to just these effects may only be applied in very short periods of time. Effect (3) plays a role when short periods between hay-cutting are considered. Effects (4) and (5) are of importance in the long run (one year or several years), although a rapid invasion of monocotyledonous weeds may occur even in short time periods after prolonged rainy weather.

Tab. 4 shows the total impact of voles in an alfalfa field in relation to the consumption of these animals. It refers to a period of 50 d between the second and the third alfalfa cuttings. The assumption has been made that consumption of each gram of the biomass results in a series of additional effects which further decrease the crop useful for man. Coefficients of destruction (DEST), unrealized growth (UNGR), succession of weeds (SUCC), and changes in the stem/leave ratio (STLEA) has been employed. The first coefficient (DEST) has been adopted from Ryszkowski et al. (1973) and modified for different phases of the crop's growth. Others are taken from a study by Tertli (1976). The way for calculating these coefficients was recently described in detail (Tertli 1977). It concerned the total biomass of alfalfa, the content of wheat biomass and also the stem/leave ratio in the final crop harvest from exposed and control plots.

Consumption (C) is connected with destruction of an additional amount of biomass; the younger the crop, the greater the loss. By multiplying C by DEST one obtains a total amount of the biomass removed from the system by rodents. The removal of biomass also reduces current growth - the amount has been determined experimentally and expressed as the UNGR coefficient. The

Tab. 4. Total impact of voles on the alfalfa cultivation – coefficients for estimation different effects.

Coefficient (symbols in parenthesis)	Alfalfa growth (in days after cutting)			
	11–20	21–30	31–40	41–50
Destroying (DEST)	1.8	1.5	1.3	1.1
Unrealized growth (UNGR)	1.25	2.41	2.70	2.33
Succession (SUCC)	2.43	3.33	1.64	1.56
Stem/leave ratio (STLEAF)	0.89	1.15	1.49	1.54
Total impact (TOTAL)	4.87	13.84	8.57	6.16

mass of alfalfa which has been superseded by the weeds is estimated by an additional, experimentally determined coefficient (SUCC) and multiplication of C by DEST and by SUCC gives total losses of alfalfa resulting from vole consumption.

However, the nutritive quality of alfalfa for domestic livestock depends mainly on the stem/leave ratio, and STLEAF has been introduced to account for the change in this ratio in the grazed plants. All these corrections may be expressed as one TOTAL coefficient, which is their multiplication product. Consumption C multiplied by TOTAL gives the IMPACT on alfalfa leaves.

The example in Tab. 4 shows that alfalfa is most resistant to vole impact in the early stages of growth. The high rate of growth at this time compensates for the losses due to rodent feeding. Moreover, grazing during this period improves the stem/leave ratio. Exceptionally high values of SUCC in the case studied resulted from an acceleration of weed succession, caused by long periods of rain in the course of experiments (Tertil 1976).

It must be emphasized that the computed TOTAL coefficients do not represent a simple decrease in loss of biomass in the field, but a combined effect, including a decrease in alfalfa biomass, a higher proportion of stems, and a partial replacement of alfalfa by weeds. SUCC strongly depends on the year's climatic conditions, and the effect STLEAF is rather small (Tab. 4). If both these coefficients are disregarded, then consumption for the four periods under consideration should be multiplied by factors of 2.25, 3.61, 3.51 and 2.56, respectively.

The impact of rodents on a cereal crop may be computed by a slightly different method. Total impact of voles on winter wheat crop from the spring onset of vegetation till harvest was calculated (Tab. 5) on the

basis of studies by Tertil (1974, 1976). The coefficients QUANT and QUAL were used to designate the quantity and quality of grain crops. They indicate the influence of consumption by voles when grazing wheat at different stages of development. QUANT reflects the influence on total weight of grain crop, QUAL on its quality (technological usability of grain), while the factor TOTAL integrates both types of damage.

Values given in the first three columns of Tab. 5 illustrates the effect of consumption of stems and leaves on the parameters of grain crop. The last column shows how the consumption of grain itself affects the total grain crop.

The very high TOTAL coefficient for 241–260 d occurs because grazing is particularly harmful to wheat at the stage of earing (Tertil 1974). Aside from this specific period wheat is quite resistant to impact of voles (Tab. 5). In addition, the number of voles is usually far smaller in cereal fields than it is in alfalfa or clover crops (Ryszkowski et al. 1973). This is why the damage of voles to cereal crops seldom exceeds the economic threshold.

4. Discussion

To estimate the impact of rodents on crops, a simulation model of consumption for a whole population of voles was used. Within this model, energy budgets of individuals were evaluated and then summed for a whole population using data on population structure and density. There was no feedback effect between the individual energy budgets and the dynamic changes in population numbers and structure. That is, a specific history of the population is given as input to the model. This seems justified since the objective of this study has

Tab. 5. Total impact of voles on the winter wheat cultivation – coefficients for estimation different effects.

Coefficient (symbols in parenthesis)	Winter wheat growth (in days of cultivation)			
	221–240	241–260	261–280	291–300
Quantity (QUANT)	1.29	5.55	1.06	2.04
Quality (QUAL)	1.91	7.14	0.95	0.96
Integrated total Impact (TOTAL)	2.11	39.60	1.01	1.96

been to estimate the total rodent consumption and impact on cultivated field and not to explain population dynamics. For the same reason, our model includes only the most important factors affecting the energy requirements of individuals, and we do not undertake any detailed analysis of the individual energy balance (e.g. the chance of survival under the given environmental conditions, Collier et al. 1975).

4.1. Simulation model

4.1.1. Energy budgets of individuals

Using the average daily metabolic rate (ADMR), simple models of daily energy budget were constructed for *Microtus arvalis*, *M. agrestis* and *M. oeconomus* (Grodziński and Górecki 1967, Gębczyńska 1970). Later, species-specific functions for the relationship between ADMR and body size were applied to the field vole (Hansson and Grodziński 1970) and also to the tundra vole (Grodziński 1971). This allometric model has been developed recently by Weiner as a more general equation (Grodziński and Wunder 1975). In this study we continue to refine the calculation of energy budgets using a simulation model, based mainly on the relationship ADMR – body size and ambient temperature.

In an individual the energy requirement for maintenance is a function of many variables, the most important of which are included in ADMR measurements (body weight, ambient temperature, seasonal changes, pattern of activity, and huddling effect). These factors could be inserted into a DEB model separately, using data from independent measurements of the particular components (e.g. cost of thermoregulation measured by RMR), but it is extremely difficult and cumbersome to assess these effects quantitatively when constructing an additive model (Gessaman 1973). A model based on ADMR has the advantage that an ADMR measurement integrates all components of the energy budget in a natural way and, consequently, includes all compensatory effects. Therefore, we concluded that ADMR, expressed as a function of body weight, ambient temperature, season and number of individuals living together, is the best estimate of the costs of maintenance under field conditions.

4.1.2. ADMR sub-model

As has been shown previously, ADMR may be expressed

as a power function of body weight, $ADMR = aW^b$. Parameters of this function (a, b) were determined in the autumn series of measurements at 20°C, and we assumed that the function is constant throughout the year.

ADMR is strongly related to ambient temperature. This relationship is curvilinear and should probably be described as a multi-dimensional model, comprising more independent variables than ambient temperature alone. Available data do not allow us to develop such an equation and, therefore, we have made use of a polynomial fitted to the winter ADMR series (Eq. 4). This procedure seems applicable because under the experimental conditions of ADMR measurement the voles develop spontaneous activity, and it is likely that the response of voles to any decrease in ambient temperature should be similar to that in the field. It appears that the slope of the RMR-temperature curve (Fig. 1) reflects the cost of thermoregulatory metabolism. Since this slope does not vary with season (Eqs 2 and 3), we assume that also the parameters other than the intercept of the ADMR-temperature curve are also constant throughout the year. Any error, caused by this assumption would be negligible since voles bear the cost of thermoregulation mainly in winter.

Data on the temperature near ground (Tab. 6) indicate that the measured thermoregulation curve nearly spans the actual range of field conditions. Since the additional cost of thermoregulation begins at 20°C, the correction has been recalculated as an additive factor:

$$\varphi(t) = (\alpha t^2 - \beta t + c) - (\alpha 20^2 - 20\beta + c) = \alpha' t^2 - \beta' t + c \quad (6)$$

where $\varphi(t)$ is the correction for thermoregulation as function of ambient temperature (t), α, β, c are parameters.

Changes of ADMR with season and with group size have been discussed above (Tab. 1, Fig. 2). In calculating the seasonal correction factors, the autumn ADMR has been assigned the value of 1.0 because the model starts with the level of ADMR determined in the autumn series of measurements. Under natural conditions the voles live in families consisting of from 3 to 15 or more individuals, and the size of these groups varies during the year (Frank 1953, Straka 1967). We assumed that during the season of intensive breeding (April till October) these groups consist of 7 or more individuals, while during other seasons the number of animals in a

Tab. 6. Annual course of soil and air temperatures on a cultivated field in Southern Poland. Data from the Experimental Farm of the Jagiellonian University for 1963 (after Olecki 1968). All values expressed as monthly means.

Temp. (°C)	Months												Annual
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	
2 m above ground	-0.5	-0.0	1.6	6.5	10.7	16.2	16.5	15.0	13.7	6.7	0.2	1.9	6.9
Ground surface	-0.7	-0.8	2.2	8.2	14.4	19.8	19.7	17.6	15.6	8.1	0.4	0.9	8.5
20 cm below surface	0.3	0.1	1.4	6.2	10.9	16.7	17.7	16.7	15.1	9.2	3.3	1.6	8.3

family averages 3 individuals. Appropriate correction factors were calculated from Eq. (5).

The combination of equations and coefficients described above yielded a universal formula for ADMR with discrete parameters changing within a yearly cycle:

$$\text{ADMR} = [aW^b + (\alpha t^2 - \beta t + c)] sh \quad (7)$$

where t is ambient temperature, W is body weight, s is seasonal correction factor, h is correction factor for social effect, b is exponent, a , α , β , c are parameters.

By substituting the actual values for the parameters (Sects 3.1, 3.2) and converting the units from $\text{ccm O}_2 \times \text{g}^{-1} \times \text{h}^{-1}$ into $\text{kcal} \times \text{animal}^{-1} \times \text{d}^{-1}$ the following equation was obtained:

$$\text{ADMR} = [2.252 W^{0.525} + (0.00303 t^2 - 0.2169 t + 3.126)] sh \quad (8)$$

$$s = \begin{cases} 1.077 & \text{for spring and summer} \\ 1.000 & \text{for autumn} \\ 0.904 & \text{for winter} \end{cases}$$

$$h = \begin{cases} 0.701 & \text{for breeding season} \\ 0.880 & \text{for non-breeding season} \end{cases}$$

where ADMR is measured in $\text{kcal animal}^{-1} \text{d}^{-1}$, W in g and t in $^{\circ}\text{C}$.

4.1.3. Energy cost of growth

Measurements of ADMR do not include growth because animals in these experiments maintained a stable weight.

Many field data suggest that voles grow throughout most of their life which, under field conditions, rarely lasts longer than 6 to 7 months. During this time their body weight reaches 42 g (Pelikan 1959, Spitz 1972). A steady increase in body weight markedly heightens the energy requirements of individuals, but only a part of this energy is deposited in body tissues.

As far as we know, there are no data available for the growth rate of the free-living common voles. However, considering the maximum body weight and the maximum life span of voles in the field (Straka 1967, Spitz

1972) we inferred that the logarithmic growth curve determined for laboratory voles from day 20 to day 70 (Drożdż et al. 1972) could be extrapolated to the maximum age (e.g. body weight estimated from the formula of Drożdż et al. (1972) for a 250-d old vole reaches 41.6 g. Therefore estimation of body weight in various age classes of voles has been done using the formula from Drożdż et al. (1972):

$$W = 2.476 X^{0.511} \quad (9)$$

where W = body weight in grams, X = age in days since birth.

For further bioenergetic computations, the animals were divided into 3 age classes: 15–49 d old (juveniles), 50–99 d old (sub-adults), and 100–250 d old (adults). The criterion for the inclusion in the first class was the onset of reproduction. According to Pelikan (1959) and Straka (1967), at 50 d, or after a body weight corresponding with this age, most females start breeding. As far as the model is concerned it seems reasonable to equate age and body weight. Drożdż et al. (1972) have also demonstrated that at this same age the voles attain "chemical maturity": body composition is constant from this age on.

The division into age classes roughly corresponds to the population structure presented by Straka (1967) whose population data are used in further computations. The model does not include the youngest voles (nestlings, age < 15 d) because the energy expended on their growth and maintenance before weaning has been added to the energy budgets of reproducing females.

For each of the three age classes the average body weight has been determined as a geometric mean of body weight, calculated for the first and the last day of age class. Average daily growth was calculated by assuming a linear growth rate in each class. Using data on body composition of growing voles (Drożdż et al. 1972), an average daily increase in the biomass of fat and non-fat tissue was determined for each class. Assuming caloric values of 9.3 and 4.7 kcal g^{-1} dw for fat and non-fat tissue, respectively, mean daily energy deposition (ΔP) was estimated (Tab. 7). Additional respiration connected with the deposition (ΔR) has been evaluated on the assumption that the efficiency of fat deposition

reaches 75%, and that of non-fat tissue (mainly protein) about 40%. The total amount of energy (EP_i) expended in each age class (i) on growth is a sum of the energy deposited (ΔP_i) and the additional respiration (ΔR) (Tab. 7):

$$EP_i = \Delta R_i + \Delta P_i \quad (10)$$

The daily energy requirement of a growing, but not reproducing, animal is a sum of the maintenance cost (ADMR) and the growth cost:

$$DEB_i = \text{ADMR}_i + EP_i \quad (11)$$

where $i = 1, 2, 3$ (subscript for a given age class).

4.1.4. Cost of reproduction

Many females in age classes II and III participate in reproduction which adds considerably to their energy budgets. As Trojan and Wojciechowska (1967) as well as Migula (1969) have shown, the energy budget of a female vole is increased 1.8 fold during both pregnancy and lactation (18 and 15 d, respectively). The estimated weighted mean of production efficiency throughout the whole reproduction period (pregnancy + lactation) amounts to 18.9% (recalculated after Migula 1969). To determine the value of production alone in this period (P_i), it has been assumed that the younger animals (age class II) produce on average of 4 young, while the older ones (age class III) produce 6 young (Straka 1967). Average body weight and caloric value of the new-born voles and of the young on the day of weaning were adopted from Sawicka-Kapusta (1970), and used to determine the average daily production for sub-adult and adult females during reproduction. Using these assumptions, the biomass of juveniles at weaning, expressed as a percentage of the adults' body weight, is almost identical in both age classes and amounts to 73%. Data from Migula (1969) indicate that reproducing females do not gain in body weight, and thus are not charged with the cost of growth (Tab. 7). The daily energy budget of a reproducing female may now be computed:

$$DEB_i = \text{ADMR}_i + P_i/0.189 \quad (12)$$

4.1.5. Consumption of energy and biomass

Daily energy budgets (DEB_i 's), calculated as a sum of the cost of maintenance (ADMR) and the cost of growth or reproduction represent assimilation (metabolized energy), according to the terminology accepted in productivity studies (Petrušewicz and Macfadyen 1970).

Consumption of energy (C) required to balance the total energy budget may be calculated as the assimilation coefficient of natural foods. In this study we use 0.6 (cf. Sect. 3.4).

Thus

$$C_i = DEB_i/0.6 \quad (13)$$

Then, the amount of biomass consumed is:

Tab. 8. Four "artificial" populations of common voles. Number of voles per ha are given.

Cultivar	Density	Spring (March)	Summer (June)	Autumn (Sept)	Winter (Dec)
Alfalfa	Normal	27	86	93	60
	Outbreak	112	1412	1450	781
Winter wheat	Normal	3	15	10	60
	Outbreak	22	84	84	60

$$\text{CBIO}_i = C_i/\text{CVAL} \quad (14)$$

where i = subscript for a given age class, CVAL = caloric value of food, kcal g^{-1} .

4.1.5. Population density and structure

The previously computed consumption by individual voles must be combined with demographic data in order to estimate the consumption of a whole population. Despite the abundance of literature on the common vole, it is difficult to find a complete account of the population dynamics, that would include both density and structure of age and/or body weight. For this reason, artificial populations were created for computations.

Estimates of seasonal changes in abundance during an outbreak and during a year of normal density were taken from Ryszkowski et al. (1973). Different vole populations were used for alfalfa and wheat crops. There were no satisfactory data for the winter season, so the density in this period was interpolated from the autumn and spring numbers. The maximum density during an outbreak reaches 1450 voles ha^{-1} in alfalfa, and 84 voles ha^{-1} in cereals, while in a normal year the density is 93 and 15 animals ha^{-1} , respectively (Tab. 8). Proportions of juveniles, subadults, adults and reproducing females from groups II and III are taken from Straka (1967). By interpolating for short time intervals (6 d), these data were used in a dynamic model to estimate the consumption of population in an annual cycle.

4.1.6. Impact sub-model

Each measure of the impact of rodents on the crops is calculated on the basis of consumption values obtained in the main model. The multiplication of consumption by the coefficients described in Sect. 3.5. yields a complete impact, TOTAL.

The pertinent equations are:

$$\text{TOTAL}_a = C \times \text{DEST} \times \text{UNGR} \times \text{SUCC} \times \text{STLEAF} \quad (15)$$

for alfalfa, and

$$\text{TOTAL}_w = C \times \text{QUANT} \times \text{QUAL} \quad (16)$$

for wheat.

Tab. 7. Calculated cost of growth and reproduction in particular age classes of common voles.

Age class (age and reproductive state)	d	I 16-49	II 50-99 non-reprod.	IV 50-99 reproducing	III non-reprod.	V 100-250 reproducing
Average body weight (range)	g	13.4 (9.9-18.3)	21.7 (18.3-25.9)		32.8 (25.9-41.6)	
Daily weight gain	$\text{g} \times \text{d}^{-1}$	0.240	0.153	-	0.105	-
Daily energy deposition (ΔP)	$\text{kcal} \times \text{d}^{-1}$	0.801	0.382	2.310	0.261	3.460
Additional respiration for production (ΔR)	$\text{kcal} \times \text{d}^{-1}$	0.441	0.249	9.912	0.170	14.850
Additional assimilation (RR + P)	$\text{kcal} \times \text{d}^{-1}$	1.242	0.631	12.220	0.431	18.307

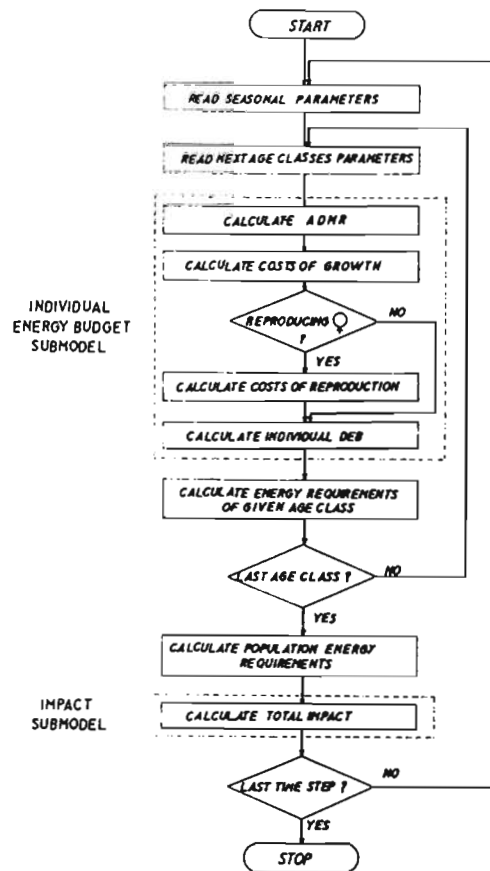


Fig. 3. Flow diagram of the program used for computations of bioenergetics and total impact of common vole populations.

The successive intermediate values have the following meaning: $C \times DEST$ represents total biomass removed, $C \times DEST \times UNGR$ represents the biomass removed plus that which did not grow and, finally, $C \times DEST \times UNGR \times SUCC$ represents the previous sum increased by the biomass of alfalfa replaced by weeds. $TOTAL_s$ is a measure of the impact of voles on the crop of alfalfa leaves, whereas $TOTAL_w$ is a measure of impact on the quality and of quantity of grain crop.

4.1.7. Computations

Computations for the populations were done by means of a FORTRAN program (Fig. 3), with parameters interpolated for 61 six-day intervals which covered a whole year. The impact on crops was simulated for 42 d

(from 1 August to 11 September) for alfalfa, and for 80 d (from late April to July) for wheat. Simulation of impact has been limited to these periods, owing to a lack of experimental data on impact for other periods.

4.2. Results of simulations

4.2.1. Individual DEB-model

Simulated energy budgets of all sex and age categories show similar changes during a yearly cycle. The lowest values occur in summer and remain more or less constant from mid-April to mid-October. The highest of energy requirements of individuals is observed in winter and is almost constant from mid-November to mid-February. In the remaining transitional periods energy budget changes markedly; energy requirements decrease considerably in spring and increase again in autumn (Fig. 4). Reproduction significantly increases the energy requirement. In summer this requirement is about 20.9 kcal animal⁻¹ d⁻¹ in subadults (21.7 g in weight) and as much as 29 kcal animal⁻¹ d⁻¹ in adults (32.8 g in weight), increases of 125% and 159% (Fig. 4). The total DEB of the animals reproducing in winter is still higher in both age classes and reaches 27.8 and 39.4 kcal animal⁻¹ d⁻¹, respectively (Fig. 5). The voles feeding on bulky food in winter would not be able to ingest enough food to satisfy their energy budget if they were reproducing; this would require a feeding rate of the order of 30–60 g biomass d⁻¹.

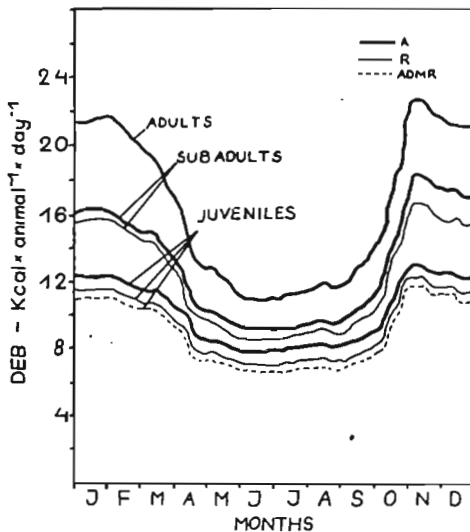


Fig. 4. Daily energy budgets of non-reproducing voles of three age classes: A – assimilation (DEB), R – respiration, ADMIR – average daily metabolic rate.

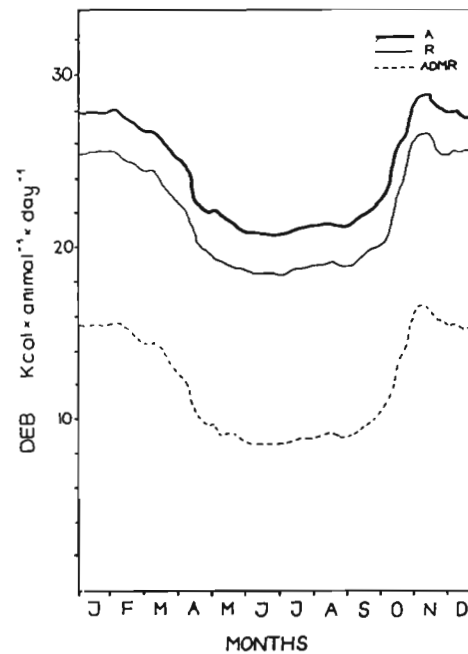


Fig. 5. Daily energy budget of a reproducing adult female. A – assimilation, R – respiration, ADMIR – average daily metabolic rate.

One way to test the validity of any model is to compare the results of model estimates with the actual figures obtained from independent measurements. Unfortunately, the energy requirement of voles living in the field have never been measured. Sawicka-Kapusta et al. (1975), however, have studied the energetics of laboratory colonies of voles kept under seminatural conditions and the values obtained are in close agreement with model estimates. For instance, the experimentally determined energy requirement of a 16.0 g vole feed on alfalfa is 8.6 kcal animal⁻¹ d⁻¹ in summer and 8.7 kcal animal⁻¹ d⁻¹ in autumn. Corresponding values computed from the model for a juvenile in mid summer and autumn are 8.14 and 8.85 kcal animal⁻¹ d⁻¹, respectively.

Tab. 9. Energy balance of four common vole populations (Mcal ha⁻¹ yr⁻¹).

Cultivar	Density	Respiration	Production	Assimilation	Consumption
Alfalfa	Normal	987.9	71.5	1059.4	1765.7
	Outbreak	13590.0	1003.1	14593.1	24321.8
Winter wheat	Normal	122.5	9.1	131.6	219.3
	Outbreak	988.1	71.3	1059.4	1765.7

4.2.2. Population energy demand

Energy demand of a vole population was simulated for normal and peak populations in alfalfa and wheat crops (Tab. 8). Total energy consumption varied considerably. In an outbreak year, animal consumption in alfalfa field was 24321.8 Mcal ha⁻¹ yr⁻¹ (Tab. 9), reaching top values (41 Mcal ha⁻¹ d⁻¹) in mid summer and falling down to about 4 Mcal ha⁻¹ d⁻¹ in early spring (Fig. 6). In a year of normal vole density in an alfalfa field, energy consumption ranged from 2.46 Mcal ha⁻¹ d⁻¹ in summer to 0.80 Mcal ha⁻¹ d⁻¹ at the turn of February and March (Fig. 6). The annual consumption by such population was 1765.7 Mcal ha⁻¹ yr⁻¹. Much lower values of energy consumption were computed for a population living in a wheat field. Even in an outbreak year, total energy consumption did not exceed 1765.7 Mcal ha⁻¹ yr⁻¹, and in a year of normal density was only 219 Mcal ha⁻¹ yr⁻¹ (Tab. 9). In all cases most energy is consumed by vole populations in June–July, and least in February–March (Fig. 6).

Particular categories of individuals have a different share in the consumption of a whole population. Fig. 7 shows the share of various age and sex categories of voles in the energy consumption of a whole population in an alfalfa field during a year of normal density. The highest share is that of reproducing adults, which are responsible for 34% of the annual consumption of the whole population, and it is at its peak in June and July. The share of reproducing subadults in the total consumption is much smaller and has a different course during the year (Fig. 7). Recall that energy budgets of these two categories of individuals include the cost of maintenance and growth of the nestlings being nursed by females. Non-reproducing adult females and males have their highest share in population energy consumption in autumn, while peaks for the juveniles and non-reproducing subadults fall in spring and autumn.

The major portion of energy assimilated by voles is dissipated as respiration (Tab. 9, Fig. 8); production averages 7.2% of respiration. Thus the production efficiency estimated by this model approximates that found in populations of many small rodent species (Grodziński and French 1974). A large portion of food consumed by voles returns to the ecosystem in the form of excreta. In various populations this portion ranges from 87.7 to 9728.7 Mcal ha⁻¹ yr⁻¹ (Tab. 9, Fig. 8).

Fig. 6. Daily energy consumption by common vole populations. A. Outbreak years, alfalfa. B. 1 - outbreak year, wheat, 2 - normal year, alfalfa, 3 - normal year, wheat.

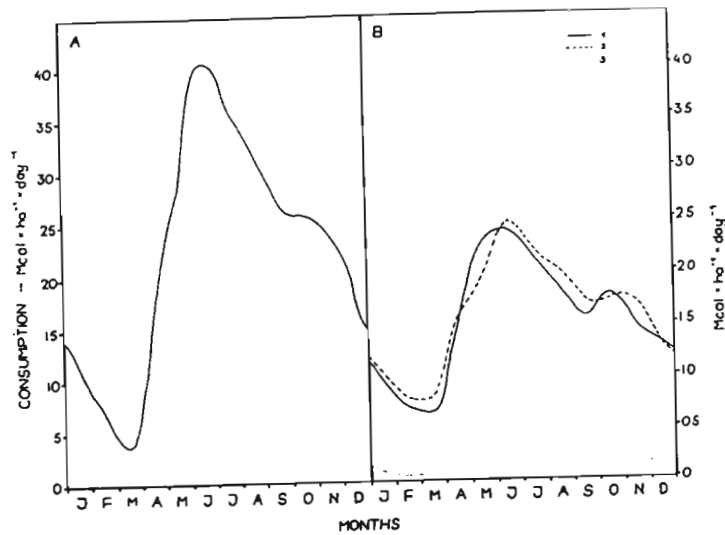
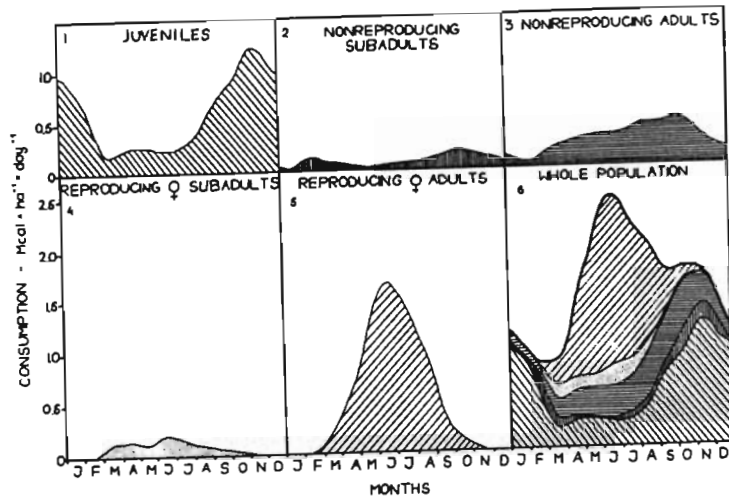


Fig. 7. The share of various age and sex categories of voles in energy consumption of a whole population (alfalfa, normal year): 1 - juveniles, 2 - non-reproducing sub-adults, 3 - non-reproducing adults, 4 - reproducing sub-adult females, 5 - reproducing adult females, 6 - energy consumption of a whole population.



4.2.3. Energetic and extraenergetic impact

Energy flow through small mammal populations represents but a few per cent in relation to the primary production available in the ecosystems (Golley et al. 1975), and this suggests a rather negligible role of rodents in the functioning of ecosystems. However, total impact may be much greater than consumption of available energy indicates. Fig. 9 shows changes in consumption itself and total impact during a period of 42 d of alfalfa growth. Maximum daily consumption by voles reaches 2.7 g of alfalfa m^{-2} and represents merely 0.18% of the potential

crop of alfalfa from this area. If, however, coefficients for destruction, unrealized growth and weed succession (see Sect. 3.5.) are taken into account, the impact on alfalfa plants reaches a maximum value of 31.8 g m^{-2} which makes up 2.14% of the potential crop of alfalfa green mass. With the inclusion of stem/leave ratio the total daily impact may be as high as 2.5% of alfalfa leaves. Thus, the impact of rodents expressed as effect on leaves is 13 times greater than that indicated by consumption during the period of highest susceptibility of

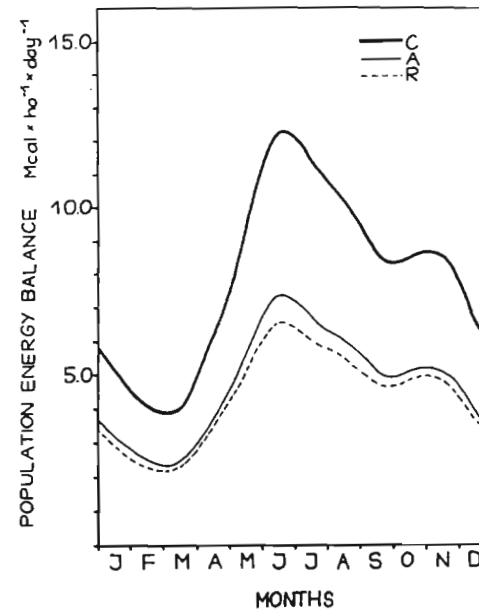


Fig. 8. Energy balance of a common vole population during a year of normal density.

alfalfa to damage. In other periods the impact exceeds consumption by 4-8 times.

The results obtained from the impact submodel for a normal density year show the daily consumption of population as 0.17 g m^{-2} , which is only 0.01% of the

available alfalfa biomass. The total impact on alfalfa crop is also limited, although its cumulative value for the whole period exceeds consumption by more than 8 times.

Fig. 9B shows the result of impact simulation for a year of outbreak in wheat fields. The curve fitted by hand indicates a considerable increase in impact phenomena in the stage of ear/head formation. The daily consumption in this period reaches 0.24 g of green mass m^{-2} and results in a maximum reduction in grain crop of 9.2 g m^{-2} , or 2.3% of the potential grain crop from this area. At other times the effect of voles on the wheat crop does not exceed 0.5 g m^{-2} , or 0.12% of the potential harvest. The decrease in consumption at the time of head ripening is due to the fact that voles switch to feeding on grain with a high caloric content as compared to the green mass. The daily grain consumption of the order of 0.05 g m^{-2} decreases the crop by 0.11 g m^{-2} , or 0.03% of the potential crop.

A similar simulation for a normal year in wheat fields has demonstrated that, in the period of the highest susceptibility to grazing, the voles reduce the grain crop by 0.41%. While feeding on grain, they consume 0.016 g m^{-2} , which is as little as 0.004% of the potential crop.

The results of these simulations agree with the observation of Ryszkowski et al. (1973) that voles have practically no effect on another cereal crop (rye). Ružić (1971) has found, however, that in autumn and winter, not considered in this study, voles may reduce the crop of wheat by as much as 12.4%. The cumulative impact of grazing over the whole period of growth for a crop may be even greater than the daily estimates suggest.

Fig. 10 illustrates the consumption by a population of voles computed for the whole year of outbreak in alfalfa as well as the impact during the period between the

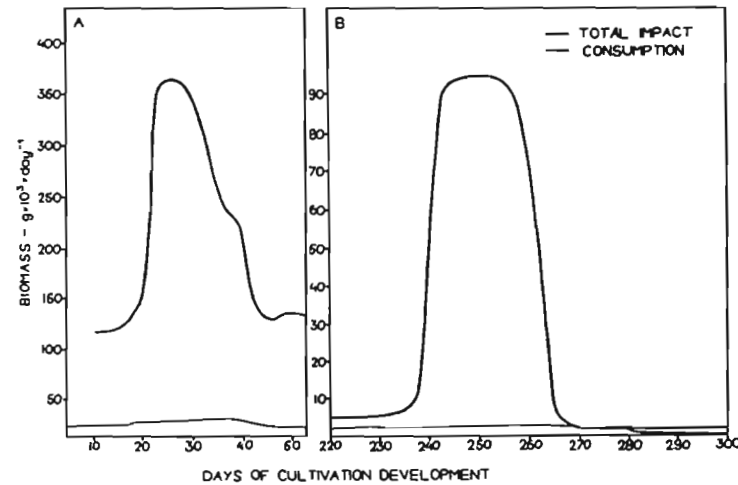


Fig. 9. Consumption and total impact of vole population in outbreak year on alfalfa (A) and winter wheat (B) crops.

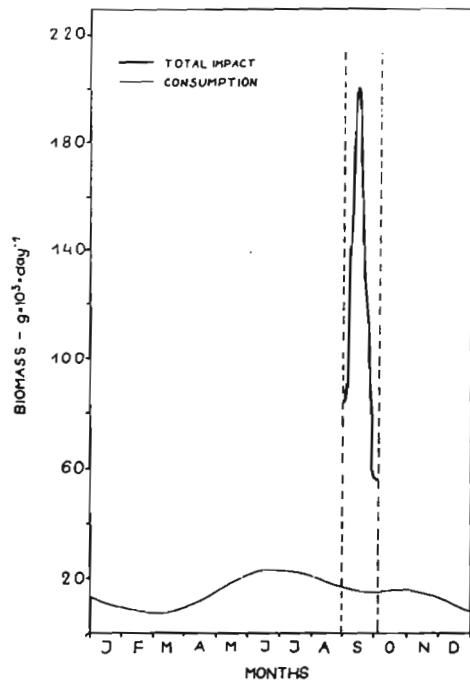


Fig. 10. Comparison of vole consumption and their total impact on third hay of alfalfa.

second and the third alfalfa cutting. The cumulative consumption of biomass during these 42 d is 170.6 g m^{-2} , which represents 11.5% of the potential crop. If the impact of voles on the crop is only considered in terms of biomass consumed, the crop should be decreased only by one. The cumulative value for total impact for this period amounts to 1135.1 g m^{-2} (76.7% of the potential crop), a devastating effect.

It is thus clear that utilization of bioenergetic data for estimation of impact of herbivores requires an understanding of extraenergetic effects on vegetation.

APPENDIX

Definition of mathematical symbols

Mathematical symbols

Symbol	Definition and unit used
a	constant in Eq. (6) [$\text{kcal animal}^{-1} \text{d}^{-1} \text{ } ^\circ\text{C}^{-1}$]
ADMR	average daily metabolic rate [$\text{cm}^3\text{O}_2 \text{g}^{-1} \text{h}^{-1}$ or $\text{kcal animal}^{-1} \text{d}^{-1}$]
b	constant exponent in Eq. (7)
c	constant in Eq. (6) [$\text{kcal animal}^{-1} \text{d}^{-1}$]

C	total biomass consumption of the population [$\text{g m}^{-2} \text{d}^{-1}$]
C_i	energy consumption in <i>i</i> -th age class [$\text{kcal animal}^{-1} \text{d}^{-1}$]
$CBIO_i$	biomass consumption in <i>i</i> -th age class [$\text{g animal}^{-1} \text{d}^{-1}$]
CVAL	caloric value of food [kcal g^{-1}]
DEB_i	daily energy budget of <i>i</i> -th age class [$\text{kcal animal}^{-1} \text{d}^{-1}$]
DEST	coefficient of crop destruction
EP_i	daily cost of growth in <i>i</i> -th age class [$\text{kcal animal}^{-1} \text{d}^{-1}$]
h	social effect correction factor for ADMR
<i>i</i>	subscript for age class
N	number of animals in a group (sample)
P_i	mean daily production during pregnancy and lactation [$\text{kcal animal}^{-1} \text{d}^{-1}$]
ΔP_i	mean daily energy deposition during growth in <i>i</i> -th age class [$\text{kcal animal}^{-1} \text{d}^{-1}$]
QUAL	coefficient of reduction in grain quality
QUANT	coefficient of reduction in grain quantity
ΔR_i	additional respiration for growth in <i>i</i> -th age class [$\text{kcal animal}^{-1} \text{d}^{-1}$]
RMR	resting metabolic rate [$\text{cm}^3\text{O}_2 \text{g}^{-1} \text{h}^{-1}$]
s	seasonal correction factor for ADMR
STLEA	coefficient of change in stem/leave ratio
SUCC	coefficient of weeds succession on a crop
<i>t</i>	ambient temperature [$^\circ\text{C}$]
TOTAL _a	total impact on alfalfa [$\text{g m}^{-2} \text{d}^{-1}$]
TOTAL _w	total impact on wheat [$\text{g m}^{-2} \text{d}^{-1}$]
UNGR	coefficient of unrealized growth
W	body weight [g]
X	age [d]
α	constant in eq. (6) [$\text{kcal animal}^{-1} \text{d}^{-1} \text{ } ^\circ\text{C}^{-2}$]
β	constant in eq. (6) [$\text{kcal animal}^{-1} \text{d}^{-1} \text{ } ^\circ\text{C}^{-1}$]
$\varphi(t)$	temperature dependent additive correction factor for thermoregulation [$\text{kcal animal}^{-1} \text{d}^{-1}$]

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