

## 8. PRODUCTIVITY AND ENERGETICS

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### 8.1. The Concept of Productivity

#### 8.1.1. General Remarks

In common language, the term "production" means making something new. Secondary biological production, discussed here for the bank vole — transforms the organic matter of food into the organic matter of the consumer to become the potential chemical energy contained in consumer's body. Then it can be transformed into kinetic energy, or heat energy, and used for all living processes of an organism, such as metabolism, growth, reproduction, foraging escape, etc.

Biological production can be measured for individual organisms, populations, or even trophic levels in an ecosystem. Obviously, production at the level of individual organisms is the same physiological process as production at the population level. Productivity processes such as production assimilation, or respiration at the population level are realized through physiological processes occurring in individual organisms.

The production of a population includes many processes organized at the population level as the phenological time progresses. Among the parameters involved are number of individuals, interactions between individuals, their age, spatial distribution, etc.

An individual that dies of old age, can realize a maximum production over its lifetime. A female can additionally increase production due to reproduction ( $P_r$ ). An individual that dies before reaching adult weight obviously has lower production. The same is true of a female that dies before delivering. Also individuals living at high densities are generally less productive than those living at optimum densities, etc.

Population mortality can be low, but it always exists. Survivorship curves usually fit the exponential models, suggesting that a constant per-

centage of the young is dying. Population production can never reach the level which is physiologically possible. The higher the mortality of offspring, the lower the total production of the population. Population production is also influenced by the shape of individual growth curves. As Figures 8.1, 8.2, and 8.3 show, production due to individual growth ( $P_0$ ) is very low above a certain age. For example, the production of an island bank vole population over six months of winter accounted for only 8% of its total annual production (Petrušewicz *et al.*, 1971). Production due to growth of spring cohorts is much higher than that of autumn cohorts (68% versus 32%, Petrušewicz *et al.*, 1971) not only because the former comprise more individuals but also due to a higher survival of the youngest offspring in spring cohorts.

Initial growth rate of individual bank voles is higher than at the age when they are approaching a weight of about 18 g. The production to assimilation ratio ( $P/A$ ) was about 46% for 9-day-old bank voles and 4.5% for 30-day-old animals (see Table 2.6). The mean  $P/A$  ratio over the lifetime of the trappable part of the population was merely 2% (Grodziński *et al.*, 1969/1970; Petrušewicz *et al.*, 1971). Hence, the higher mortality of the youngest, the lower the total production of the population.

Biological production is a highly complex process occurring by steps. Thus we must consider many parameters, often inter-related, when studying it. Production due to body growth is a result of continuous processes.

Before we proceed to a more detailed review of parameters and concepts used in productivity studies, three comments are needed: (1) In productivity studies, which are influenced by ecosystem studies, we usually speak about the flow of energy and the cycling of matter. It is worth remembering that matter is cycling only at the ecosystem level. With reference to individuals both matter and energy only flow. It is true that the fates of the matter flowing through an individual differ from the fates of energy. Energy, as we shall see later, is mostly dissipated. For example, about 98% of the energy assimilated by the bank vole is lost from the system in the form of heat for the so-called maintenance costs or respiration ( $R$ ). Matter, instead, remains within the ecosystem and can be used by other trophic levels. (2) It frequently happens that the terms "productivity" and "production" are misused, although their definitions have been given many times (Petrušewicz, 1967; Petrušewicz & Macfadyen, 1970). According to these definitions, we use "productivity" to denote all the concepts (parameters) such as consumption ( $C$ ), assimilation or energy flow ( $A$ ), respiration or costs of maintenance ( $R$ ), changes in standing crop ( $\Delta B = B_T - B_0$ ), elimination

of individuals ( $E$ ), and finally "production" ( $P$ ), that is, the organic matter produced over a period of time by individual organisms and not used for their costs of living. The term "secondary production" (net production) is reserved for the actual accumulation of organic matter in the bodies of animals over a definite time. (3). The general schemes suggested by Petruszewicz (1967) and Petruszewicz & Macfadyen (1970), rather commonly used in some studies on matter flow have proved useful. Although this monographs is concerned only with the bank vole, we use this occasion to introduce some corrections to them, following proposals by Petruszewicz (1978).

### 8.1.2. Parameters of Productivity

Living organisms, including bank voles, occupy habitats with a food supply. It is defined as "the food available, readily eaten and assimilated by an animal", and denoted by  $FA$  (Grodziński, 1975). Some of this food,

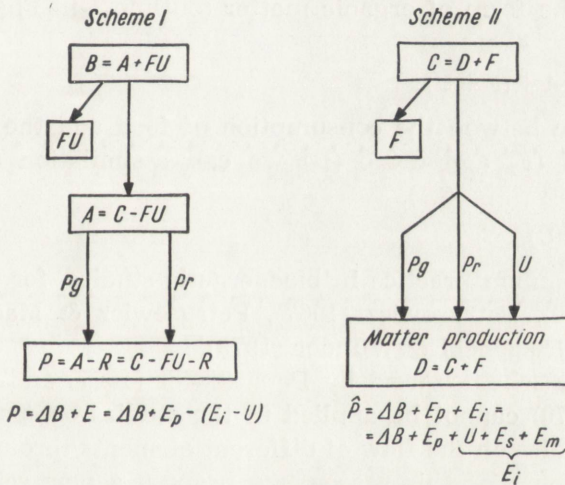


Fig. 8.1. Diagrams of matter and energy flow through a population;  $C$  — consumption,  $A$  — assimilation (energy input),  $FU$  — faeces and urine,  $P$  — production,  $R$  — respiration (maintenance costs),  $D$  — digested energy (assimilated),  $P$  — production and energy content of urine,  $P_g$  — production due to body growth,  $P_r$  — production due to reproduction,  $E$  — elimination of individuals from population,  $E_i$  — individual elimination (part of individuals),  $E_s$  — elimination in the form of secretions such as urine, mucus produced by snails, etc.,  $E_m$  — elimination of organic matter in the form of sloughs, spider webs, peeled epidermis, etc.,  $\Delta B$  — difference between standing crops. Diagram I is most frequently used in the field studies, diagram II can be used to analyse matter flow (but not energy flow) (after Petruszewicz, 1978).

usually a major part of it, remains untouched by consumers. Some is consumed ( $C$  in Fig. 8.1), and some is not used but damaged ( $NU$ ). Therefore, the material removed from the available food supply is given by

$$MR = NU + C \quad (8.1)$$

To date we do not know how much of the available food is only damaged by the bank vole and not used ( $NU$ ). Therefore, the impact of these rodents on their food resources can only be measured by their consumption ( $C$ ). Under different conditions it ranges between 0.6 and 13% of the food available (Grodziński, 1971). These amounts usually cannot threaten forest ecosystems. Damages caused by bank voles can be of economic importance only in the earliest stages of forest growth as a result of foraging on growing seedlings.

But consumption by an individual or a population is not equivalent to the matter and energy input to them. A part of the food intake is excreted in the form of faeces ( $F$ ), while the other part is digested and assimilated ( $D$ ). Also urine is rapidly excreted and returned to the ecosystem in the form of organic matter (outline I in Fig. 8.1). This can be expressed as

$$C = D + F = A + (F + U) \quad (8.2)$$

A difference between the consumption of food and the excreta in the form of faeces ( $F$ ) and urine ( $U$ ) we call assimilation ( $A$ ), or energy input (scheme I in Fig. 8.1).

$$A = C - (F + U) \quad (8.3)$$

This is a common practice in bioenergetic studies, for example, those of Golley (1960), Petruszewicz (1967), Petruszewicz & Macfadyen (1970), Odum (1971), Grodziński & Wunder (1975).

Energy flow schemes used by Petruszewicz (1967) and Petruszewicz & Macfadyen (1970) cannot be applied in the studies on matter flow, particularly in studies on the flow of different elements through an organism and a population. For this reason, we propose a new scheme (Fig. 8.1) after Petruszewicz (1978), which can be useful in studies on the flow of particular elements, except for carbon, oxygen and nitrogen.

Before discussing the parameters needed to calculate the energy and matter budgets for a population or an individual, we want to stress again that the concept of productivity refers to physiological processes that are ecologically organized. Physiological potential of the population can be realized in different ways and provides different productivity parameters, depending on the ecological organization.

To estimate productivity we need many parameters, which can be classified into two large groups: physiological and ecological.

Physiological parameters, for example, litter size, gestation period, or indices as  $P/C$ ,  $P/A$ ,  $K_1$  and  $K_2$  used, in hydrobiological terminology, e. g., by Grodziński, Klekowski & Duncan (1975) and  $R/A$ , are significantly less variable than ecological parameters. Physiological parameters are specific and more or less stable in different habitats. Ecological parameters such as numbers ( $N$ ), proportion of mature or pregnant females, sex ratio, mortality, or natality are much more variable.

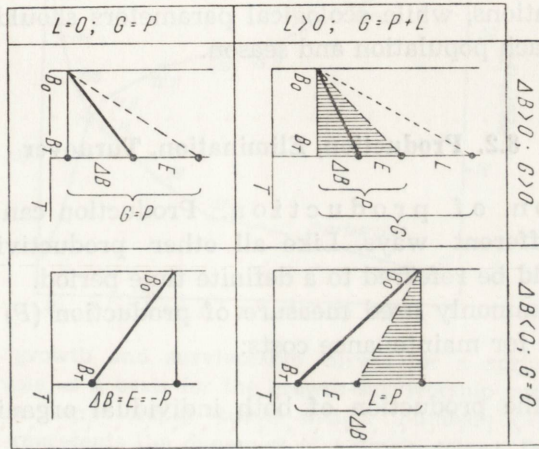


Fig. 8.2. Relationship between the total biomass growth ( $G$ ), production ( $P$ ), elimination ( $E$ ), and weight loss ( $L$ ), when  $\Delta B \geq 0$ ,  $\Delta B$  — biomass change,  $T$  — time.

We shall illustrate this with an example. It is known that the litter size of the bank vole can range from one to ten offspring, that is, it is highly variable. At the same time, Zejda (1966) points out that the mean litter size is highly stable in particular months, being for example 5.1 in April, 5.2 in May, 4.2 in September. In studies carried out at the Institute of Ecology PAS (unpublished data), the mean litter size was not significantly different from that reported by Zejda (1966). Therefore, the litter size once calculated from a sufficiently large set of data can be used as a reliable parameter in calculations made for bank voles living in different areas.

A high species-specific stability has also been found for assimilation efficiency ( $A/C$ ), as well as for  $P/A$  and  $P/C$  (Grodziński & Wunder, 1975).

Ecological parameters such as numbers ( $N$ ), proportion of pregnant females, sex ratio, age structure (especially in abnormal years), survival

and mortality show large fluctuations. To give an example, let us take numbers as illustrated by the studies carried out in Poland. The peak of bank vole numbers was 100 per ha on Crab-Apple island. In the Kampinos Forest their numbers ranged from 5 to 20 per ha, and in the Niepołomice Forest from 2 to 65 per ha (Andrzejewski, 1963; Petruszewicz *et al.*, 1971). The proportion of pregnant females was almost 100% in the second half of April, 10% in August-September, and zero in late autumn and in winter.

In short, physiological parameters once calculated can be used for different populations, while ecological parameters should be determined separately for each population and season.

## 8.2. Production, Elimination, Turnover

**Definition of production.** Production can be defined and estimated in different ways. Like all other productivity parameters, production should be referred to a definite time period.

The most commonly used measure of production ( $P$ ) is the input of energy not used for maintenance costs:

$$P = A - R \quad (8.4)$$

This refers to the production of both individual organisms and populations.

The production of any population is due to individual growth and reproduction (Petrusewicz & Walkowa, 1968; Petruszewicz & Macfadyen, 1970).

$$P = P_g - P_r \quad (8.5)$$

where  $P_g$  is production due to body growth, and  $P_r$  is production due to reproduction. In mammals, particularly in altricial mammals, it may be difficult to make a difference between these two kinds of production. Newborn mammals entirely depend on the food collected by their mothers and transformed into milk. For this reason the growth of sucklings is usually considered as production due to reproduction. In this case there is no clear division between production due to growth ( $P_g$ ) and production due to reproduction ( $P_r$ ) as the young become self-feeding only gradually.

Population production consists of the body tissue not used for costs of maintenance ( $R$ ) of all population members, independent of whether they survived over the period considered (e. g. by spring) or died at any time instant during this period. This is given by the formula

$$P_T = B_T - B_0 + E_T = \Delta B_T + E_T \quad (8.6)$$

where  $B_T$  is the standing crop at time  $T$ ,  $B_0$  is standing crop at time  $T_0$ ,

and  $E_T$  is elimination over period  $T - T_0$ . Elimination  $E$  in formula (8.6) is always positive. The difference in standing crops between the two time moments can be either positive or negative, depending on the situation. The possible relationships among,  $P$ ,  $B$ , and  $E$  are presented in Figure 8.2. In animals that grow and reproduce like the bank vole,

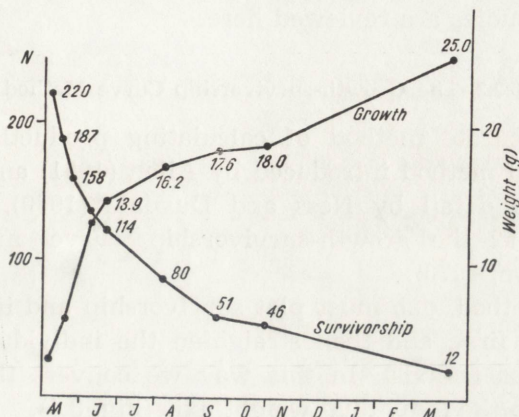


Fig. 8.3. Individual growth and survivorship curves for a spring cohort of the bank vole as a basis for the growth-survivorship curve.

The figures on the survivorship curve denote numbers ( $N$ ) of individuals ( $\gamma$ ) since this curve represents the dynamics of a single cohort. Data from Gliwicz *et al.* (1968) and Bujalska & Gliwicz (1968).

Table 8.1

Average daily metabolic rate ( $ADMR$  in  $\text{cm}^3 \text{O}_2/\text{g h}$ ) of the bank vole as a function of body weight in four seasons of a year (after Górecki, 1968 and unpubl. data).

Season	$N$	Range of body weight in g	$ADMR = aW^b$	Confidence interval of $b$
Spring	14	17.2—32.2	$35.97 W^{-0.68}$	(-0.86, -0.50)
Summer	16	19.9—32.6	$31.96 W^{-0.63}$	(-0.85, -0.41)
Autumn	16	17.2—22.0	$21.16 W^{-0.59}$	(-0.74, -0.44)
Winter	17	16.2—25.4	$5.61 W^{-0.13}$	(-0.47, 0.21)

the differences in standing crops ( $\Delta B$ ) for a period of one year is negligible as compared with elimination. Therefore for long periods it may be accepted that  $P = E$  in equation (8.6).

### 8.2.1. Calculation of Production

In ecological studies it is not possible to determine production empirically. We can, however, find empirically the values of ecological parameters (numbers, survival, time of the presence in the population

during the study period), and also the values of physiological parameters such as growth, energy content of the body, or natality.

Based on these two sets of parameters, the production of the population can be calculated. A detailed list of the principles for calculating production is given by Petruszewicz & Macfadyen (1970), and Petruszewicz & Hansson (1975), so only the most frequently used methods in small mammal studies are reviewed here.

### 8.2.2. The Growth-survivorship Curve Method

The most accurate method of calculating production for a cohort was the graphical method introduced by Allen (1951) and then described and discussed in detail by Ness and Dugdale (1959). Nowadays it is usually known as the growth-survivorship curve method (Petruszewicz & Macfadyen, 1970).

Using this method, one must plot survivorship and individual growth curves (Fig. 8.3) first, and then straighten the individual growth curve along the abscissa ( $x$ -axis). In this way we convert the abscissa from the time axis into the individual weight axis (Fig. 8.4).

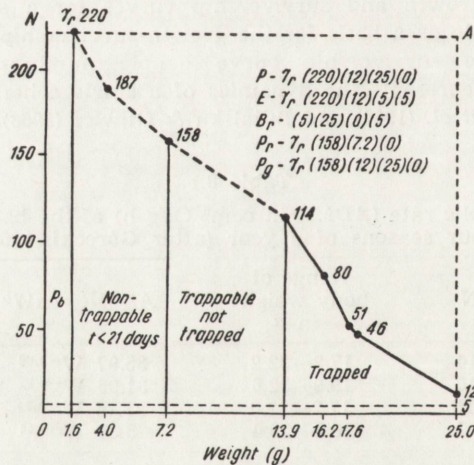


Fig. 8.4. A growth-survivorship curve calculated from data in Figure 8.3. The growth curve is straightened on the abscissa and the number of individuals is plotted against weight; the area below the growth-survivorship curve represents production (from Petruszewicz & Hansson, 1975).

The consecutive numbers of survivors in a population (cohorts) are plotted against the corresponding average weights. The area between the curve and the co-ordinate system represents production in weight units. A simple mathematical treatment of this relationship was demonstrated by Petruszewicz & Macfadyen (1970) and Petruszewicz *et al.* (1971).



Generally, different cohorts, born in various seasons, must be treated separately as they have different growth and survival rates.

This method of calculation is easy to use and has great advantages. It permits the calculation of production for any period of the cohorts life. For example, the biomass (production) of newborn individuals in Figure 8.4 is represented by the rectangle  $\nu_r$  (220) (1.6). Production of trappable animals, overwintered animals, or others, can be estimated by this method (see Fig. 7.4). The difficulty is in finding data for individual growth and survivorship curves. Especially the data of the latter kind are not easy to get for small mammals as they breed throughout the growing season and even throughout the year at highly variable rates.

The starting point to calculate production is the estimation of the total number of animals born in the population or a cohort, or the total number of overwintered animals at the beginning of the breeding season. Overwintered bank voles may be considered as one cohort because differences in their mortality and growth rates are very small, despite differences in their age (Bujalska & Gliwicz, 1968; Petruszewicz *et al.*, 1971).

The next step is the estimation of growth and survival. For this purpose we need individually marked animals or reliable age indices or unmarked ones. Data for laboratory raised animals are sometimes used to construct growth curves as it is easy to find a relationship between their age and growth. However, the extrapolation of these data to the field may result in large errors (Bujalska *et al.*, 1968; Petruszewicz & Macfadyen, 1970). To reduce these errors, we can use the modified laboratory growth curve to accommodate the body weights of the smallest trappable voles in the field. Such growth curves have usually been smoothed between successive weight measurements (Bujalska & Gliwicz, 1968; Bobek, 1969; Hansson, 1971a).

The turnover method. As we have previously stated (see section 8.1.2) one of the formulae describing production is

$$P_{(T)} = \bar{B}_{(T)} \cdot \Theta_B \quad (8.7)$$

where  $B_{(T)}$  is the average biomass for the time period  $T$ , and  $\Theta_B$  is the turnover of biomass.

It is usually impossible to determine the turnover of biomass in small mammals directly in the field, and this essential index, characterizing important ecological features of the population, can only be found when production and average biomass have been determined in other ways. Nevertheless, various modifications of equation (8.7) have been used to estimate production.

The production of an individual born during time period  $T$  is its maximum weight in that time; for individuals dying in this period,

it will be their weight at the moment of death, and for individuals that live longer than time  $T$  it will be the weight at the end of time period  $T$ . Now, the production of  $\gamma$  individuals will be equal to the product of the number of individuals and their average maximum weight  $W^+$  (the weight at the moment of death or at the end of the study period)

$$P_t = \gamma \cdot W^+$$

To calculate the total production, we should add the production of adults (usually overwintered) present in the population at the initial time instant.

### 8.2.3. Values of Production and Turnover

Total production is already known for many bank vole populations (Bobek, 1973). The mean production of a well known bank vole population isolated on an island in Masurian Lakeland north Poland was about 3000 g biomass/ha·year over a three-year period (Petrušewicz *et al.*, 1971). In oak-hornbeam stand of the Niepołomice Forest, the mean production of a bank vole population varied between 600 and 1980 g biomass/ha year (Bobek, 1973). Usually production due to reproduction is somewhat higher in bank vole populations than production due to individual growth. In the bank vole population on the Crab-Apple island, production due to reproduction ( $P_r$ ) accounted for 58% of the total production (Petrušewicz *et al.*, 1971). Bobek (1973) found an identical figure for the bank vole in oak-hornbeam stand of the Niepołomice Forest.

A striking feature of bank vole populations, as well as populations of rodents in general, is a high production due to animals less than 21 days old, thus prior to the trappable age. On Crab-Apple island they accounted for 81% of the total production (Petrušewicz & Macfadyen, 1970). Thus, the non-trappable part of the population plays an important part in total production, and it can be calculated when some assumptions, especially about the number of newborn animals are made. Hence large errors are made when we try to estimate any parameters of productivity in any part of the population for which empirical data are virtually unobtainable. This also shows that data concerning curves of population dynamics should be considered with caution. In many cases we determine the dynamics of only the "trappable" part of the population, while the independent but very young and infrequently trapped individuals are missed.

Turnover of biomass. This is an instructive population parameter

indicating how many times the biomass of a population is exchanged in a given period ( $T$ ).

$$\Theta_B = P/\bar{B} \quad (8.8)$$

Turnover characterizes production per unit population biomass. The value of turnover depends on survival "strategy", already discussed in section 5.1: a high reproduction at a high mortality, and a moderate or small reproduction in species with low mortality. The bank vole, like other rodents, has high mortality and high reproduction. The turnover of an isolated, island population (Petrušewicz *et al.*, 1971) for a whole year was:

$$\Theta_B = P/\bar{B} = \frac{11379 \text{ g biomass}}{3027 \text{ g biomass}} = 3.76$$

The turnover of a bank vole population in the Niepołomice Forest was 3.9 (Bobek, 1973). Therefore, the mean standing crop biomass is exchanged about four times over a year.

Recall that the turnover of individual bank voles ( $\Theta_N$ ) is about 4.7 (see section 5.1). The higher value of individual turnover ( $\nu/N$ ) as compared with biomass turnover ( $P/\bar{B}$ ) is an effect of a high mortality of the youngest, not fully grown animals ( $\nu$  is the number of individuals present in the population at a given time, see section 5).

### 8.3. Metabolism and Costs of Maintenance

There are several measures of metabolism, which are well defined in physiology. In small mammals, we can measure basal metabolic rate (*BMR*), resting metabolic rate (*RMR*), fasting metabolic rate (*FMR*), and average daily metabolic rate (*ADMR*). These measurements differ in their duration, ambient temperature, feeding regime applied to animals, and the level of activity allowed. For this reason, these measures of metabolism differ in the number of metabolic components (Gessaman, 1973). The most ecological measure of metabolism seems to be the average daily metabolic rate, *ADMR* (Grodziński & Górecki, 1967; Grodziński & Wunder, 1975). *ADMR* represents the mean value of metabolism over 24-hours, that is, the mean value for active and resting periods in the daily cycle (Górecki, 1968). It consists of the basal metabolism (*BMR*), the metabolic equivalent of energy for thermoregulation and activity, as well as of the energy of SDA (specific dynamic action or the calorogenic effect of food; Gessaman, 1973). Such measurements were used as the basis for constructing daily energy budgets of small mammals, and the balances of energy flow through their populations (Grodziński & Górecki, 1967; Grodziński *et al.*, 1969/1970).

*ADMR* is measured in large chambers, where animals are relatively free to move. Usually the chamber is equipped with nests, food, and water and also an activity wheel. Measurements are taken at nest temperature, usually at 20°C (Morrison & Grodziński, 1975).

Daily metabolism has been determined for a few vole species such as *Clethrionomys rutilus* (Grodziński, 1971; Whitney, 1977) or *Clethrionomys gapperi* (Pearson, 1947; Buckner & Bergeron, 1973). In the bank vole (*C. glareolus*), it has been thoroughly measured for a large number of animals from southern Poland (Górecki, 1968; Górecki, unpubl. data). The measurements have been taken in four seasons of the year at 20°C. The animals had a possibly wide range of body weights (from about 16 to 33 g). Intraspecific relationship between the metabolism and body weight was computed for all the seasons. The resultant allometric functions of the form  $ADMR \text{ (ccm O}_2\text{/g h)} = a W^b$  are listed in Table 8.1. Results obtained by the using these functions can be easily expressed in energy units (calories) by means of the so-called oxygen energy equivalent (usually when the animals are supplied with a mixed diet, this equivalent equals to 4.8 kcal/ccm<sup>3</sup> O<sub>2</sub>).

The daily rhythm of metabolism in the bank vole varies over the year. The ratio of the metabolic rate in periods of maximum activity (so-called maximum metabolism) to the minimum metabolic rate (usually for sleeping animals) was similar in all the seasons and ranged from 1.6 to 2.0 (Górecki, 1968). The patterns of the daily rhythm, as determined by oxygen consumption in the annual cycle, are shown in Figure 8.5. Generally these patterns have two peaks, at dawn and dusk.

In addition to the *ADMR*, the energy budget of a rodent should also contain the costs of thermoregulation in the time spent outside the nest, and the costs of reproduction.

### 8.3.1. "Group Effect" and Reproduction in Relation to Metabolism

Small homiotherms have various forms of behavioural thermoregulation. In bank voles, this is generally huddling together in some periods within the nest. This allows the animals to reduce their daily energy losses and is called the "group effect". Ponugaeva (1960) found that huddling can reduce the resting metabolic rate (*RMR*) of a group of bank voles by about 8 to 17%. *ADMR* can be reduced in this way by 13.5% (Górecki, 1968). As bank voles stay in their nests most of the day, this is an important energy conservation measure.

The gestation and lactation period costs much in terms of energy. The bioenergetics of this period in the bank vole was studied by Kaczmariski (1966). To produce and rear an average litter, the female must

additionally assimilate 346 kcal, including as many as 289 kcal during lactation which lasts for 18–20 days. Thus, energy expenditures in females rise by about 24% during pregnancy and by as much as about 92% during the lactation period. On the average, the assimilation in females increases by 58% over the breeding season (Kaczmarek, 1966), of which almost 50% goes for respiration, and about 8% for production

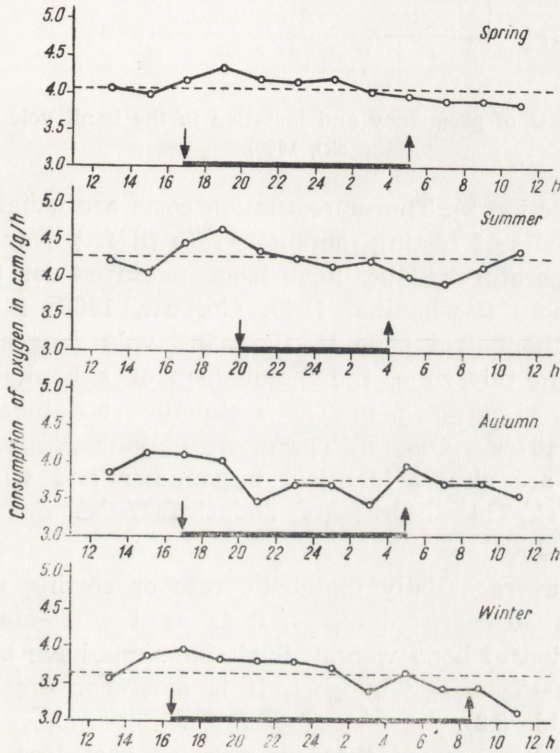


Fig. 8.5. Average daily metabolic rate (ADMR) of the bank vole in different seasons ((after Górecki, 1968).

of the young, including placenta and foetal membranes (Grodziński & Wunder, 1975). The increase in the energy requirements of reproducing females is shown in Figure 8.6.

### 8.3.2. Thermoregulation

Maintenance of a high constant body temperature is an important component of the energy budget in small mammals. The annual mean body temperature in adult bank voles is 37°C (Górecki, 1968), and in their first month, it increases from about 34° to about 38°C (Gębczyński,

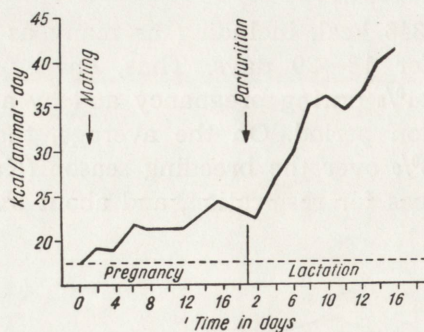


Fig. 8.6. Energy costs of pregnancy and lactation in the bank vole (after Kaczmar-ski, 1966).

1975; see also section 2). Thermoregulation costs are usually determined from measurements of resting metabolic rate (*RMR*) over a wide range of ambient temperatures. They have been measured for the bank vole by several authors (Bashenina, 1966; Górecki, 1966, 1968; Vişinescu, 1967). The thermoneutral zone in the bank vole ranges between  $28^{\circ}$  and  $32^{\circ}\text{C}$ . Within this zone, the metabolism of a bank vole weighing 24 g is  $2.33 \pm 0.25$  cc  $\text{O}_2/\text{g h}$ . The metabolic rate measured at  $0^{\circ}\text{C}$  reaches almost 10 ccm  $\text{O}_2/\text{g h}$ . Thermoregulation costs within a range of  $0^{\circ}$  to  $25^{\circ}\text{C}$  are almost identical in summer and winter, reaching  $0.967$  cal/g  $\cdot$  h  $\cdot$   $^{\circ}\text{C}$ . This represents about  $5.6\%$ / $^{\circ}\text{C}$  on average over a year (Górecki, 1968).

To use the average daily metabolic rate or resting metabolic rate for computation of energy budgets, it is most convenient to express them as a function of body weight. Such functions have been developed for computation of energy budget, it is most convenient to express temperature (Table 8.2).

It is commonly assumed that the rate of heat loss by an animal is proportional to thermal conductance (*TC*) and to the difference between

Table 8.2

A relationship between resting metabolic rate (*RMR*) and body weight at different ambient temperatures for the bank vole (after Górecki, 1966, 1968 and unpubl. data).

Ambient temperature	N	<i>RMR</i> , ccm $\text{O}_2/\text{g}$ $h = aW^b$	Confidence interval of <i>b</i>
0	8	4.64 $W^{-0.67}$	(-1.67, 0.23)
5	51	32.96 $W^{-0.44}$	(-0.60, -0.28)
10	54	27.93 $W^{-0.44}$	(-0.62, -0.26)
15	54	22.13 $W^{-0.42}$	(-0.62, -0.22)
20	52	12.96 $W^{-0.29}$	(-0.45, -0.13)
25	55	2.32 $W^{-0.37}$	(-0.57, -0.17)
30	54	1.33 $W^{-0.52}$	(-0.78, -0.26)

the body temperature and ambient temperature (Swan, 1974). Thermal conductance is defined as the specific rate of the heat transfer and it is usually measured in  $\text{kcal/g} \cdot 24 \text{ h} \cdot ^\circ\text{C}$  (Hart, 1971). Therefore, the relation of thermal conductance to temperature is linear in animal of a given body weight. To find the relationship between  $TC$  and the body weight, the resting metabolic rate ( $RMR$ ) has been calculated for animals of different sizes at ambient temperatures ranging from  $5^\circ$  to  $20^\circ\text{C}$ , using equations from Table 8.2. Then  $TC$  has been calculated from the formula

$$TC = \frac{RMR(t) - RMR(20)}{t - 20} \quad (8.9)$$

$t$  is the temperature of  $RMR$  measurement for bank voles weighing from 17 to 30 g. The following relationship was found from these formulae, using a logarithmic regression technique

$$TC = 3.53 W^{-0.20} \quad (8.10)$$

where  $W$  is body weight in grams, and  $TC$  is thermal conductance in  $\text{ccm O}_2 \cdot \text{h}$ . The exponent of this intraspecific function differs from that given by Hart (1971) for interspecific functions calculated for rodents ( $b = -0.5$ ). The comparisons made by Hart for tens species of rodents shows, however, that the value of this exponent for intraspecific functions can vary considerably.

### 8.3.3. Energy Costs of Activity in Bank Voles

There are two important questions we have to answer when doing bioenergetic studies: (1) what is the effect of normal activity of an animal on its metabolism, and (2) what fraction of the day does this activity last and what is the pattern of this activity? Janský (1965) found that the metabolism of bank voles forced to run on the activity wheel for a long time was about four times as high as the basal metabolic rate ( $BMR$ ), and as much as seven times as high during short, maximum efforts. But under natural conditions animals are not so forced and the increase in their metabolism varies from only about 50% to 100% of the resting metabolic rate ( $RMR$ ) (Górecki, 1968).

There are many laboratory data on the daily activity in the bank vole, unfortunately field data are almost completely lacking. Daily sums of activity are usually lower in winter than in summer, and, furthermore, in winter, rodents usually are more active during the warmer part of the day (Osterman, 1956; Saint Girons, 1960b, 1961; Pearson, 1962).

The total time spent outside the nest has been treated as a daily

activity of animals. This parameter was measured in metabolic chambers and the average value calculated for the entire year was 227 minutes. In summer, the daily sum of activity was higher (264 min) than in the other seasons (Górecki, 1968). Therefore, the time of the bank vole activity outside the nest did not exceed 20% of the daily cycle. These laboratory results are consistent with the results obtained by Buchalczyk (1954) under natural conditions. He determined the activity of bank voles from measurements of their trappability at 2-hour intervals. This method provides a rather good indication of the activity pattern, but only a rough estimate of the sum of activity. Bank voles are mostly active at night, and there are two peaks in their daily activity rhythm (Górecki, 1968, Fig. 8.7).

Two methods have been developed that allow measurements of rodent activity in the field. One consist of continuous tracking of animals labelled with metal radio-cobalt (Nikitina *et al.*, 1972). The other one is a continuous measuring of temperature in the nest by means of thermocouples, this temperature being higher when the animal is in the nest (Flowerdew, 1973). Such measurements were taken for only a few voles (*Microtus* sp.), and their activity proved to be much higher in the wild than in the laboratory. We may thus expect this to also be the case for the bank vole (Ashby & Vincent, 1976).

#### 8.4. Consumption, Digestibility, and Assimilation of Food

Bank voles are polyphagous rodents feeding on different plant parts (tree seeds, berries, greens, fungi, buds, and bark) and on animals (insects, snails) (see section 3). They can use this diversified food due to the specific structure of their alimentary canal with both small intestine and caecum well developed (Grodziński, 1962).

Consumption and utilization of food energy in the bank vole were mostly studied under laboratory conditions, using the classic balance method (Drożdż, 1968). This method is based on equations (8.2) and (8.3), which state that consumption (gross energy in nutrition terminology) is equal to the sum of assimilation (metabolizable energy) and energy excreted with feces and urine. Practically such measurements are made in metabolic cages, in which we can determine exactly the daily food intake and separately the daily production of feces and urine for single animals. During 7- to 10-day experiments the animal should not change its weight ( $P=0$ ), otherwise some corrections are needed to compensate energy equivalents of gains or losses in body weight. Then the energy content of food, feces and urine, as well as ash content are determined



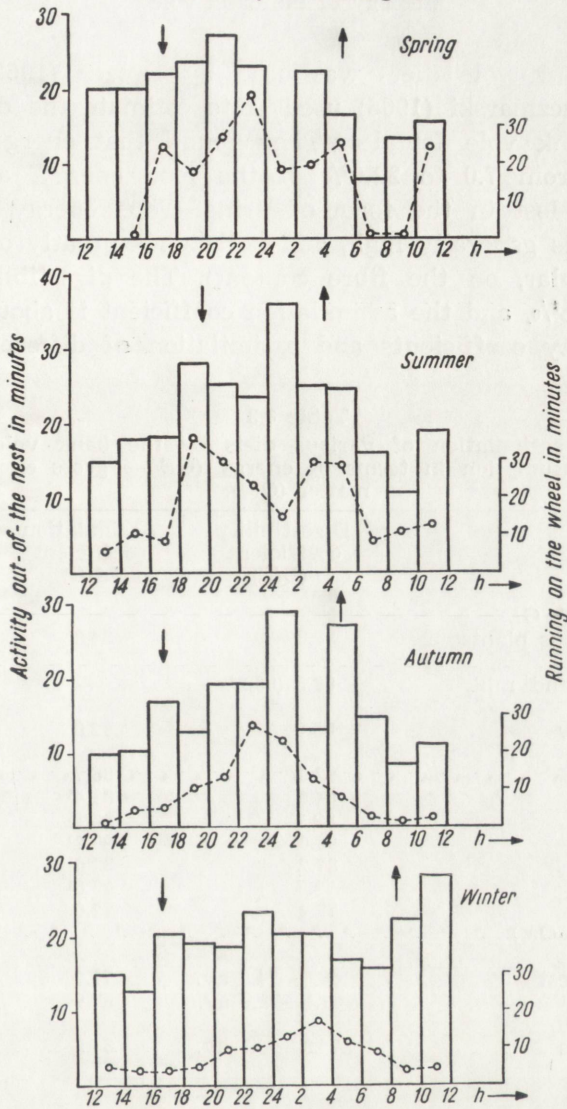


Fig. 8.7. Seasonal changes in the pattern of daily activity as measured in respiratory chambers for the bank vole (after Górecki, 1968).

using a bomb calorimeter. This allows the estimation, in terms of energy and/or organic matter, of the total consumption ( $C$ ), digestibility ( $D$ ), and assimilation, which here equals costs of maintenance ( $A=R$ ), and also the calculation of digestibility and assimilation coefficients ( $D/C$  and  $A/C$ ). All these variables are necessary physiological parameters for estimating productivity of the entire rodent populations (Grodziński, 1975).

The balance method for estimating the digestibility and assimilation

of different bank vole diets was used by Drożdż (1968) and Meese (1971). Also Kaczmariski (1966) used it to estimate the digestibility in reproducing bank vole females. They found that energy losses with feces ranged from 7.0 to 22.6% of the food energy, and additional 2.2—5.4% was lost in the form of urine. Thus energy utilization in the bank vole is generally high, and it depends greatly on the type of diet (in particular, on the fibre content). The digestibility of mixed diets reaches 88%, and the assimilation coefficient is about 85% (Table 8.3). Digestibility coefficients and assimilation of different diets com-

Table 8.3

Digestibility and assimilation of various diets by the bank vole, expressed as percentage of consumption in terms of energy (*GE* — gross energy) or organic matter (*OM*).

Method and diet	Digestibility coefficient (D/C)	Assimilation coefficient (A/C)	Reference
Balance method (% <i>GE</i> )			
Mixed (herbaceous plants and seeds)	87.8	84.8	Drożdż, 1968
Wheat, carrot and milk	88.5 (86.2) <sup>2</sup>	—	Kaczmariski, 1966
Laboratory chow	85.0	82.8	Malinowska, 1978
Beechmast	92.9	88.7	Drożdż, 1968
Acorns	84.0	81.4 <sup>1</sup>	Meese, 1971
Oats	89.1	86.1 <sup>1</sup>	Drożdż, 1968
Oats	93.0	90.2 <sup>1</sup>	Meese, 1971
Wheat	87.2	84.6 <sup>1</sup>	Meese, 1971
Bluebell corns	79.7	75.6 <sup>1</sup>	Meese, 1971
Greens	77.4	72.0	Drożdż, 1968
Tracer method (% <i>OM</i> )			
Natural diets <sup>3</sup> :			
deciduous forest	66.6—74.5 av.	71.2	Sikorska, 1975
pine woods	61.1—72.9 av.	67.9	Malinowska, 1978
Laboratory diets	75.8—90.7 av.	84.9	Drożdż, 1968 (Grodziński & Wunder, 1975)

<sup>1</sup> Corrected for the energy of urine according to Davies & Golley (1963) and Drożdż, (1968), <sup>2</sup> Digestibility in highly lactating females, <sup>3</sup> Range for various seasons.

prising tree-seeds (beechmast, acorns) or grain (oats, wheat) are even higher, 84—93% and 81—89%, respectively. The digestibility of greens, e.g., plants of the forest herb layer, is markedly lower (77—80%), the same being true of their assimilation (72—76%). According to Drożdż (1968), the mean values he obtained for four diets (digestibility coefficient of 86.8% and assimilation coefficient of 82.9%) can be used in computations of energy flow through bank vole populations. This implies that to get a total consumption of the population, the assimilation calculated

as the sum of the costs of maintenance and production should be increased by about 17% in terms of energy (Grodziński *et al.*, 1969/1970).

New possibilities of estimating digestibility in small mammals under field conditions have been discovered by Johnson & Maxell (1966). They developed a tracer method, using the content of ash in food and feces as a natural tracer. Natural food and feces for analyses can be collected in the field (Johnson & Maxell, 1966) or directly from stomachs (food samples) and colon (feces samples) of the animals obtained from snap traps (Johnson & Groepper, 1970). This method should be used with caution, checked for different elements, and tested for natural diets in the laboratory (Kaufman *et al.*, 1976). The animal has to be in mineral balance. The tracer method was used to examine digestibility in bank voles inhabiting deciduous and coniferous forests of the Niepołomice Forest (Sikorska, 1975; Malinowska, 1978). A large (61–74%) seasonal variability in digestibility coefficients was found. Digestibility also depended on the forest type and the associated available food supply. Mean annual digestibility in coniferous and deciduous forests was 68 and 71% of the organic matter consumed by the bank vole (Table 8.3). Digestibility coefficients expressed in terms of organic matter differ by 1–3% from those calculated in energy units (Grodziński & Wunder, 1975). Table 8.4 shows for comparison the results obtained by Drożdż for laboratory diets; the mean digestibility coefficient for all diets reaches 86%.

Due to the natural ash tracer method we have found that wild bank voles utilize only about 70% of the energy consumed in food. This is much less than in all laboratory feeding trials in which the balance method was used (83–85% on average). The reasons for this discrepancy are not clear yet. It is possible that the natural diet of the bank vole is not as well assimilated as is the diet tested in the laboratory. Similarly, a lower digestibility was obtained by this method for the boreal redback vole, *Clethrionomys gapperi*, in America (Johnson & Groepper, 1970). Therefore, about 30% should be added to the value of assimilation when estimating total consumption for a bank vole population in a forest.

Feeding trials also allow the determination of the cost of maintenance ( $R$ ) in small rodents kept under laboratory conditions. Measurements of consumption and assimilation in metabolic cages were sometimes considered as a control for more precise respirometric measurements (Drożdż, 1968; Górecki, 1968; see also section 8.3). Table 8.4 shows daily energy requirements in the bank vole, as calculated from food assimilation (Drożdż, 1968; Meese, 1971), and expressed in kcal/g body weight to compare them easily with the results based on oxygen consumption presented in section 8.3. As we can see, the daily food consumption in

the bank vole ranges from 0.505 to 1.090 kcal/g day, depending on diet, while costs of maintenance corrected for changes in body weight ( $A=R$ ) are 0.401—0.467 kcal/g day (Table 8.4). These values are slightly higher than the average daily metabolic rate (*ADMR*). For example, assimilation of a mixed diet was 11.5% higher than *ADMR*. Drożdż (1968) explains this difference by the insulating properties of the nest that was available in the metabolic chamber during *ADMR* measurements, but absent in the metabolic cage for feeding trials. Energy requirements in *Microtus*,

Table 8.4

Daily energy requirements in the bank vole (*Clethrionomys glareolus*), measured as consumption (C) and assimilation (A) of food energy (all values in kcal/g day). Recalculated from Drożdż (1968) and Meese (1971).

Diet	Consumption (C)	Assimilation (A)	Assimilation corrected for body weight changes (A = R)	Reference
Mixed	0.657	0.558	0.446	Drożdż, 1968
Beechmast	0.584	0.519	0.462	Drożdż, 1968
Acorns	0.553	0.450	—	Meese, 1971
Oats	0.568	0.489	0.422	Drożdż, 1968
Oats	0.806	0.726	—	Meese, 1971
Wheat	0.716	0.606	—	Meese, 1971
Bluebell corns	0.570	0.432	—	Meese, 1971
Greens	0.569	0.392	0.401	Drożdż, 1968

as calculated from food consumption in out-of-doors experiments, can be considerably lower than when obtained from respiratory measurements (Sawicka-Kapusta *et al.*, 1975; Ferns, 1979).

### 8.5. Energy Budget of Individual Voles and Their Populations

In this chapter we will finally deal with joining the physiological parameters discussed earlier and ecological parameters at the population level. Physiological parameters determined by respirometric, feeding, and calorimetric methods can be used for developing energy budgets. As already mentioned, the daily energy budgets (*DEB*) are just based on the average daily metabolic rate (*ADMR*). The bank vole is a classic example of an animal for which such energy budgets were calculated (Grodziński & Górecki, 1967; Górecki, 1968). We will discuss here the data obtained by Górecki (Table 8.5). The energy budget for a winter day comprised the value of *ADMR* and was corrected only for the additional cost of thermoregulation during four-hour activity outside the nest. The energy budget for a summer day was corrected for thermore-

gulation outside the nest (lasting for a longer time but at higher ambient temperatures) and for the cost of reproduction, calculated as an average value for all population members. As the result, the winter and summer *DEB* for an average bank voles (weighing 21 or 19 g) was 10.21 and 10.56 kcal/day, respectively.

Improved energy budgets for voles are based on the relationship between *ADMR* and body weight (Grodziński, 1971), which makes them independent of "an average animal in the population". Intraspecific functions were calculated, e. g. for the redbacked vole, *Clethrionomys rutilus* (Grodziński, 1971), as well as interspecific functions for small

Table 8.5  
Daily energy budget (*DEB*) of the bank vole on a winter and a summer day (after Górecki, 1968).

Items	Winter (kcal/g day)	Summer (kcal/g day)
<i>ADMR</i> (20°C) in the nest, including group effect (13%)	20 h × 3.65 ccm 0 <sub>2</sub> /g h = 0.0351	19.5 h × 4.29 ccm 0 <sub>2</sub> /g h = 0.401
Metabolic rate during periods of out-of-the-nest activity (0°C or 15°C)	4 h × 7.03 ccm 0 <sub>2</sub> /g h = 0.135	4.5 h × 5.57 ccm 0 <sub>2</sub> /g h = 0.121
Cost of female reproduction	—	6.5% <i>ADMR</i> = 0.034
Corrected <i>DMR</i> values × average body weight	0.486 × 21.0 g	0.556 × 19.0 g
<i>DEB</i> in kcal/vole day	10.21	10.56

rodents or insectivores (Grodziński & Wunder, 1975). The slopes of these functions were close to 0.50, therefore they have been rounded off to this value. These functions, like those developed by Górecki (1968), were corrected for the cost of thermoregulation outside the nest and for female reproduction. Using this technique, Grodziński (1971) found that the mean daily energy budget of the redbacked vole (*C. rutilus*) is 13.5 kcal/day in snow-free periods and 10.1 kcal/day in winter (at body weights of 22 and 19 g). In section 8.3, Górecki developed new *ADMR*—body weight functions for the bank vole, using different slope values for different seasons. The energy budgets based on these functions for both vole species are shown in Figure 8.8. As we can see, they range between 9 and 13.5 kcal/animal·day in different seasons.

So far, the daily energy budgets (*DEB*) presented here have not been verified in the field. They have been tested only by feeding methods (see section 8.4). Mullen (1973) developed the D<sub>2</sub><sup>18</sup>O technique which allows precise measurements of energy requirements of small mammals in the field. This technique has already been used to verify energy budgets calculated from energy measurements similar to those we used (respirometric) but for desert rodents. The results proved to be highly consistent, with differences ranging between 1—21% (Mullen & Chew,

1973). We can thus expect that the daily energy budgets for the bank vole also approximate reality.

The application of *DEB* to the productivity estimates of entire populations, and in particular to their respiration, has been methodologically discussed by Grodziński (1975). He uses as an example populations of the bank vole and yellow-necked field mouse (*Apodemus flavicollis*)

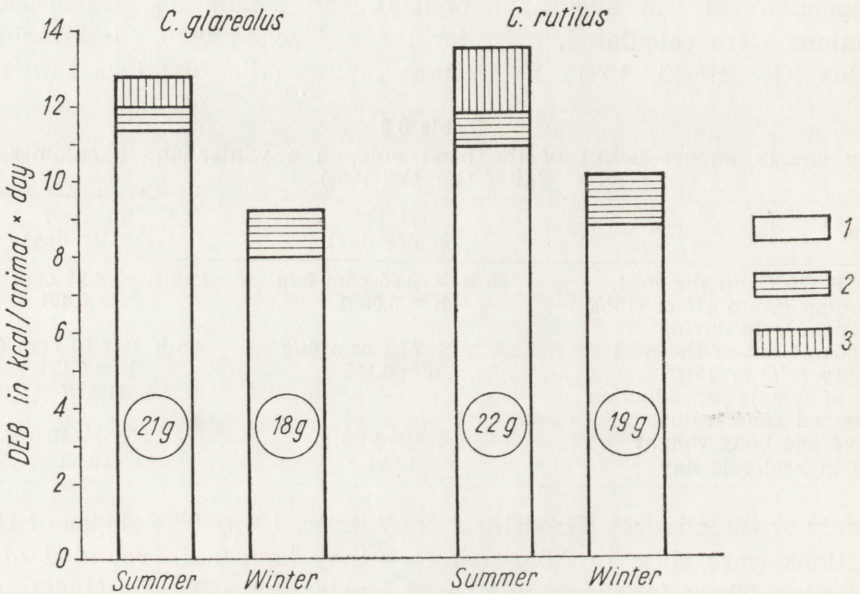


Fig. 8.8. Daily energy budget (*DEB*) of the bank vole (*Clethrionomys glareolus*) and the tundra redbacked vole (*C. rutilus*) in summer and winter. These are budgets for adult voles of an average body weight (encircled figures); 1 — *ADMR*, 2 — thermoregulation costs in periods of activity beyond the nest, 3 — additional costs of reproduction per average population member (after Górecki, 1968 and Grodziński, 1971, recalculated and simplified).

living in beech forests of the Ojców National Park (Grodziński *et al.*, 1969/1970; Grodziński, 1975). For technical details the reader is referred to the IBP Handbook, edited by Grodziński, Klekowski & Duncan (1975). But the principle itself is worth quoting here. The cost of maintenance (*R*) of the bank vole population was calculated as a product of its mean biomass, *DEB* and the time period (number of days); population biomass and number of days could be multiplied and used as “biomass-days” (Petrušewicz & Macfadyen, 1970). The technique for calculation of net production is explained in section 8.2. Energy flow through the population (assimilation) has been computed as the sum of respiration and production. To estimate the total consumption in the population, its assimilation

has been divided by the assimilation coefficient ( $A/C = 0.70$ ) discussed in section 8.4. Such simple methods for estimating respiration, assimilation and consumption in rodent populations have been used in many papers on their productivity (e. g. Grodziński *et al.*, 1969/1970; Gębczyńska, 1970; Hansson, 1971a; Grodziński, 1971; Górecki, 1977; for a review see Grodziński & French, 1983).

Such methods of calculation based on physiological parameters for individual species or even on interspecific functions (Grodziński & Wunder, 1975) usually provide satisfactory results (Kozłowski, Górecki & Bobek, 1980). In this way we can easily calculate sums and mean values of annual budget, but it would be a laborious task to follow in this way the dynamics of population productivity in annual or multiannual cycles. For this reason, simple computer programs have been developed to analyse the dynamics of respiration, production, and consumption in rodent populations. The first such model was constructed for rodent populations living in North American grasslands (French *et al.*, 1976) and the second one for microtine voles in European croplands (Grodziński *et al.*, 1977). In the next section (8.6) we will present a new model for productivity dynamics in bank vole populations. It has been used for an open population and for a population isolated on an island.

## 8.6. Productivity Dynamics in Bank Vole Populations

Population numbers of the bank vole vary considerably in time and space. The general pattern of population dynamics, however, is fairly similar from year to year (see section 4.1). Similarly, there are seasonal changes in the age structure and the related distribution of body weights in the population. Also reproduction is a seasonal event (see section 6.2). It is thus obvious that production, respiration, assimilation, and consumption of the population will vary with time. Analysis of these changes requires not only knowledge of many physiological and ecological parameters, but also tedious calculations. Therefore, a simple model has been developed for studying the dynamics of all the components of population productivity.

### 8.6.1. The Model

The model presented here was developed and tested for a bank vole population (Kozłowski, Górecki & Bobek, 1980). This is a simulation model, the general structure of which is illustrated in Figure 8.9. Omitting the description of the computer program written in *FORTRAN*,

we will describe here its structure and functioning. It uses data of three types: physiological, ecological (see section 8.1), and climatic. Physiological data can be considered as relatively stable over large areas and are species-specific. Ecological data, however, should be individually determined for each population. We tried to develop a program that can use the necessary ecological data collected in the simplest possible way, and that can also work when these data are inaccurate, for example, when they are insufficient for construction of life tables and individual growth curves.

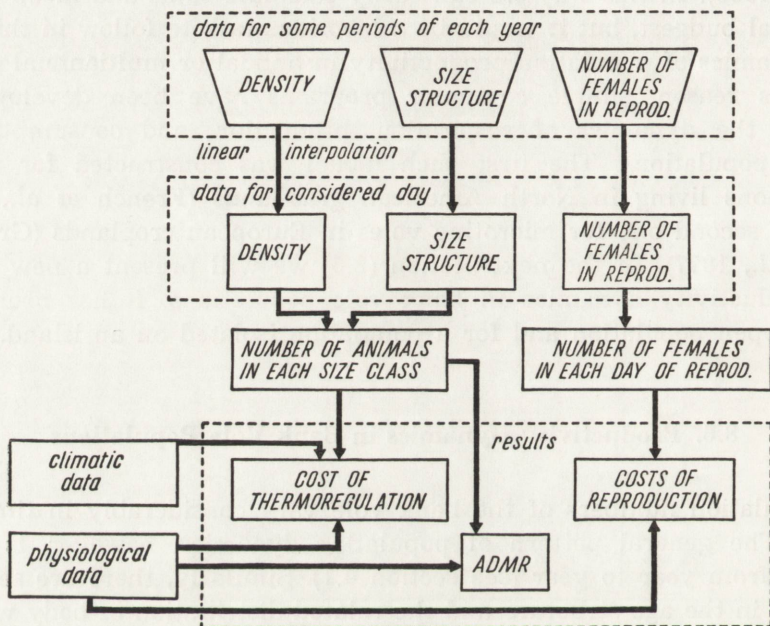


Fig. 8.9. Computation scheme of respiration at the population level.

Physiological data have been described in detail in section 8.3—8.5. Average daily metabolic rates (*ADMIR*) for animals in different weight classes have been calculated from equations given in Table 8.2 (section 8.3), which describe relationships with body weight and change in season. The *ADMIR* for consecutive days of the year was linearly interpolated from the *ADMIR* calculated from the two nearest seasons. The costs of thermoregulation (*THERMO*) for animals of each body weight category were calculated from the equation:

$$THERMO = TC \cdot AP \cdot (t - 20) \quad (8.11)$$

where *TC* is thermal conductance ( $\text{kcal/g} \cdot \text{hr} \cdot ^\circ\text{C}$ ), which is a function of body weight (equation 8.10, section 8.3), *AP* denotes the part of the



day spent outside the nest, and  $t$  is the ambient temperature at the ground level. It has been assumed that  $AP$  equals to 0.17 day, that is, about 4 hours (Górecki, 1968). Thermal conductance is multiplied by the difference between  $20^{\circ}\text{C}$  and actual ambient temperature. The thermoneutral zone in the bank vole is close to  $30^{\circ}\text{C}$ , but the costs of thermoregulation between  $20^{\circ}$  and  $30^{\circ}\text{C}$  are included in the  $ADMR$  measurement itself.

Additional costs of reproduction are taken from Figure 8.6. They were lowered by 12% for gestation period and by 8% for lactation period because such a part of the costs of reproduction in females will, in some way, be incorporated into the production realized by the offspring (Grodziński & Wunder, 1975). The percentages have been calculated on the assumptions that: mean litter size is about 5 young (Bobek, 1973), body weight is 1.6 g at birth (Drożdż, 1963) and 7 g at leaving the nest (Bujalska & Gliwicz, 1968) and that the weight of placenta and foetal membranes can be assumed from general physiological data.

**Field data.** Population density and the frequency distribution (structure) of body weights in the bank vole population are of basic importance. These variables must be known for a few time instances during a year, and they are linearly extrapolated to the other periods. Data on numbers and on the distribution of body weights allow calculation of the costs of maintenance, except for costs of reproduction. Obviously, to estimate the costs of thermoregulation we have to know temperature near the ground, that is, at a height of about 5 cm above the ground. If such data are not available for the study area, they can be calculated from the following equation for European forests of the temperate zone (Klein, 1978)

$$T_5 = -0.75 + 0.98 T_{200} \quad (8.12)$$

where  $T_5$  denotes temperature at a height of 5 cm,  $T_{200}$  is temperature at a height of 200 cm, thus according to the standard. Temperature at the ground level is also affected by the depth of snow cover. It can be assumed that when the snow cover is more than 5 cm thick, the temperature at the ground is about  $+0.5^{\circ}\text{C}$ , independent of the ambient temperature (Formozov, 1946; Klein, personal communication).

To calculate the cost of reproduction, we have to know the number of pregnant females at the selected time instants of the year. The number of animals in successive days of the breeding season was calculated on the assumption that the gestation period lasts 18 days, lactation lasts 18 days, and that the probability of death for both pregnant and lactating females is 0.02/day. Let  $n_i$ ,  $i$  ( $i=1, \dots, 36$ ) be the number of females in the  $i$ -th day of the breeding cycle at time  $t$ . Then the number of females

on the  $i$ -th day of the cycle at time  $t+1$  can be calculated from the equation

$$n_{t+1,i} = n_{t,i-1} (1.0 - 0.02) \quad (i = 2, \dots, 36) \quad (8.13)$$

and the number of females on the first day of pregnancy from the equation

$$n_{t+1,1} = N - \sum_{i=2}^{18} n_{t+1,i} \quad (8.14)$$

where  $N$  is the total number of pregnant females, as found by linear interpolation from the available field data.

Computation of population maintenance cost (respiration). Figure 8.9 illustrates the way of calculating cost of maintenance for the whole population. Field data were available for eight separate periods during the course of a year for the population living in the Niepołomice Forest, and for five periods for the population on the Crab-Apple island. The values of the variables for any given day were obtained by linear interpolation of the input data obtained for the nearest time instants. Then the number of animals in particular weight classes was calculated, as were the numbers of females in successive days of the breeding cycle. Using the climatic and physiological data described above,  $ADMR$  and additional cost of thermoregulation were calculated for each of body weight, and then they were summed for the whole population. The number of females on consecutive days of the breeding cycle was then multiplied by the additional cost of reproduction on respective days.

Calculation of population production. To calculate net production in a population, the detailed data on animal survival and growth are needed. The graphical method for calculating production from data has been described in section 8.2. Such detailed data, which allow the construction of life tables, are rarely available. To get at least a rough approximation of the net production dynamics in the population when the respective data are lacking, we used the following procedure in the model. A pattern of the percentage distribution of production over the year and the total annual production were introduced. The latter can be calculated by the graphical method if the data are available, and if not, it can be estimated from the  $P/R$  ratio, which is rather constant (Petrušewicz & Hansson, 1975), and for small mammals is described by the equation

$$P = 0.00643 R^{1.116} \quad (8.15)$$

where  $P$  and  $R$  are expressed in kcal/ha year (French *et al.*, 1976. In addition, Bobek (1973) has calculated a specific equation for the bank vole, which provides quite accurate estimates of net production from

mean annual numbers of trappable animals ( $N$ )

$$P = 92.4 \bar{N} \quad (8.16)$$

where  $P$  is in kcal/ha year, and  $\bar{N}$  in individuals per ha.

If the appropriate data are not available, the pattern of production distribution can eventually be taken from another area or another year. It can also be intuitively conceived, when we know the phenology of the species and have some information on changes in the number of pregnant females over the year.

**Calculation of assimilation and consumption.** The assimilation of rodent populations is usually calculated as the sum of respiration and production (Grodziński, 1975). If the body weight decreases in winter, assimilation is reduced by the corresponding energy value. This is related to the fact that actual respiration can be covered in part from the energy stored in individual animals.

Consumption was calculated by dividing assimilation by the coefficient of assimilation. The estimated value of assimilation coefficient was 0.83 in the laboratory and 0.70 in the field (see section 8.4). The latter value has been used in the model (see section 8.4).

To express the amount of oxygen used in terms of energy, it was assumed that the energy equivalent of oxygen is 4.8 cal/ccm<sup>3</sup> O<sub>2</sub> (see section 8.3). To express the biomass of animals in energy units, it was assumed that the energy content of the bank vole tissue is 1.454 kcal/g (Górecki, 1965).

**Energy flow** through bank vole populations inhabiting Niepołomice Forest and Crab-Apple island. The described model was used to simulate the dynamics of productivity in two rather well known populations of the bank vole. One of them is an open population inhabiting deciduous forests of the Niepołomice Forest, dominated by oaks, limes, and hornbeams (*Tilio-Carpinetum*). The total number of animals, number of animals born, and net production and its distribution in time have been given by Bobek (1973). These data have been supplemented with the distribution of body weights in the population (Bobek, unpublished data). Temperature at ground level and the thickness of snow cover are given by Klein (1978).

For comparison, energy flow was analysed in an isolated population of the bank vole inhabiting Crab-Apple island on Beldany Lake, near Mikołajki. The island is dominated by a deciduous forest of *Tilio-Carpinetum* type. The number of animals and annual net production are taken from Petruszewicz *et al.* (1971), and the number of pregnant females from Bujalska (1970). The description of body weights in the population has been calculated from the dynamics of particular cohorts (Gliwicz

*et al.*, 1968) and individual growth curves (Bujalska & Gliwicz, 1968). The same distribution of production over particular seasons was assumed for all the years according to Petruszewicz *et al.* (1968), who described the production of this population in 1966/1967. Climatic data were provided by the Institute of Meteorology and Water Economy, Mikołajki.

The dynamics of vole numbers in the two populations are presented in Figure 8.10. In 1967/1968, there was an outbreak of bank voles in Niepołomice Forest. Population density in May of that year reached 65 voles/ha, while in other years peak numbers did not exceed 23 voles/ha. In addition, in the year of outbreak the shape of the curve of population dynamics was different — peak numbers occurred in May and not in September as in other years. The lowest numbers always occurred at the advent of spring, when they ranged from 2 to 5 voles/ha. Therefore, the density dropped over winter as much as 11 times on the average.

The density of the confined island population was much higher than in the Niepołomice Forest in normal years. Generally, confined populations, even if only in part, have higher densities. A more detailed explanation of this, considering also other factors than lack of emigration, has been given by Petruszewicz (1967, 1978) and Petruszewicz & Uchmański (1980). Maximum numbers on the island in successive years were about 70, 50, and 100 voles per ha, and the minimum was about 15 individuals. Thus the density dropped in winter only about four times. This lower elimination of voles in the island during winter may be related to a reduced impact of predation as it may be difficult for some predators to reach the island.

Standing crop (*B*) of the bank vole population obviously follows changes in numbers of animals. But peak standing crops are a little lower than the peaks of numbers (Fig. 8.10) as there are many young, thus small animals in the population during the breeding period.

The maximum daily production was 37 kcal/ha for both the island and mainland populations, but in the year of the outbreak of the mainland population, maximum production was merely 10 kcal/ha day (July, 1968) and 6 kcal/ha day (July, 1969) (Fig. 8.10B).

The consumption by the island population largely varied from 360 to 1800 kcal/ha day. For the mainland population it was 1100 kcal/ha day at peak numbers in the outbreak year, 450 and 370 kcal/ha day at peak numbers in other years, falling to only several dozen kcal as winter turned to spring (Fig. 8.10). The estimate of population consumption significantly depends on the estimate of the population cost of maintenance (respiration) and on the coefficient of assimilation, and only to

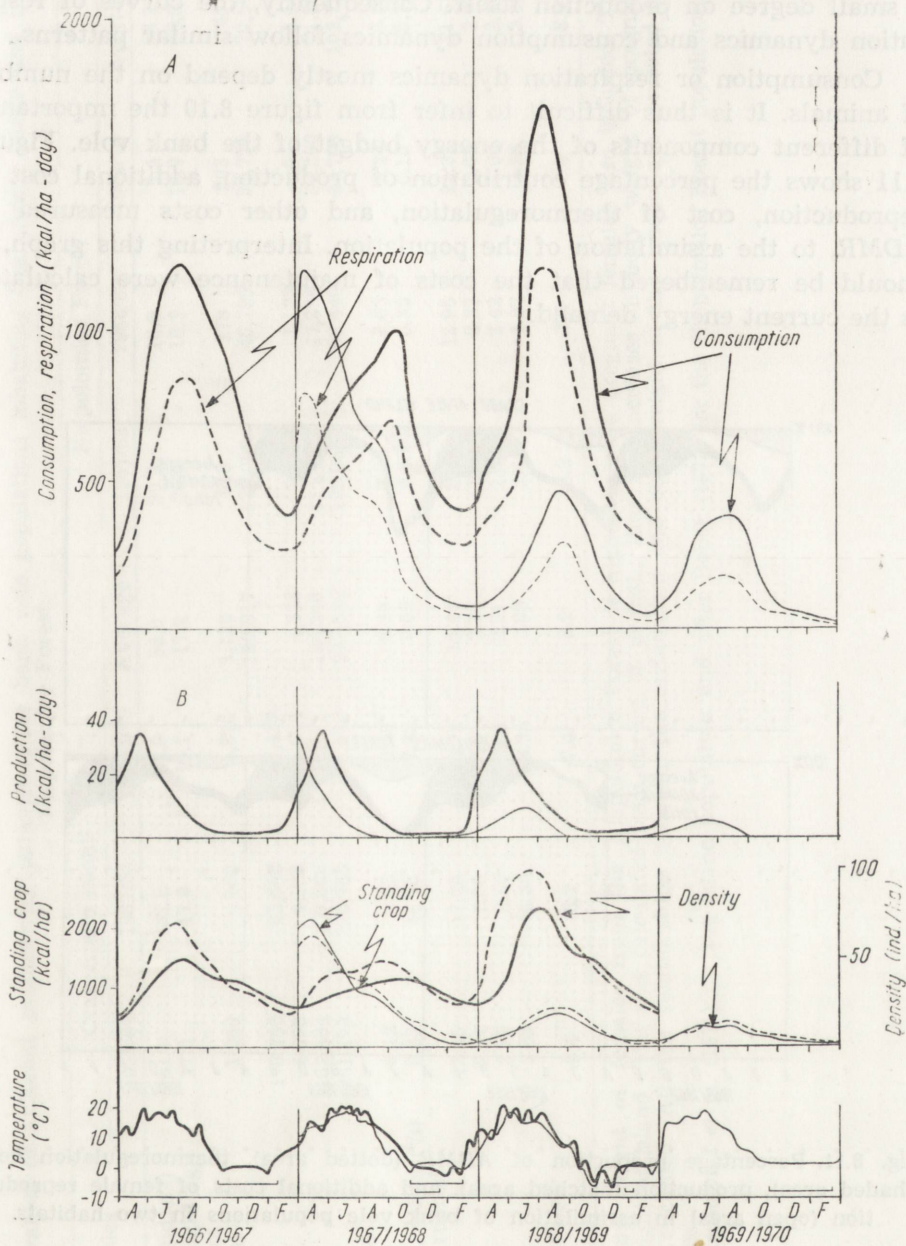


Fig. 8.10. Dynamics of consumption and respiration (A), production (B), numbers and standing crop (C) for bank vole populations on the Crab-Apple island (thick lines) and in the Niepołomice Forest (thin lines). Fig. 8.10 represents mean 10-day temperatures at the ground level (thick and thin lines are for the respective populations) and periods of snow cover, denoted by horizontal lines.

a small degree on production itself. Consequently, the curves of respiration dynamics and consumption dynamics follow similar patterns.

Consumption or respiration dynamics mostly depend on the number of animals. It is thus difficult to infer from figure 8.10 the importance of different components of the energy budget of the bank vole. Figure 8.11 shows the percentage contribution of production, additional cost of reproduction, cost of thermoregulation, and other costs measured as *ADMR*, to the assimilation of the population. Interpreting this graph, it should be remembered that the costs of maintenance were calculated as the current energy demand.

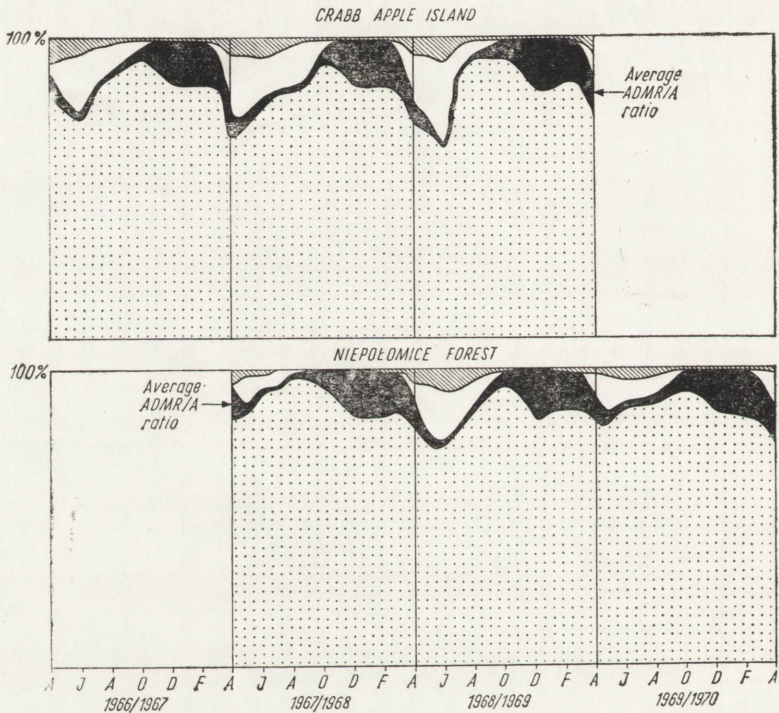


Fig. 8.11. Percentage proportion of *ADMR* (dotted area), thermoregulation costs (shaded area), production (hatched area), and additional costs of female reproduction (open area) in assimilation of bank vole populations in two habitats.

Figure 8.11 clearly shows that the costs of thermoregulation and reproduction replace each other in some way; the annual variability in the proportion of the cost of reproduction and cost of thermoregulation taken separately is much larger than the variability of the sum of these two components. It seems, therefore, that the total assimilation is physio-

Table 8.6

Mean annual values of different productivity parameters for bank vole populations inhabiting Crab-Apple island and the Niepołomice Forest.

Variables	Crab-Apple island				Niepołomice Forest			
	1966/67	1967/68	1968/69	Average	1967/68	1968/69	1969/70	Average
Mean density (ind./ha)	41.1	37.2	58.9	58.9	30.9	10.5	7.4	16.3
Mean body weight (g) <sup>1</sup>	17.5	17.9	16.1	17.2	20.5	18.3	18.9	19.2
Standing crop of biomass (kcal/ha)	1,040	960	1,370	1,128	918	278	203	466
Respiration (kcal/ha-year)	178,706	163,608	227,437	189,917	132,099	46,795	32,726	70,540
Production <sup>2</sup>	4,098	4,198	4,674	4,323	2,419	1,133	682	1,411
Assimilation	182,804	167,806	232,111	194,240	134,421	47,899	33,390	71,903
Consumption	261,190	239,760	331,530	277,530	192,060	68,440	47,700	102,730
Costs of thermoregulat./A (‰)	6.12	6.53	6.40	6.35	4.82	6.63	6.24	5.90
Costs of reprod. + P/A (‰)	9.23	10.73	7.32	9.09	4.65	6.33	6.15	5.71
(C. therm. + c. reprod. + P)/A (‰)	15.35	17.26	13.72	15.44	9.47	12.96	12.39	11.61
P/A (‰)	2.24	2.50	2.01	2.25	1.80	2.37	2.04	2.07
P/R (‰)	2.29	2.57	2.06	2.31	1.83	2.42	2.08	2.11
Turnover (P/B)	3.88	4.30	3.35	3.89	2.63	4.07	3.36	3.35
Mean ground temperature (°C)	8.4	8.7	7.4	8.2	8.5	7.6	7.8	8.0

<sup>1</sup> Mean body weight of females from the Niepołomice Forest is higher because pregnant females also included. The mean body weight of island voles was calculated from curves of growth, thus the increases in body weight of pregnant females were excluded. All the relationships between the metabolism and body weight in the model are corrected for these differences.

<sup>2</sup> After Petruszewicz *et al.* (1971) for the island population and after Bobek (1973) for the Niepołomice Forest population.

logically limited. Reproduction can occur only when the cost of thermoregulation is very low or absent.

The proportion of *ADMR* in the total assimilation is particularly high in late summer and early autumn, thus at the peak of vole numbers. There may be several reasons for this. When the density is high, bank voles can use much energy for local migrations in search of places to live in. Such additional costs are not included into the model. Another reason may be due to a less effective searching for food by young voles, which are abundant in periods of high densities, or to utilization of energy for storing food before winter (see section 3). Perhaps adult animals would be able from the energy viewpoint to continue reproduction in this period, but there would be little chance for offspring to survive winter. A better strategy would thus be to reduce activity, and due to this also to lower the chance of predation. Górecki (1968) has found that under laboratory conditions bank voles are least active in autumn. A particularly low contribution of *ADMR* to assimilation was found for spring and early summer.

The annual cost of maintenance of the entire island population is about 190,000 kcal/ha year, on the average, thus it is more than 2.5 times higher than for the mainland population (about 70,000 kcal/ha year) (Table 8.6). Population consumption is 277,000 and 103,000 kcal/ha year, respectively (Table 8.7). In the mainland population, the proportion of the cost of thermoregulation, total production, and additional cost of reproduction in the annual energy budget almost does not vary from year to year (Table 8.6). In the island population the proportion of thermoregulation cost was always slightly lower.

The net production of the island vole population is several times higher than of the mainland population. It exceeds 4000 kcal/ha year for the island population, while merely 2500 kcal/ha year even in the year of the outbreak for the mainland population, usually it is much lower (Table 8.6).

The ratio of annual production to annual respiration does not vary much from one year to another for the island population and in the years of normal numbers also for the mainland population. It is slightly higher than 2%. Production can thus be quite accurately predicted from respiration, as proposed by Petruszewicz & Hansson (1975), French *et al.*, (1976), Grodziński & French (1983). In the year of outbreak the *P/R* ratio was a little lower. It is understandable as the study was started when the population reached peak numbers (Bobek, 1973), thus the increased production prior to the peak was missed.

Also the biomass turnover is rather stable for the two populations. On the average, it is 3.8 for the island population and 3.7 for the



mainland population in the years of normal numbers (Table 8.6). This implies that we may accurately estimate net production of the bank vole population from its standing crop as well.

However, as it has been shown in this chapter, there are many quite distinct differences between these two free-living bank vole populations inhabiting rather similar forest habitats. It may be expected that these differences are primarily due to the isolation of the island population.