Polish Academy of Sciences
Institute of Ecology and Mammals Research Institute

Ecology of the Bank Vole

Editor: Kazimierz Petrusewicz

Acta Theriologica, vol. 28
Supplement No. 1

Polish Scientific Publishers
WARSZAWA

This supplement has been prepared as a joint work of the editors of "Polish Ecological Studies" (editor-in-chief: Jadwiga Łuczak, editor: Leszek Grüm, secretary: Janina Totwen-Serafińska) and "Acta Theriologica" (editor-in-chief: Zdzisław Pucek, deputy editor and scientific secretary: Marek Gębczyński)

Suggested reference form:

Gliwicz J, 1983: Age structure [In: "Ecology of the bank vole", ed. K. Petrusewicz]. Acta theriol., 28, Suppl. 1: 66-75.

PREFACE

In the early 1970s, Professor Kazimierz Petrusewicz came to the conclusion that the ecology of *Clethrionomys glareolus* was rather well known by a group of his co-workers. Thus, the data collected and the views inferred from them provided a good basis for preparing an ecological monograph of this species. In the mid-1970s the manuscript of the monograph was submitted to the editorial board of Polish Ecological Studies.

However, Professor Petrusewicz fell ill, and this delayed the completion of the editorial work. For this reason the volume presented reflects the state of knowledge on the bank vole ecology while the International Biological Programme was under way. After the death of Professor Petrusewicz in March, 1982, the editorial work on the monograph was continued by his followers.

Dr. G. Bujalska did the final editorial work in the spirit of Professor Petrusewicz's thought, and Dr. M. Gębczyński co-operated with her. The monograph was translated into English by B. Diehl. Dr. G. Dryden of Slippery Rock State College, U.S.A., kindly reviewed the final version of the text. Prof. Dr. Z. Pucek kindly provided space in Acta Theriologica for this monograph.

The efforts of all these people who helped to prepare the "Ecology of the Bank Vole" as soon as possible are greatly appreciated.

Jadwiga Łuczak

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1. INTRODUCTION

Kazimierz PETRUSEWICZ

From the foundation of the Department of Ecology in 1952, then transformed into the Institute of Ecology PAS, population studies constituted an important part of its investigations. These studies were first headed by two successive directors of the Institute, K. Tarwid and K. Petrusewicz, then subsequently by R. Andrzejewski, who was succeeded by L. Ryszkowski, and finally by both Andrzejewski and Ryszkowski. These studies, first laboratory-experimental, were rapidly expanded into the field, and field experiments were often carried out. The main object of the field studies became the bank vole, the most common and ubiquitous species of small mammals in Poland.

Independent investigations were conducted at the Department of Agrocoenology at Turew, which has finally been transformed into an independent Department of Agrobiology and Forestry PAS in Poznań, headed successively by Z. Wilusz, P. Trojan, and L. Ryszkowski.

Also many ecological studies on small mammals were conducted at the Chair (then the Department) of Ecology and Evolutionism of the Institute of Zoology, University of Warsaw (headed by K. Petrusewicz, then by K. Dobrowolski).

At the same time, intensive morpho-physiological studies with deep ecological inclinations were developed at the Mammals Research Institute PAS at Białowieża (headed by A. Dehnel, then by Z. Pucek).

In the early 1960s, a specific field of physiological ecology (not ecological physiology) was developed at the ecological research centre in Kraków (headed by W. Grodziński), where both laboratory and field investigations were conducted.

It is worth emphasizing that parallel studies in the same areas and in the same vole populations were carried out on endoparasites (K. Kisielewska, Department of Parasitology, PAS) and ectoparasites (S. M. Janion, Institute of Ecology, PAS) of small rodents.

Population studies of small mammals were greatly intensified in the 1960s and in the first half of the 1970s due to the International Biological Programme (IBP). Studies carried out in different centres were coordinated for many national symposia. As the result, they were of a complementary character, and the co-operation was so close that we can speak about common Polish studies, which yielded 102 papers on the bank vole, and, more importantly, a detailed review of the literature on this species was compiled. Polish studies on small rodents, particularly on *Clethrionomys glareolus*, started to occupy an important position on the world scale. As a consequence of this development of population studies, the IBP Small Mammals Working Group was established at the symposium of the PT (Productivity of Terrestrial Ecosystems) section of the IBP at Jabłonna in 1966. K. Petrusewicz was the head and L. Ryszkowski the scientific secretary of this group.

The IBP Small Mammals Group was very active. A non-periodical bulletin, Small Mammals Newsletters was issued. Every other year, international symposia were organized: Jabłonna 1966, Oxford 1968, Helsinki 1970, and finally Warsaw-Dziekanów 1973. The first three symposia produced the following publications: Jabłonna — "Secondary productivity of terrestrial ecosystems"; Oxford — "Energy flow through small mammals populations"; Helsinki — "Proceedings of IBP meeting on secondary productivity in small mammal populations". Workers from 27 countris were involved in the IBP Small Mammals Working Group. The result of these joint studies was an advanced standardization of methods and terminology, coupled with a great diversity of study problems.

These intensive studies were summarized in the Vth volume of IBP synthesis: "Small mammals, their productivity and population dynamics" (Cambridge University Press, 1975).

In the course of these studies a huge body of empirical data was collected and a number of theoretical concepts were developed concerning population dynamics and the underlying regulatory mechanisms. A basic theoretical concept — widely though not commonly accepted — is the view that the population is not only the sum of individuals satisfying a certain criterion, but it is an integrated whole, the properties of which cannot be explained using even a complete knowledge of all individuals living in it. The population is a super-organismal unit in a cybernetical sense, an organized system. This organization determines or co-determines population dynamics, the fate of the population. There is also a large body of empirical material concerning the productivity of small mammals in a general sense of the word, and also the ecological role of small mammals in the functioning of ecosystems. As *Clethrionomys glareolus* is one of the most common and widely distributed species in Europe and Asia, we have accumulated a large set of data on the ecology of this species. Hence, an idea was born among Polish ecologists to prepare an ecological monograph of the bank vole. This book is the result of their efforts in this direction.

2. CHARACTERISTICS OF THE SPECIES

2.1. Taxonomic Position, Geographical Range, and the Ecology of Distribution

Jan RACZYŃSKI

2.1.1. Taxonomic Position of the Bank Vole

The bank vole, *Clethrionomys glareolus* (Schreber, 1780), represents the most abundant group of recent rodents — voles. The voles are most frequently classified as the subfamily *Microtinae* of the family *Cricetidae* (Simpson, 1945; Gromov & Polyakov, 1977; Corbet, 1978, and others). Simpson (1945) characterizes the taxonomic position of the bank vole as follows:

Cohort	*Glires*	Linnaeus, 1758
Order	*Rodentia*	Bowdich, 1821
Suborder	*Myomorpha*	Brandt, 1855
Superfamily	*Muroidea*	Miller *et* Gidley, 1918
Family	*Cricetidae*	Rochebrune, 1883
Subfamily	*Microtinae*	Miller, 1896
Tribe	*Microtini*	Simpson, 1945
Genus	*Clethrionomys*	Tilesius, 1850

According to Gromov (Gromov & Polyakov, 1977) the genus *Clethrionomys* belongs to the tribus *Clethrionomyini* Hooper *et* Hart, 1962, which is subdivided to three subtribes: *Pliomyi, Alticoli,* and *Clethrionomyi* (all names nov., Gromov, 1977). Thus, red-backed voles (after Corbet, 1978) are phylogenetically related to the genera *Pliomys* (forms abundant in the late Pliocene and extinct in the Pleistocene) and *Dinaromys,* now represented by *Dinaromys bogdanovi* in high reaches of the Balkan Mountains, Europe (both *Pliomyi* groups), and also to sister species of the genus *Alticola,* represented by the recent mountain voles of central Asia, with scarce species of the genera *Hyperacrius* (high-mountain Himalayan forms) and *Anteliomys* which are mountain forms living in south-east Asia (Group *Alticoli).*

The group *Clethrionomyi* is geographically much more widely distributed than other groups due to the species diversity of the main genus *Clethrionomys.* The genus *Eothenomys,* which belongs to the same group, consists of few high-mountain species inhabiting south-eastern Asia. Thus, except for a few genera spread over mountain habitats of the Old World, only the genus *Clethrionomys* is characterized by a large geographical expansion and high ecological adaptability. This genus is abundantly represented in the Pleistocene fauna of Eurasia and North America, and it constitutes an important component of the known faunas of the glacial epoch. The present distribution of the subspecies of the bank vole in Europe is ascribed to the effects of the last glaciation.

Within this family only the genus *Microtus* is more abundant and diversified than the genus *Clethrionomys.*

2.1.2. Geographical Distribution of the Genus *Clethrionomys*

At present, the genus *Clethrionomys* consists of 7—9 species ranging over vast areas of the northern Holarctic.

The New World is inhabited by:

Clethrionomys gapperi (Vigors, 1830) — the species representing a distinct line of American red backed voles. It is the Nearctic counterpart of *Clethrionomys glareolus.* It inhabits North America within a large belt from the east to the west coasts of Canada and northern United States, and along the Appalachian and Rocky Mountains southwards to 34° northern latitude.

Clethrionomys occidentalis (Merriam, 1890) — the range of this species is limited to a narrow strip western coastal Canada and the United States (British Columbia and northern California) (Hall and Kelson, 1959).

The species inhabiting both Palaearctic and Nearctic are represented only by:

Clethrionomys rutilus (Pallas, 1779) — a Holarctic species living in northern parts of Eurasia and North America, i.e., from northern Scandinavia through Siberia and Japan to Alaska and northern Canada. In Europe, the southern range extends to Karelia, in Asia to southern reaches of the Urals, southern Kazakhstan and Mongolia, and south-eastern China. It inhabits tundra and taiga to the north and forest-steppe to the south. This species exemplifies the invasion of Siberian fauna to North America.

The group of Palaearctic species consists of:

Clethrionomys rufocanus (Sundevall, 1846) — the species living in northern part of Scandinavia, northern part of the European USSR.

Siberia and Far East (Kamchatka, Sakhalin), and to the south extending to southern part of the Ural and Altai Mts., northern Mongolia, and southeastern China. The form typical of taiga extends northwards to tundra nad forest-tundra. In Europe it occupies the boreal part of the *Clethrionomys glareolus* range, occurring there sympatrically with *Clethrionomys rutilus.*

Clethrionomys glareolus (Schreber, 1780) — the species typical of Europe, except of its southernmost nad northernmost parts. Its southern range crosses Asia Minor. Eastwards it covers European part of the Soviet Union, southern Urals, western Siberia, and mountains of central Asia (Altai, Sayan) to Lake Baikal. The southern part of its range in eastern Europe and in Asia is poorly documented. In addition to these widely distributed species, two species have been distinguished in Japan (Corbet, 1978):

Clethrionomys rex Imaizumi, 1971 — on Hokkaido, and

Clethrionomys andersoni (Thomas 1905) — on Honshu.

Two more species inhabits Asia (Gromov and Polyakov, 1977):

Clethrionomys sikotanensis Tokuda, 1935 — the species described from southern Sakhalin and Shikotan.

Clethrionomys frater Thomas, 1908 — the species occurring in the Thian Shan Mts.

2.1.3. Geographical Distribution of *Clethrionomys glareolus*

The European range of the bank vole (Fig. 2.1) is presented on the basis of the available original data, especially in border areas, thus it contains more detail than the popular book by van den Brink (1972) and the monograph by Bashenina (1981). This range is shown in a generalized form. Obviously, within this range there are areas not occupied by the bank vole. This situation is an effect of both man-induced enviromnental changes and local habitat heterogeneity, along with geographically conditioned patterns of physiocoenoses not suitable for this species (tundra, steppe, or high mountains). Geographical reasons for discontinuous distribution are of particular importance at the edges of the continuous distribution and in the regions with a strongly diversified relief. In some geographical regions the mammal fauna is poorly studied and the distribution of the bank vole remains unclear.

In the northernmost part of their range bank voles extend beyond the Arctic Circle, where they live in deciduous forests (Siivonen, 1967). In northern Scandinavia, however they do not inhabit the zone of subalpine birch scrub, a typical habitat of *Clethrionomys rufocanus* (Kalela *et al.*, 1971). At the northern border of forests, bank voles occur sympatrically with *C. rufocanus* and *C. rutilus.* They do not occur in Iceland, although their distribution is continuous over mainland Europe, being restricted southward in the Mediterranean climatic zone. On the British Isles they occupy all of England and Scotland, except northern islands of the archipelago, while in Ireland they occupy only an isolated area in the southwestern part of the island. This suggests that the island is being colonized by this species as a result of introduction. The duration of this process and the ways of invasion are not known, however (Fairley and O'Donnel, 1970). Well known populations of the bank vole occupy such British islands as Jersey, Rassay, Skomer, and Mull. They are taxonomically well defined and exhibit a high morphological diversity. According to recent views, the bank vole is a secondary faunal element there, due to a casual introduction by man (Corbet, 1964).

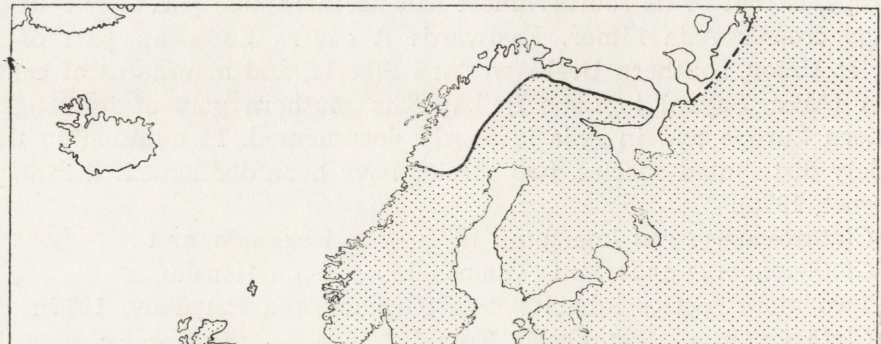

Fig. 2.1. A schematic map of the distribution of *Clethrionomys glareolus (Schreber,* 1780) in Europe (Original data). Uncertain boundaries of the range are denoted by a dashed line.

In the Mediterranean zone the range of the bank vole is not continuous for ecological reasons. On the Iberian Peninsula, which has been little studied so far, bank voles were recorded behind the Pyrenees and in the Cantabrian Mountains (Malec and Storch, 1964; Niethammer, 1956).

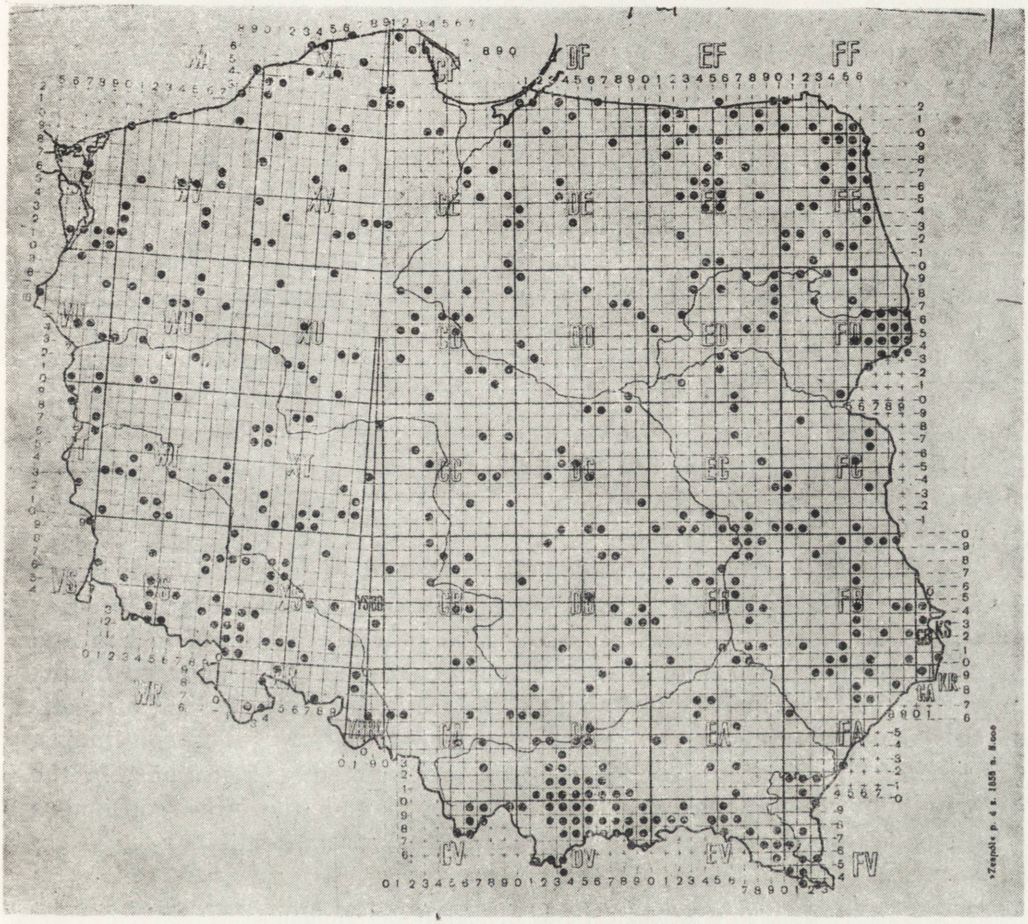

Fig. 2.2. A point map of the distribution of *Clethrionomys glareolus* (Schreber, 1780) in Poland.
The sites are cumulated in squares of 10×10 km in the UTM grid (after Raczyński, 1983).

On the Apennine Peninsula, the range of the bank vole is not contiguous. Its distribution in mountain and forested areas depends on the local bioclimate resembling that of the temperate zone. This species does not occur on small and large islands of the Mediterranean Sea (Amori *et al.*, 1983). Bank vole population of the Monte Gargano shows, like other faunal elements of this region, some similarity to the Dalmatian populations of the Balkan Peninsula (Hagen, 1958). Major parts of the Balkan region (Dulić and Tortić, 1960; Atanassov and Peschev, 1963) and western coast of the Black Sea are occupied by this species. The southern limit of distribution passes through Macedonia in northern Greece (Felten and Storch, 1965; Ondrias, 1966). The Adriatic coast on the Balkan Peninsula, extending from Istria (Dulić, 1962) southwards along the Dinaric Alps is inhabited by mountain populations of the bank vole (Dulić, 1961, 1971). In some parts of its Balkanian range, this species does not occur. This is the case of north-eastern part of Yugoslavia (Petrov, 1968). Pontic populations, occupying a narrow belt of the most humid southern and partly eastern coast of the Black Sea are of similar origin as the Balkanian populations. In Asia Minor, the occurrence of the bank vole is limited to the already mentioned Pontic region (Neuhäuser, 1936; Spitzenberger and Steiner, 1962), reaching Batumi on the north. This species was not recorded in the Caucasus region (Ognev, 1950). Further investigations are needed of the distribution of the bank vole on the southern coast of the Black Sea, in Crimea, in the Sea of Azov region, between the Don and the Caucasus, in Transcaucasia, and also in the northern part of the range, along the European coast east of the White Sea as no records of the bank vole are available about these areas (see Bobrinskij *et al.*, 1965).

The distribution of the bank vole in Poland is presented on the map with a UTM (Universal Transverse Mercator) grid with 10 km squares (Fig. 2.2). About 720 sites of bank vole occurrence (literature data and collections) are distributed over the whole country. The degree of the coverage of the map reflects only the state of the investigation of particular regions of Poland where the range of this species is continuous. Detailed distribution depends only on environmental conditions. In the mountains, bank voles reach the upper boundary of the contiguous range of the dwarf mountain pine (in the Tatra Mountains).

2.1.4. Ecological and Biological Determinants of Distribution

Ecological success in terms of increasing number of occupied habitats, depends mostly on adaptability, a high ecological flexibility which enabling survival and often also expansion of the species. Dynamic expansion processes usually occur under variable habitat conditions in both time and space. The present distribution of *C. glareolus* was influenced by the ice age with its successive periods of glaciation alternating with interglacial periods, coupled with respective changes in the plant cover. In historical times, even more violent changes in physiocoenoses occurred as a result of human activity. In this way, the biological capacity of the species, on the one hand, and changes in the biotic environment, on the other, determine geographical distribution of the species. The considerations below deal with some general problems of the bank vole distribution. A detailed analysis of habitat preference will be presented in section 3.1.

The bank vole belongs to the rodents that colonized the zone of primaeval forests of Europe, and forest habitats determined its geographical range. They now inhabit both boreal coniferous forests of taiga and high mountains and broad-leaved oak and beech forests on the south. Deforestation related to the development of human settlements and agriculture accounts for the contraction of bank vole habitat, and at the same time it releases the ability to occupy secondary habitats. On the British Isles, bank voles inhabit shrubby escarpments, embankments, and hedegerows, and they do not avoid places covered only with forbs and grass (Southern, 1964; Corbet and Southern, 1977). Also in western Europe they occupy hedgerows and shrubberies, and rarely croplands. Some cases are known, however, where they occupied croplands as well, in the absence of competition with other voles. This was noted on Belle-Ile in France (Saint Girons & Beaucournu, 1970), However, a typical habitat of the bank vole is forest with dense undergrowth providing shelter and secret runways. These features of the habitat are stressed by many workers as particularly preferred. Wrangel (1940) lists the following habitat requirements of this species: forests with dense undergrowth, forest edges, shrubberries, park gardens, and parks. Dense forests without undergrowth (e.g. old pine forests) are not a suitable habitat; bank voles are more abundant in mixed or deciduous forests on humus soils and in beech forests, being most abundant at the edges of these forests.

Undoubtedly, the areas covered with ferns on the Skomer Island in Great Britain, represent secondary habitats of the bank vole (Fullgar *et al.*, 1963). This is also the case of uncultivated meadows far northwards in Scandinavia (Hansson *et al.*, 1978). In southern parts of their range, bank voles distribution is closely related to forest habitats, and in the Mediterranean region, also to climatic conditions. In the Balkan area and in Asia Minor, these rodents live in dense forests covering mountain ranges, thus under cooler climatic conditions. In the Balkan and Appenine Peninsulas, bank voles prefer habitats with low temperature amplitudes. These are interiors of dense forests in ravines, where the forest bottom is cooler than in warm coniferous forests on exposed slopes (Hagen, 1958; Dulić, 1971). They also occupy such microhabitats as crevices in rocks and stones, where thermal conditions are more uniform. According to Dulić (1971), the presence of suitable shelters determines the distribution of the bank vole in this extreme part of the range of this species.

Among environmental factors influencing the occurrence of the bank vole, most important are those determining the possibility of burrowing, providing shelters, and securing food. The burrowing ability of the bank vole is relatively poor, so they prefer soft, humus soils in deciduous and mixed forests, easily accessible corridors within root systems of trees growing in clumps in alder forests, or suitable shelters among stones in mountain forests. Their preference for a good shelter in the form of plant cover or stony ground might be related to their relative poor agility and prolonged activity period, which includes some daylight hours. Wrangel (1940) analysed a number of morphological adaptations related to the activity pattern in the bank vole.

The diversity of habitats is closely related to the diversity of food available for bank voles. Broad possibilities of using natural resources are discussed in detail in section 3.1 on the diet. A typical example of adaptative changes in the diet is given by Koshkina (1957) from the Kola Peninsula. In northern areas sparsely covered with herbaceous plants, bank voles commonly use lichens growing on trees, fungi, and roots of trees, with an addition of animal food. The bulk of the diet of this species consists of green plant parts, seeds, and fruits of herbaceous plants (Gębczyńska, 1976).

A large variability in the diet of the bank vole over the annual cycle and from one geographical zone to another suggests that food is not a factor limiting geographical distribution of this species. It is probable that an entire set of ecological factors in forests has an effect on the occurrence of this species. The geographical range of this species at least in Europe, seems to be filled with respect to the geographical distribution of the habitats occupied. Possibilities of a further expansion of this species seem very limited, particularly in view of increasing urbanization and other kinds of human impact. Forests will remain the principal refuge of this species, including pine monocultures especially of lower age classes, which provide suitable habitat conditions. Agrocoenoses, independent of the crop structure, do not seem to ensure much chance for a future expansion of the living space for the bank vole.

2.2. Morphological Variability and Taxonomic Differentiation

Jan RACZYŃSKI

2.2.1. Morphological Characteristics

The genus *Clethrionomys* comprises small and medium voles characterized by many specific features, particularly as compared with the genus *Microtus*, which is rich in species numbers. These features include:

- closing of the molars root with age, and the development of roots (only *C. rufocanus* produces roots at an older age and the Japanese forms, *C. rex and C. andersoni*, produce roots only in the very oldest age groups),
- rounded loops of enamel on the wearing surface of molars,
- the palate in the form of flat lamina is ended by a distinct rim closer to anterior edges of the crown of M^3 (Fig. 2.3),
- a delicate skull, rounded, with shortened facial part, without frontal crest (*crista frontalis*),
- relatively large ears, protruding from the fur,
- rusty-red coloration of the back in some species (*C. rutilus, C. glareolus*).

Particular species of the genus *Clethrionomys* vary slightly in size, in body-tail proportions, details of skull and dental morphology, and first of all in the coloration of the fur.

Clethrionomys glareolus (Schreber, 1780) — the bank vole, is characterized by medium body size: Head and body 80—129 mm, tail 40—60 mm (about 50% of the body), hind foot 14—18 mm, body weight 15—20 g, in summer sometimes more than 30 g (the size of animals from populations living in Poland is given in the next subsection).

The dentition of the bank vole is shown in Figure 2.4. It differs from the dentition of other *Microtinae*, and particularly from European forms of the genus *Microtus*, in many characters such as:

- gentle design of the enamel lines forming rounded loops in the front and hind parts of the tooth, and rounded triangles on both lateral edges (only in young individuals are these edges sharper),
- enamel loops of M_2 form three joined fields of dentine due to a specific configuration of opposite triangles (in the genus *Microtus* these triangles are always separated),
- enamel triangles of M_1 (denoted by numbers 2-3 and 4-5) form dentine fields clearly joined with each other,
- The last upper molar, M^3, does not protrude much from the bony

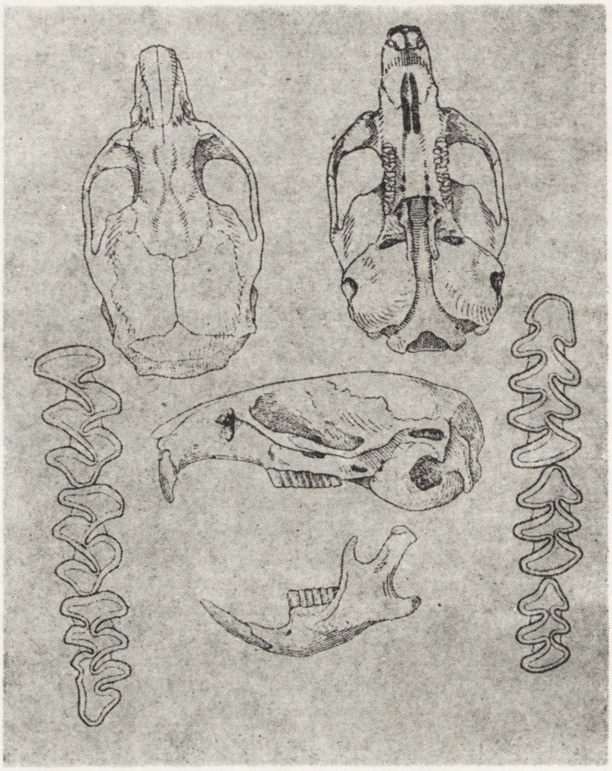

Fig. 2.3. A bank vole skull. The proportions between the cranial and visceral parts, and the hard palate margin are denoted (after Gromov and Polyakov, 1977).

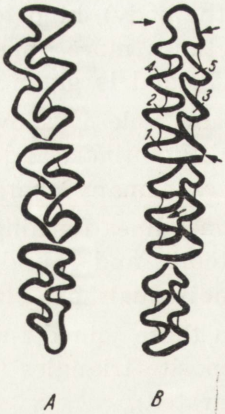

Fig. 2.4. An outline of the structure of wearing surface of molars in the bank vole. A — upper molar row, left side; B — lower molar row, right side (after Chaline *et al.*, 1974).

edge of the jaw, and it varies greatly in wearing surface structure (Fig. 2.5).

Bank vole fur is rusty-brown on the back, often with a reddish tint. Sides are paler, with a grey tint, belly light silvery grey, sometimes whitish with yellow tint. The zone separating the coloration of the back and belly is well demarcated. The tail is bicoloured, lighter beneath, crested with hair at the tip. The pelage of young individuals is generally more grey and with less contrasting shades. Moulting occurs in spring and autumn, typically from the back region towards the head.

The coloration of the bank vole fur varies relatively little over the wide range of this species. For example, voles from England, Germany, and France cannot be distinguished from each other on the base of their coloration (Corbet, 1964). On a vast geographical area from the Białowieża Forest to Arkhangelsk and the Pechora basin, Rossolimo (1964) did not find any trends in coloration variability. Local forms differing in colour were described only in a few, usually isolated populations, (Corbet and Southern, 1977). Albinisms and melanism occur rare as they are due to genetic anomalies. Non-agouti forms are due to recessive alleles (eight at least) and they are phenotypically expressed in homozygotes. One case of an extreme non-agouti mutation (black colour of the fur) in the bank vole has been described from southern Poland by Bobek and Bartke (1967); other melanistic individuals are reported by Husson (1953) and Hanak (1957). One albinotic specimen from Germany was described by Reichstein and Kulicke (1958). Differences in coloration between lowland and mountain populations considered as taxonomic features often are not confirmed in larger series of material (Prychodko, 1951).

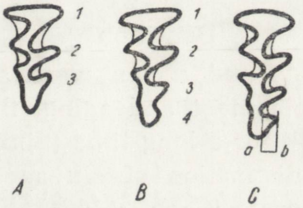

Fig. 2.5. Types of the structure of enamel loops of M^3. Lingual corners are denoted by numbers 1—4.
A — "simplex" type; B, C — "complex" types. Line a-b denotes the degree of the development of the fourth lingual corner (triangle) of enamel. The measurement of line a-b provides a quantitative characteristic of this feature (after Corbet, 1963).

The number of chromosomes in the bank vole is relatively constant as compared with that in the genus *Microtus*. The karyotype of the nominative subspecies, *C. glareolus glareolus*, from Germany, Hungary, and different regions of Czechoslovakia is 2N = 56 chromosomes, incloding 2 metacentric autosomes and a metacentric Y chromosome (NFa=56, NF=58, Kral, 1972). The karyotype of south-European subspecies, *C. g. istericus* and *C. g. garganicus*, has the same number of chromosomes (2N=56), and differs only by the acrocentric Y chromosome. The latter feature has been recorded in peripheral populations of Palaearctic species, and it is a suitable genetic marker in these populations (Voroncov *et al.*, 1978). Chromosomally Palearctic *C. glareolus* and Nearctic *C. gapperi* are identical (Matthey, 1956), but this evidence is insufficient to suggest conspecifity of these forms.

2.2.2. Morphological Variability

Dentition

Growth of molar roots and crown wear are continuous processes related to postnatal development and aging, therefore they have been used for age determination for a long time (Zimmermann, 1937) *. Tooth morphology allows the distinction of six age classes illustrating the developmental stages of roots (Corbet, 1964). For this purpose, usually the roots of M_1 (Prychodko, 1951; Wasilewski, 1952) or M^2 (Koshkina, 1955; Tupikova *et al.*, 1968) are used as they are easier to extract from the jaw. The problem of age homogeneity in particular classes of root length is related to the rate of root growth and crown wear which are species specific and often population specific. The most important is the different growth rate of animals in the spring and autumnal vole generations. In view of this fact, absolute values of monthly tooth increases under laboratory conditions (Mazák, 1963), or in the wild (Tupikova *et al.*, 1968) used as the basis for estimating the absolute age of animals should be cautiously considered. Large differences in the growth rate of root length between the spring generation (0.23 mm/month) and the autumnal generation (0.16 mm) are described by Zejda (1961, 1971), and the differences in growth between summer (0.2 mm) and winter (0.1 mm) by Claude (1970).

Another age-related feature in the development of molar roots was noticed by Hinton (1926). This is the disappearance of the alveolar capsules with age (Fig. 2.6). This is an arched swelling of *processus alveolaris maxillae*, visible within the temporal fovea (Prychodko, 1951; Koshkina, 1955). This morphological feature, easily seen on prepared

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* Other ways of age determination from morphological features of the bank vole are described in section 6.2.

skulls, can facilitate the distinction between adult and young bank voles in some ecological investigations.

Variability in the structure of the grinding surface of M^3 in the bank vole was noticed by Rörig & Börner (1905) and classified in detail. For some species (e. g. *Microtus arvalis*) this feature was used to interprete population dynamics of this species in different areas, assuming that particular variants are of selective value (Stein, 1958), and considering them as taxonomic features of subspecies.

In the bank vole, two basic types of the M^3 crown are described: 1) "Simplex", which is a shortened form with three triangles of enamel on the labial and lingual sides of the tooth; 2) "Complex", which is a developed form of the tooth with four lingual and four labial triangles.

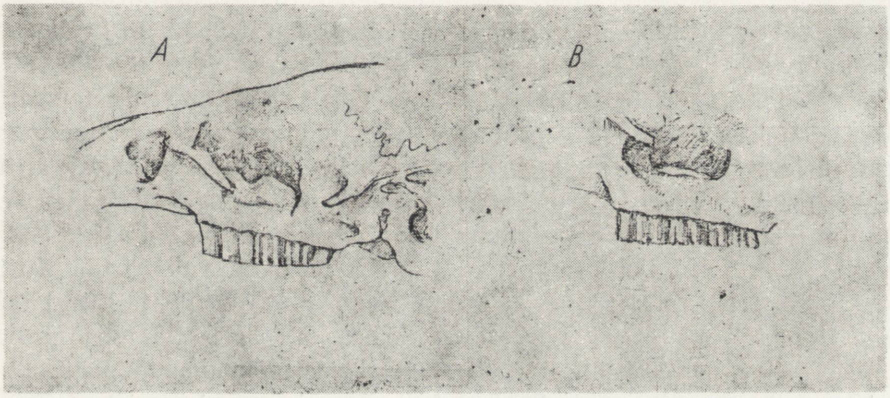

Fig. 2.6. The structure of the alveolar capsule, which is a convenient feature to visually estimate the age of bank voles from the skull material (Original). A — young individual, strongly arched alveolar capsule, B — old individual with well-developed roots, the capsule flattened and reduced.

There are, however, many intermediate forms between these extremes (Prychodko, 1951), which indicate a complex character of inheritance of this feature (see Fig. 2.5). Bank vole populations living in England are characterized by a high proportion of the simplex form (Steven, 1955). Detailed studies have shown, however, that neighbouring populations can markedly differ in the proportion of the two forms, which reduces the taxonomic importance of this feature (Corbet, 1963). An additional limitation is due to the fact that it is difficult to classify these variants in older age classes because of tooth wear (Zejda, 1960).

Body and skull sizes

Among body measurements, only the length of hind foot and ear are fairly constant, thus of taxonomic value. The body length and weight can vary greatly, depending on geographic location and population variability. The intrapopulation source of variability is related to sexual activity of individual bank voles and to the age structure of the population. It also shows a clear seasonal aspect. This variability is discussed in detail by Kubik (1965). The relationship between the body weight and sexual activity is analysed by Zejda (1965).

According to Rossolimo (1964), the geographical variability of the skull is low over a large area from central Europe to the Pechora river in the east, and from Yugoslavia to Arkhangelsk. Some skull measurements, e. g. inter-orbital breadth or rostrum breadth do not vary. Variability in condylo-basal length is more distinct but it has no trend and is not large enough to indicate subspecific differentiation in the population. Instead, seasonal differences are clearcut: difference between the summer and winter specimens are higher than differences between geographically distant populations (Rossolimo, 1964). In relatively thoroughly studied populations of the British bank vole, the skull and body size tend to increase northwards (Corbet, 1964), a distinct position being occupied by isolated forms from small islands (see section 2.2.3).

A different aspect of geographical variability is revealed by altitudinal distribution. Differences in the body-tail proportions between mountain and lowland populations were described by Schaefer (1935). Claude (1968) compared Swiss populations of bank voles from Zurich and Göschnerlap, and found an isometric growth of the tail and body length for high mountain populations, contrasting with allometric growth populations inhabiting lower regions. This phenomenon cannot be explained by the effect of physical factors or by a subspecific differentiation. Bank voles living in the mountains are larger than those from lowlands (Claude, 1967; Haitlinger, 1970). According to the ecological interpretation of this fact by Claude (1967, 1970), alpine populations have a different age structure; they are predominated by older individuals as their winter mortality is lower in the mountains than in the lowland, and in addition they reach maturity in the next calendar year. The two-step growth of these voles promotes greater body size. A similar situation was observed by Jewell on the Skomer Island, where the reproductive period of voles was short and delayed, and the animals were larger than in England (cit. after Claude, 1967). Other authors argue that the larger size of Scandinavian and high-mountain forms is due to the Bergmann rule (Saint Girons, 1973).

2.2.3. Subspecific Differentiation

Ellerman and Morrison-Scott (1951) distinguished 72 forms of Palaearctic *Clethrionomys,* including 23 subspecies of *Clethrionomys glareolus.* A taxonomic analysis of subspecies is beyond the scope of this paper as it would require some revision; recently there is a tendency to integrate minor groups on the basis of modern craniometry and variability analyses in representative series of material from various parts of the species range. Such a revision on the scale of the entire range has not been carried out so far, and partial analyses have provided a basis for some simplifications of the complex and often controversial division of subspecific forms.

For a long time the differentiation of *C. glareolus* in the European part of its range was interpreted on the basis of a zoogeographic-phylogenetic concept. According to this concept, in the Pleistocene continental Europe was inhabited by a larger form of *Clethrionomys* ("*nageri*" group), which was replaced in the postglacial period by a smaller race from the east. Relicts of the original from were to survive in the high Alps, in western Norway, and on isolated islands off the British coast (Hinton, 1926; Zimmermann, 1950; Matthews, 1952). This concept was not consistent with later findings.

Prychodko (1951) challenged the distinction of the mountain race, *C. g. vesanus,* described by Hinton from Bavaria. Claude (1970) joined *C. g. vesanus* with *C. g. ruttneri* in the subspecies *C. g. helveticus,* on the basis of body and skull measurements, and coloration. He also suggests that large alpine forms can only be an ecological race (Claude, 1967). Steven (1955), who experimentally crossed the form representing the *nageri* group (British and Norwegian) with the form from England (*C. g. britannicus*), found no differences in their biology. Corbet (1964) questioned the distinction of the main British form, *C. g. britannicus,* and included it with *C. g. glareolus.*

Outlining the problem of taxonomic division of the European forms, it can be stated that the nominative subspecies inhabits the bulk of the continent, while the morphologically distinct subspecies either are geographically isolated (islets, mountains) or inhabit suboptimal habitats at the margin of their geographic range.

Unquestionable subspecies now include the races described from the British Isles (Steven, 1955; Corbet, 1964):

C. g. caesarius — from Jersey (Channel Islands),
C. g. skomerensis — from the Isle of Skomer (Wales),
C. g. alstoni — from the Isle of Mull (Inner Hebrides),
C. g. erica — from the Isle of Rassay (Inner Hebrides). They are distinguished by their body and skull size (all are larger than British forms) and by M^3 structure. *C. g. skomerensis* is differently colored (lighter, with cream-colored belly in winter). According to present views on their origin, they are not relicts but were casually introduced, probably by man, and then geographically isolated (Corbet, 1964).

According to karyotaxonomic criteria, forms living in southern parts of the species range: *C. g. garganicus* from Italy and *C. g. istericus* from the southern Carpathians, can be considered as distinct (Král, 1972; Král *et al.*, 1972), though according to Rossolimo (1964) there are no morphological differences in the body and skull structure between the latter and *C. g. glareolus*. Probably *C. g. ponticus* from Asia Minor or *C. g. curcio* from southern Italy are distinct forms, but this separation requires some conclusive evidence. A detailed analysis of alpine forms carried out by Gruber and Kahman (1968) indicates that it is necessary to fuse into larger groups the units distinguished so far, this being a conclusion from the statistical analysis of biometric data. The ultimate subdivision of the species *Clethrionomys glareolus* living in central Europe (the Alps, Balkan) and, in particular, over vast areas of the eastern range of this species, has to be based on reliable material analysis. A supplementary list of the subspecies described so far was provided by Corbet (1978).

2.2.4. Characteristics of Bank Voles Living in Poland

Two bank vole populations from Poland have detailed biomorphological descriptions: one in Białowieża (Wasilewski, 1952; Kubik, 1965) and another one in the Wrocław region (Haitlinger, 1965). To characterize these two populations, the basic body and skull measurements are given in Table 2.1.

Both these characteristics are based on the mechanism and differentiation of growth rate of particular parameters of skull in relation to seasonal events occurring in these populations. Wasilewski (1952), using the least squares method for the craniometric analysis, distinguished 12 "types" of skull structure in the Białowieża population that differ in the proportions of linear dimensions. This method of analysis, however, does not allow far reaching taxonomic conclusions because the range of the variability of the Białowieża population covers also other forms of European *Clethrionomys glareolus*.

A comparison of the parameters of skull growth between the Białowieża and Wrocław populations reveals few noticeable differences. According to Haitlinger (1965), the specific features of the Wrocław population include the length of nasal bones, saggital suture, and palatial length. In both populations the growth rate of the spring generation was higher than autumnal generation (Kubik, 1965; Haitlinger, 1965). Sexual dimorphism in the bank vole occurs during the breeding season; it concerns the body weight, which is higher at the end of winter for males and in spring for females. Craniometric differences between sexes are difficult to prove (Haitlinger, 1965). The body weight also undergoes seasonal changes. It is lower in winter for all age classes by about 6 g as compared with the maximum value reached in summer. The body weight increases in March and it attains maximum values in June and July (Haitlinger, 1965).

Table 2.1.
Morphological characteristics of *Clethrionomys glareolus* from Poland.

Białowieża (Wasilewski, 1952)			Wrocław (Haitlinger, 1965)		
Age group	Range	$\bar{x}$	Age group	Range	$\bar{x}$
Body length (mm)					
overwintered	79.0—117.0	—	IV (4-7 months old)	77.8—100.0	89.0
			V (6-9 months old)	75.4—101.5	91.4
			VI (8—14 months old)	84.1—106.8	95.7
			VII (14 months old)	82.0--107.0	96.8
Tail length (mm)					
I—V	22.0—51.0	—	IV—VII	34.9— 51.5	—
overwintered	33.0—48.0	—			
Hind foot length (mm)					
I—V	14.6—18.0	—	IV—VII	16.0— 18.6	—
Ear length (mm)					
I—V	10.0—15.0	—			
Body weight (g)					
I—V	6.1—32.7	—	IV	10.1— 23.3	15.3
			V	11.1— 28.6	15.8
			VI	11.9— 28.8	18.0
			VII	12.9— 29.0	18.9
Condylo-basal length (mm)					
overwintered	21.6—24.9	—	IV	21.3— 24.4	22.7
III (4-8 months old)	21.7—24.1	22.8	V	21.7— 24.5	22.9
IV (8-11 months old)	22.3—24.5	23.3	VI	22.1— 24.9	23.4
V (11-15 months old)	22.1—24.9	23.6	VII	22.9— 24.7	23.7
Total length of skull (mm)					
III	22.1—24.3	23.1	IV	21.5— 24.6	22.9
IV	22.7—24.1	23.4	V	21.5— 24.6	23.3
V	22.7—24.5	23.8	VI	22.3— 25.8	23.8
			VII	23.1— 25.1	23.8

As only few populations from Poland were morphologically studied, it is not possible to estimate the range of variability of different forms and to characterize trends in body and skull sizes over the country.

Poland, however, lies in the centre of the bank vole range, is small relative to the range of this species, and so is not likely to be a good place to follow such trends. Nevertheless, it has been found that bank voles from mountain populations in the Karkonosze Mts. are larger than those from Wrocław and submontane regions. These are, however, allometric relationships. The interpretation of this phenomenon should consider the degree of isolation of mountain forms as the bank voles inhabiting some peaks (e. g. Ślęża peak — 718 m above sea level, raising from a lowland) do not differ from those living in the lowland, and the voles inhabiting submontane areas have intermediate characters (Haitlinger, 1970).

Although the bank vole population from the Wrocław region is characterized by smaller body sizes than that from Białowieża, their subspecific position does not rises objections. Wasilewski (1952) classifies Polish bank voles to the nominative subspecies. In the same way, Haitlinger (1970) classifies the populations from the Carpathians and the Sudetes. Stein (1931) classifies voles from western Poland (Rybocice on the Oder river) to *C. g. glareolus* as well. Voles from south-eastern Poland were not classified to subspecies. Kowalski (1964) suggests that voles of the Kraków region may belong to the subspecies *C. g. istericus,* which includes the voles from western Ukraine (Tatarinov, 1956).

2.3. Individual Development

Marek GĘBCZYŃSKI

The period from onset of embryonic development to sexual maturity is called the period of individual development. From another point of view, individual development is considered as the whole individual life span, that is, it also includes the phase of maturity and aging. However, the sequence of changes in shape and functioning is most rapid until sexual maturity, therefore this period of life is of particular interest. In the bank vole it covers about 60 days, including 17—22 days of the embryonic (prenatal) development and then the postnatal development.

2.3.1. Embryonic Development

The gestation period in the bank vole varies from 17.5 days (Drożdż, 1963) to 18 days (Wrangel, 1940). In nursing females, it can be longer because the implantation of fertilized eggs is delayed (Brambell & Rowlands, 1936). Such a prolonged pregnancy usually lasts for 19—23 days (Drożdż, 1963; Buchalczyk, 1970), but sometimes up to 35 days (Buchalczyk, 1970). It may be assumed that the gestation period in the wild covers 22 days (Bujalska & Ryszkowski, 1966) (more information see section 7.2).

On day 3 after fertilization, the conceptus is divided into eight cells. Within 96 hours after fertilization, the blastocyst consists of about 50 cells (Mystowska, 1975), and it moves down the oviduct reaching the uterus. Implantation takes place on day 5 of the development, when the blastocyst is elongated. After implantation the blastocyst grows rapidly, particularly in length. At the same time the polar trophoblast folds into the blastocoel. The allantoic cavity begins to develop on day 5 or 6, and during day 6 its particular parts join together to form a tube opened into the uterine lumen. The trophoblastic giant cells also develop on day 5 or 6, first from the peripheral trophoblast and later from the ectoplacental cone also. The number of these cells gradually increases so that they form a loose layer surrounding the embryo (Ożdżenski & Mystkowska, 1976a). In the bank vole also a phenomenon of the reversal of germ layers occurs. In the early stage of its forma-

Table 2.2
Basic morphological characters used for aging embryos 15—18 days old (after Ożdżenski & Mystkowska, 1976b).

Character	Age of embryos (day of pregnancy)									
	9	10	11	12	13	14	15	16	17	18
Branchial arches	+	+	+							
Auditory vesicle	+	+								
Auditory vesicle, open			+	+	+	+				
Auditory vesicle, covered							+	+	+	+
Pigment in the eye			+	+	+	+	+	+	+	+
Eye-lid open				+[1]	+	+	+			
Eye-lid, closed								+	+	+
Physiological hernia				+	+	+	+[2]			
Vibrissae				+[3]	+	+	+			
Vibrissea protruding from the skin								+	+	+
Skin folds								+	+	+
Body weight mg		11	41	91	192	323	437	933	1056	1815
Crown-rump length, mm		4.5	7.0	9 5	11.0	12.5	14.5	19.5	20.0	26.5

[1] In some foetuses eye-lids are not yet developed, [2] Some foetuses are without hernia, [3] Visible in some foetuses only.

tion, the embryo is, unlike the embryos of most mammals, semicircularly bent with its dorsal surface to the inside. Other rodent species show different degrees of the reversal of embryonic layers, and the bank vole belongs to highly specialized forms in this respect. It is not until the 9th day of development that the embryo assumes the shape characteristic of most mammalian embryos. Individual embryos can differ in the degree of their developmental advancement, but their characteristic features allow the determination of their age (Table 2.2).

Changes in the size and appearance of embryos, as well as changes observed in reproductive organs of the female allow the assessment of the stage of pregnancy during the post-implantation period; this is not possible earlier. On day 5 of gestation, implantation swellings are formed in the uterus. The gestation period can be dated by the size and appearance of embryos only between days 9 nad 15 (Ożdżenski & Mystkowska, 1976b). In the last three days of embryonic development, this aging estimation is not reliable because external morphological changes are small and the sizes of embryos are higly variable (Table 2.2). Prenatal development in size, weight and shape of bank voles as well as development of the skeleton show the same pattern of ontogenesis as do other altricial mammals (Sterba, 1976).

2.3.2. Morphological Changes in Postnatal Development

New-born bank voles are naked, blind, and virtually helpless. For the first dozen or so days of life they do not leave their nests, where the whole litter is attentively nursed by the mother. During that time their bodies become covered with fur, the eyes open, thermoregulation improves, and their diet changes. At the end of the third week, the young voles are sufficiently independent to leave the nest.

During postnatal development, young voles undergo a characteristic sequence of changes on consecutive days (Fig. 2.7).

One day of age. The skin of a newborn vole is naked and dark pink. Eyes are closed, but dark eyeballs are visible through the skin. The pinnae are not separated from the body, the acoustic meatuses are closed, toes are fused, and there are no teeth. The size (length in cm): body — 2.5—4.2; foot — 0.5—0.6; tail — 0.5—0.8.

Three days of age. No fur, but there is dark pigment in the dorsal skin. Upper parts of the tail and feet are grey. The size: body — 3.5—4.7; foot — 0.6—0.8; tail — 0.8—1.1.

Five days of age. The upper part of the body becomes dark and hair start to pigment (brown). The underside continues to be pink, with faint, whitish down. The incisors begin to erupt. The size: body — 3.7—4.8; foot — 0.7—1.0; tail — 0.8—1.2.

Seven days of age. Upper part of the head and the back are covered with short, dense, rusty grey fur; the venter is still pink but already covered with whitish hair. The pinnae are clearly separated, but the acoustic meatuses still closed. The toes partly separated. The upper and lower incisors are fully srupted. The size: body — 3.9—5.2; foot — 0.8—1.2; tail — 1.4—1.8.

Ten days of age. The body totally covered with short, dense pelage, rusty on the dorsal side and dark grey on the ventral side. Toes completely separated. The size: body — 4.8—6.0; foot — 1.0—1.3; tail — 1.8—2.2.

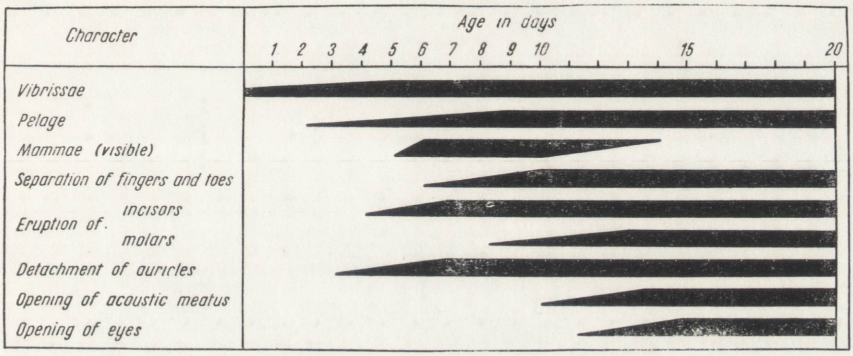

Fig. 2.7. Postnatal development of some morphological characters in the bank vole (after Sviridenko, 1959; Petrov & Ajrapetyanc, 1961; and Mazák, 1962).

12—13 days of age. The eyes are open and the animals respond to light. The acoustic meatuses are also open, and the response to sounds begins. Molars are protruding. The size: body — 5.4—6.2; foot — 1.2—1.4; tail — 1.9—2.2.

15 days of age. Fur coloration as in adults. Clear-cut response to vocal and visual stimuli. They run well and leave the nest for a short time. They begin to feed on solid food. The size: body — 5.3—7.1; foot — 1.5—1.6; tail — 2.2—3.3.

18 days of age. The teeth are completely developed, and the animals rely on themselves for food, though under laboratory conditions they sometimes continue to nurse. The size: body — 5.8—7.8; foot — 1.5—1.7; tail — 2.7—3.4.

20 days of age. The size: body — 7.7—8.0; foot — 1.6—1.7; tail — 2.8—3.5.

26 days of age. The size: body — 6.9—8.0; foot — 1.6—1.7; tail — 2.8—3.6.

30 days of age. The size: body — 7.3—8.4; foot — 1.6—1.7; tail — 3.0—3.6.

35—40 days of age. The size: body — 7.6—8.7; foot — 1.7—1.8; tail — 3.4—4.2.

2.3.2. Growth Rate

Body weight of bank voles in their first month increases rapidly, being a little less than 2 g at birth (Sviridenko, 1959; Mazák, 1962; Zejda 1968; Ożdżeński & Mystkowska, 1976b) and 11—15 g (Fig. 2.8) at the age of 30 days (Mazák, 1962; Drożdż, 1965; Bujalska & Gliwicz, 1968; Fedyk, 1974a, 1974b; Sawicka-Kapusta, 1974).

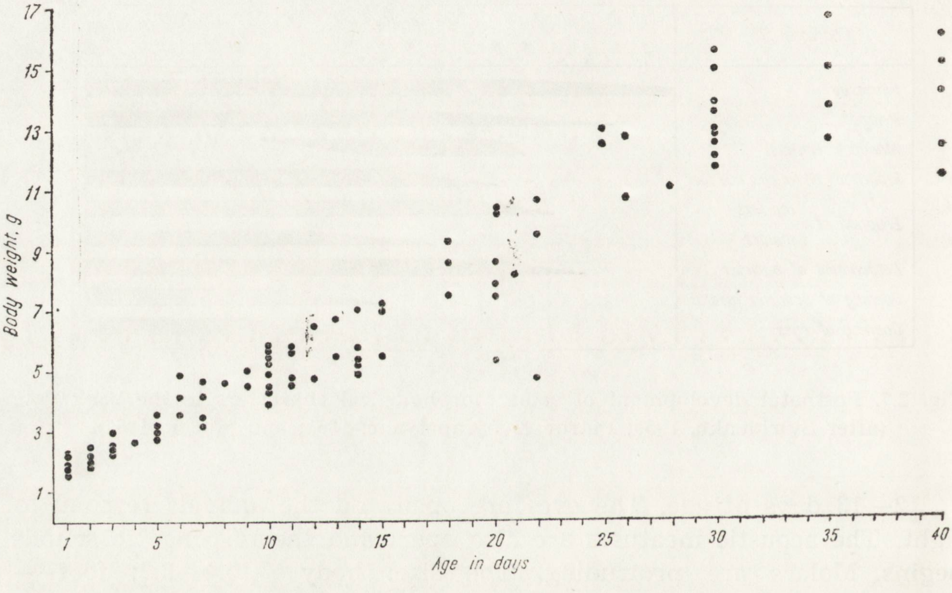

Fig. 2.8. Growth rate of body weight in the bank vole during the first weeks of life (after Sviridenko, 1959; Petrov & Ajrapetyanc, 1961; Mazák, 1962; Pearson, 1962; Drożdż, 1965; Bujalska & Gliwicz, 1968; Fedyk, 1974a, 1974b, Sawicka-Kapusta, 1974).

It is not known whether under natural conditions the growth of bank voles in their first month depends on the season. Although the season has an effect on the rate of the development of physiological maturity, it seems that there are no significant differences in the growth rate between spring and summer generations. Under experimental conditions, a decrease in the costs of rearing offspring in terms of energy is due to a decrease in their growth rate (Gębczyński, 1975). Under natural conditions, however, the same effect may be reached by a decrease in the litter size. The latter view is conistent with the fact that in autumn the litter size is smaller than in spring by 40% (Zejda, 1966; Ryszkowski & Truszkowski, 1970). It may thus be expected that the growth rate during nesting development is similar, independent of the season at birth. It is possible that an individual of small body size would have little chance for survival after weaning.

It is well known, however, that the further growth, when the animals are two and three months old, is more rapid for the spring cohort as compared with the autumn one (Wasilewski, 1952; Ilyenko & Zubchaninova, 1963; Bergstedt, 1965; Kubik, 1965). Experimental evidence shows that both poor food conditions (Sviridenko, 1959) and low ambient temperature (Gębczyński, 1975) can inhibit the growth of young voles. Nonetheless, it is suggested that under natural conditions the growth rate of the bank vole is stable over the first 3—4 weeks, independent of the season (Bujalska & Gliwicz, 1968; Zejda, 1971; Fedyk, 1974b; Sawicka-Kapusta, 1974). A different view is presented by Bergstedt (1965). It should be emphasized, however, that all the statements on the rate of growth in the nest are in fact based on laboratory data, or they are extrapolations from values for the voles caught in their second month. How difficult it is to determine the age of growing voles under natural conditions may be indicated by the fact that according to Bergstedt (1965) ten-day-old bank voles can leave their nest for a short time. Existing data on postnatal development, however, document that at this age they are still blind.

The body weight of 20-day-old bank voles from litters of 3—5 young is higher than those from litters of 6—9 (Korabelnikov, 1972). But the litter size dose not seem to have an unequivocal effect on growth rate. Vetulani (1931) discovered that mice kept singly grew less rapidly than those kept together. Moreover, as indicated above, the rate of growth depends markedly on many other factors, therefore it cannot be related to the litter size in a simple way. The data collected by Pearson (1962) and Mazak (1962) reveal that 10 to 12-day-old bank voles grow more slowly than do older animals. Many other data (Bujalska & Gliwicz, 1968; Fedyk, 1974a, 1974b; Sawicka-Kapusta, 1974) show that the growth rate is variable over the first 40 days, but it is not possible to distinguish fixed periods of faster and slower growth. Observations of many litters seem to suggest rather that growth rate depends on the varying ability of females to nourish their offspring.

2.3.4. Physiological Development

New-born bank voles are physiologically immature, and different functions develop on consecutive days after birth. Only some of them have been thoroughly studied. They include morphological parameters of blood that determine the respiratory function of this tissue. The highest hemoglobin level (20g %) occurs immediately after birth. Then it rapidly decreases to a minimum of 13 g% on days 6—7. In older voles it elevates to about 16 g% at the age of 30 days (Kostelecka-Myrcha, 1967). Similarly, clear-cut changes were observed in the number of erythrocytes and in the hematocrit index (Table 2.3). The rate of oxygen consumption by homogenized heart and kidney varied with age, but there were differences between the two organs (Table 2.4). Another interesting feature observed in some rodent species, including the bank vole, is the ability to utter ultrasounds at low ambient temperatures (Okon, 1972). This may be interpreted as a means of communication between the young and the mother when their body temperature drops and they want her to return to the nest to warm them. This suggestion concurs with the fact that the ability to produce ultrasounds disappears when their thermoregulatory system is well developed.

Table 2.3.
Age-related variability of some blood indices in the bank vole (after Kostelecka-Myrcha, 1967).

Index	Age in days			
	0—1	4—6	30—32	68—70
Haemoglobin, g%	20.0	13.0	16.0	16.7
Number of erythrocytes, × 10^6	5.33	4.12	10.93	11.52
Haematocrit, %	49.6	32.3	46.3	45.9

Table 2.4.
Rate of oxygen intake (μl/dry mg·hr) by homogenized heart and kidney during postnatal development of the bank vole (after Gębczyński, 1976).

	Age in days				
	1—3	10—12	19—21	28—30	31—45
Heart	4.48	4.47	4.08	3.86	3.64
Kidney	2.96	2.79	2.92	2.42	2.15

The rate of physiological development also depends on the season in which the young are born. Bank voles born in spring are characterized by more mature body composition (as expressed by the protein to water ratio) than those born in autumn (Fedyk, 1974b). This implies that the autumn generation is physiologically younger than the spring one.

Similar measurements of tissue metabolism indicate that the autumn generation is physiologically younger than the spring generation of the same absolute age, and that this generation develops at a lower rate (Gębczyński, 1977).

The development of homeothermy. A specific physiological feature of postnatal development is the increasing ability to maintain a stable body temperature. It depends on the formation of mechanisms of heat production (chemical thermoregulation), ability to control heat losses (physical thermoregulation), and the development of the temperature regulation centres.

Table 2.5

Age-related changes in oxygen intake (ccm/g·hr) in bank vole litters at different ambient temperatures (calculated from data by Gębczyński, 1975)

Litter size	1—9	10—18	19—33
	Age in days		
	Ambient temperature 15°C		
1—2	3.96	4.70	4.54
3—6	3.04	3.97	3.73
	Ambient temperature 20°C		
1—2	2.09	3.87	3.50
3—6	2.13	3.24	3.45
	Ambient temperature 25°C		
1—2	4.20	3.38	2.96
3—6	1.85	2.75	3.12
	Ambient temperature 30°C		
1—2	3.26	2.66	2.72
3—6	1.60	2.54	2.82
	Ambient temperature 35°C		
1—2	2.38	3.00	3.05
3—6	1.38	2.93	3.22

The rate of heat production in the bank vole increases with age (Bashenina & Borovskaja, 1963), but it also largely depends on the litter size (Gębczyński, 1975). Young bank voles from small litters (1—2 individuals) differ in their metabolic level from those raised in larger litters (3—6 individuals). These data (Table 2.5) clearly show that bank voles are able to increase their heat production in response to low temperatures already in the first days of life. This metabolic reaction is certainly not sufficient to maintain a stable body temperature for a longer period as both the energy reserves of a young organism are small and the loss of heat is relatively rapid. The rate of heat loss gradually diminishes during the first ten days as the bodies of originally naked animals become covered with the fur (Sviridenko, 1959; Mazák, 1962). It should be added that pelage development is accomplished at an age of 19—20 days, coinciding with a complete development of thermoregulation. The body temperature of young bank voles during their first nine days is about 4.5°C lower than that of adults. It undergoes only small changes, though the ambient temperature varies greatly (Fig. 2.9). The body temperature of 10—18-day-old bank voles increases daily, and reaches the adult body temperature on day 19.

Factors compensating for the lack of efficient thermoregulation in young voles involve an extensive parental care (*e. g.* complicated nest structure in close relation to ambient temperature and by attending the young for most of the day). Another important factor is the huddling behaviour of the young. They form a densely packed group responding as a unit to thermal cues during the nesting development (Gębczyński, 1975). All these factors account for relatively stable living conditions in the nest, which may be necessary for normal growth and development of the bank vole.

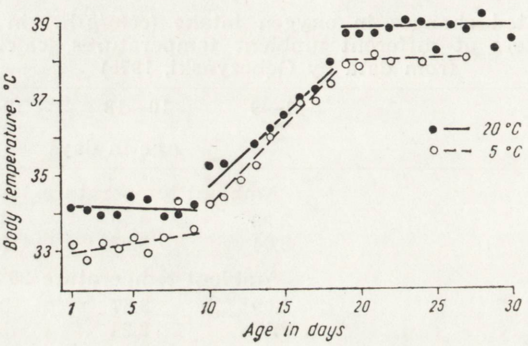

Fig. 2.9. Body temperature of the bank vole in relation to age and thermal conditions (after Gębczyński, 1975).

Bioenergetics of growth. The cost of maintenance of well protected bank voles permanently staying in their nests is small. It may be expected, therefore, that their rapid growth is an energetically efficient process. An index of this efficiency can be the ratio of the energy stored in the body to the energy assimilated from food. The assimilated energy (A) is used for costs of maintenance (R = respiration) and it can also be stored in the form of body components (P = production). From these two values, the coefficient of production efficiency can be calculated as follows:

$K = P/A \cdot 100$

The amount of energy stored in the body tissues (P) of a growing organism can be precisely measured as it is equal to the product of the body weight and its energy content per unit weight. The energy content of the body varies markedly during the first few weeks of life. Although the energy content of fat and proteins is constant and independent of age (Fedyk, 1974a), the relative water content drops with age. A six-fold increase in the content of water is coupled with a four-fold increase in the content of protein and a 50-fold increase in the content of fat (Fedyk, 1974b).

It has been calculated (Gębczyński, 1975) that during the first nine days of life (when the young do not leave their nest, their metabolism being relatively low and the rate of growth not lower than later, 60% of the assimilated energy is allocated for production (Table 2.6).

In 10-18-day-old voles the efficiency of production is significantly reduced, but still high. In older *C. glareolus* it does not exceed 5% (see also section 8), and it is equal to that of *Microtus arvalis* (Drożdż *et al.*, 1972).

Table 2.6

Energy requirements and growth efficiency in bank vole litters consisting of four individuals in successive periods of postnatal development (after Gębczyński, 1975). $K=P/A \cdot 100$ and $A=P+R$; K denotes the coefficient of production efficiency, P is tissue production (weight increase), R is respiration (maintainence costs), and A is assimilation (sums production and respiration)

Age in days	Mean litter wt., g	Oxygen intake ccm/g·hr		kcal/litter per day	Effeciency K, %	
		at 30°C[1]	at 35°C[1]		1[2]	2[3]
1—2	12.4	1.51	1.30	1.98	59.5	46.5
10—18	25.2	2.27	3.02	8.22	19.3	9.4
19—33	44.0	2.90	3.31	33.87	—	4.5

[1] It has been assumed that the female is outside the nest for about six hours a day, and the nest temperature in this time is 30°C. It has also been assumed that when the female is in the nest, the temperature for the young is about 35°C. To simplify the calculations, it has been assumed that the group of the oldest bank voles live in the same ambient temperature as younger individuals do, though the former remain in the nest only for some part of the day.

[2] Changes in the body composition after data by Sawicka-Kapusta (1974)

[3] Changes in the body composition from data of Fedyk (1974b).

Thus, bioenergetic parameters of the bank vole undoubtedly undergo substantial changes within a short time after birth. The efficiency of tissue production is very high until homeothermy is eventually developed. The cost of tissue production are highest for individuals with completely developed thermoregulation.

The developmental stage at birth can influence the differentation of the rate of growth and physiological maturation during ontogeny. The period of growth *in utero* and during postnatal development are complementary. This plasticity in reproduction, enabling adult bank voles to shift their care from the prenatal to the postnatal period, is a sign of a high evolutionary adaptability of this species. The shift is, perhaps one of the mechanisms which enabled the bank vole to spread over many different Eurasian habitats. This pattern of individual development largely alleviated the energy problems related to small body sizes (at the expense of temporary vulnerability) not only for the bank vole but also for many other small mammals.

3. HABITAT OF THE POPULATION

3.1. Habitat Preference

Michalina PUCEK

Published data on habitat preferences of bank voles are fragmentary and rather scarce, although they can be found in a large number of papers dealing with populations of this species. Generally, these are descriptions of the vegetation in terms of phytosociological characteristics serving as a background for qualitative and quantitative analyses of mammal communities.

Habitat preference depends on the abundance of the species, and the fertility and conditions prevailing in the habitat. Most generally, the issue of habitat preference involves the indication of places, sites, or biotopes, as they are called by different authors, in which a species lives. Relationships between plant and animal communities within biocoenoses have for a long time interested ecologists, but these relations remains unclear.

Many small mammals are associated with specific biotopes. We can thus say that some biotopes are preferred and other avoided or sporadically occupied. Some species, however, including the bank vole, can inhabit a wide range of biotopes, even different ecosystems. For example, in Poland, the bank vole can be abundant in wet habitats, e. g. in continental bog pine forests, bog alder forest, or raised bogs (Skuratowicz, 1948; Haitlinger & Korzeniowski, 1962; Aulak, 1970), as well as in ruderal sites (Haitlinger, 1965).

According to many authors, the bank vole prefers wet habitats (Turček, 1960; Bergstedt, 1965; Chełkowska, 1969; Lozan, 1971; Bock, 1972; Bolshakov & Vasilev, 1975). Others report that they are most abundant in dry sites (Brink, 1972, Skar *et al.*, 1971), or that they are eurybionts (Aulak, 1970; Quinet, 1971).

It is not easy to determine the optimum biotope for this species as this needs long-term studies in a wide spectrum of different habitats within its geographical range.

3.1.1. Habitat Preference vs. Dominance

Empirical establishment of habitat preference involves a trappability coefficient, that is, the ratio of the animals trapped to the number of traps; the proportion of individuals of one species trapped in a given biotope to the total number of individuals of the same species trapped in all the biotopes under study at the same time; or the number of individuals trapped per 100 trap-nights (Formozov, 1948; Naumov, 1948; Pivovarova, 1955; Koshkina, 1957; Popov, 1960; Lapin, 1963; Petrov, 1965; Aulak, 1970; Zejda, 1973; Ivanter, 1975). Using the same criteria of trappability, we can distinguish different biotope types: native, co-native, frequently occupied, sporadically occupied, randomly occupied or avoided/absent (Aulak, 1970).

Also the dominance of a species in a given biotope can be determined as a percentage contribution of this species to the total number of the mammals trapped. On the basis of these calculations we can say that a given species is dominant, co-dominant accessory, sporadic, random, or not encountered (Aulak, 1970).

It is necessary to differentiate between habitat preference and the dominance of a species in a community inhabiting the biotope. Generally, these two parameters do not coincide, but sometimes they may change in the same direction. Aulak (1970) has shown that in the Białowieża Primeval Forest, bank voles are eurybionts, and they occur everywhere, except for exceptionally wet biotopes such as forest ponds, sedge bogs, bog alder forest, or floodplain forest. They prefer bog pine forest and moist deciduous forest, where they are dominant. But in the bog alder forest, which is classified as a sporadic biotope of the bank vole, they belong to the group of co-dominant species. Pine forests (continental pine forest and its subboreal variety, continental pine-oak mixed forest, central European acidophilous oak forest) as well as deciduous forest of the Białowieża Forest are frequently occupied by the bank vole, but it is the dominant small mammal species there.

3.1.2. Factors Affecting Habitat Preference

Many data show that the bank vole is a common species associated with forests. Beyond forests, these rodents occur in shrubberies, at forest edges, and in old parks and orchards. They can also occasionally be found in other biotopes. Skar *et al.* (1971), argue that the occurrence of the bank vole in these unusual habitats in Scandinavia may be due to intraspecific competition and spatial expansion of this species. The occurrence of bank voles in atypical habitats is probably related to changes in numbers of animals, available resources, cover, shelters, nesting sites, etc.

Effects of population dynamics

Factors determining numbers of small mammals can vary from year to year and this can have an effect on numerical interspecific relations. For this reason both dominance and habitat preference of individual species must be determined only on the basis of long-term studies.

Population density has an effect on dispersal. At low population densities, bank voles occupy only the best, thus typical sites (Evans, 1942; Naumov, 1948; Koshkina, 1957; Lapin, 1963; Ivanter, 1975). In years of high population numbers they also migrate beyond these sites, including croplands close to forests. Occasionally, they are found 0.5—2 km from the nearest forest (Mohr, 1931; 1939 quoted in Naumov, 1948; Naumov, 1948; Popov, 1960; Lapin, 1963). According to Koshkina (1957), bank voles inhabit spruce-birch forests of the subalpine zone and riverside shrubberies of the tundra only in the periods of high vole numbers. The same is true of flooded meadows (Naumov, 1948) and dry, steep valley-walls (Bergstedt, 1965). Similarly, Ivanter, (1975) found that bank voles living in Karelia usually avoid wetlands as well as dry lichen-pine forests and forest plantations, except during the end of summer and in autumn when their numbers are high these habitats are also occupied. In winter, bank voles often aggregate in buildings, cellars, sheds, stacks of straw and hay close to forests, while in summer their numbers in such places can be very low (Formozov, 1948; Koshkina, 1957; Lapin, 1963; Saint-Girons & Saint-Girons, 1970; Ivanter, 1975). Therefore, bank voles can disperse widely, depending on their numbers and season.

Food

Many authors have found that the distribution and dispersal of the bank vole depends on food resources of the habitat. According to Turček (1953), the concentration of animals increases and migrations are reduced when food is abundant, while food shortage instigates population dispersal.

Some authors (Bashenina, 1947; 1951; Formozov, 1948; Naumov, 1948) relate increases in bank vole numbers to the periods of seed abundance on trees. Popov (1960) observed a very high trappability of bank voles, reaching 59.3 animals per 100 trap-nights in linden-spruce forests of the Volga-Kama region. This was a result of the bank vole mass appearance coupled with a high yield of spruce seed and linden mast.

In the following year, this index dropped to 3.2 voles per 100 trap-nights. In clearings covered with secondary growth, trappability indices for the same two years were 1 vole per 100 trap-nights and 1.7 per 100 trap-nights, respectively. The author explained this by the migration of bank voles to marginal habitats as a result of food shortfall in the previously productive forest independent of vole numbers.

Shelters

Curry-Lindhal (1959) suggests that the occurrence of bank voles in different sites depends on the avaliability of shelter from predators. These rodents do not burrow much, thus they search for natural shelters in their environment. Most often these are old logs, dry twigs, fallen branches and trees, entangled roots, tree holes, or spaces under the bark of fallen trees, dense weed cover, piles of stones, natural depressions covered with moss, dense cover of herbaceous vegetation or shrubs. All these structures provide protection from predators and adverse weather conditions (Koshkina, 1957; Lapin, 1963; Petrov, 1965; Ivanter, 1975). Skar *et al.* (1971) point out that shelters among stones, rocks, nad other structures of the alpine zone are good substitutes for trees and shrubs of the lower zones.

Type of vegetational cover

The importance of vegetational cover to the bank vole has been discussed by many authors. Some found these rodents abundant in habitats rich in dead plant remains, branches, needles, and pine cones (Turček, 1960; Venables & Venables, 1965; Birkan, 1968), or logs and fallen trees (Kratochvíl & Gaisler, 1967).

According to Lapin (1963), the distribution of the bank vole depends on the character of the area, and especially on its relief, the density of vegetational cover, and on the intensity of forest management. Kikkawa (1964) observed seasonal changes in ground cover correlated with vole distribution, thus the size of the area occupied by the population declined with reduction in the vegetational cover in winter.

Curry-Lindahl (1959) points out that the size and shape of home ranges in the bank vole varies not only from one biotope to another but also within the same vegetation type. Ivanter (1975) came to a similar conclusion. Bank voles have patchy distribution in some biotopes, depending on the relief, composition of tree stand, and degree of the development of shrub and herb layers. In dense deciduous, spruce, and mixed forests, bank voles prefer more open parts, with diversified tree stands. Also roadsides, clearings, and forest edges, particularly when they adjoin croplands, are most frequanted habitats. Studies in different parts of Karelia have shown that vole numbers at forest edges can sometimes be higher than in centres of vast forests (Table 3.1).

Also Lapin (1963) has recorded more rodents, including bank voles, at forest edges. It happens that the number of voles in such ecotones is ten times as high as in central parts. Croplands adjoining forests are of basic importance here, particularly during years of few tree seed, berries, and fungi. Forest edges lined with ditches, depressions, shrubs, thickets, stacks of hay, all provide good shelters for rodents. Jurgenson (1937) (quoted in Naumov, 1948) found that the number of bank voles at forest edges can be 2—4 times as high as inside these forests. Ashby (1967) found on the basis of 12-year material that the distribution of the bank vole is closely related to the density of plant cover, but independent of vegetational type providing the cover. Evans (1942) pointed out that the distribution of bank vole populations is not random, and the species is atracted to the fern-dominated community. Similar relationships were indicated by Miller (1958), Newson (1963) and Birkan (1968).

Table 3.1

Numbers of the bank vole (individuals/100 trap-nights) at forest edges nad in central parts of forest (after Ivanter, 1975).

Forest type	Edge	Centre
Dry pine forest	3.1	0.5
Moist pine forest	4.4	1.0
Bog pine forest	2.0	0.3
Boreal spruce forest	6.0	1.3
Mixed forest	7.3	1.5
Deciduous forest (old stand)	4.1	1.7
Thicket	6.4	0.8

There are differences in the colonization of different types of clearings by the bank vole (Ivanter, 1975). On new, open clearings they can occur sporadically. But during the first ten years, as food and living conditions improve, bank voles become dominant species there. On average, this species accounted for 47.8% of the small mammal community (2.7 per 100 trap-nights) in clearings of differrent ages. According to Lapin (1963), the index of trappability of the bank vole was 0.7/100 trap-nights in 1 to 3-year-old clearings, while 5.4 on 7 to 10-year-old clearings. A predominance of bank voles in 6 to 10-year-old clearings with saplings of broad-leaved trees was also recorded by Formozov (1948).

Birkan (1968) analysed the trappability of the bank vole in seven habitats predominantly covered with Scots pine, *Pinus silvestris*, that differed in age. The highest trappability was recorded in the pine plantation 30 years old. Bank voles rarely occupied plantations more than 35 years old and they were poorly represented in plantations less than 15 years old. Detailed phytosociological analysis has shown that these plant communities were evolving into *Quercetum* type, thus bank vole trappabliity peaked in the plant community approximating *Quercetum* climax forest, independent of the age of the tree stand.

3.1.3. Geographical Variability in Habitat Preference

The range of the bank vole generally covers broad-leaved forests of the western Palaearctic, that is, the forests of Europe and south-western Siberia. This is a common species in almost all biotopes, but a distinct geographical zonation characterizes its distribution.

Bank vole occurrence in taiga has been described by Koshkina (1957) (on the Kola peninsula) and Ivanter (1975) (in Karelia). On the Kola peninsula, this species reaches its northern boundary (Koshkina, 1957), and in coniferous forests, where it can be the dominant species accounted for as much as 99.8% of the small mammal community. The main refuges of the bank vole are moderately dense spruce forests (mean canopy cover of 3.0 to 0.4, density scale 0 to 1) where the ground layer mostly consists of mosses 7—13, some times as high as 25 cm, bilberry, and different grasses. For example, the trappability of the bank vole in these habitats was 35.3/100 trap-nights in 1941, 26.6 in 1947, and 16.0 in 1949. In the years of low population numbers, bank voles persisted only in these spruce forests. Their density there can be 2—3 times higher than in moist pine-spruce forests rich in mosses. They can also occur in burned-over pine forests with some living trees, and in spruce forests with dense deciduous shrubs. In the spruce-birch scrub of the subalpine zone they occur only in the periods of high numbers. However, they do not occur in mountain tundra.

In north-western taiga, the bank vole prefers spruce forests and mixed forests dominated by spruce, pine and birch, with a dense canopy (0.6—0.8) and well-developed shrub and herb layers (Ivanter, 1975). A relatively high index of trappability was also recorded in deciduous thickets invading clearings (1.4/100 trap-nights) and in open clearings (2.7/100 trap-nights).

Lapin (1963) emphasized the importance of spruce forests as refuges of the bank voles living in the subzone of northernmost predominately coniferous mixed forests. In these regions, bank voles chiefly inhabit *Piceetum oxalidosum*, where in addition to the spruce there are deciduous trees such as aspen, birch, and also alders (*Alnus incana* and *A. glutinosa*), the undergrowth consists of *Frangula alnus*, *Sorbus aucuparia*, *Corylus avellana*, and *Lonicera xylosteum*, while the field layer contains many grasses and *Oxalis acetosella* — a characteristic component of these forests. The mean trappability of bank voles in these habitats was 6.3/100 trap-nights and the total index of trappability of all small mammals was 7.3. In the three successive years of low vole numbers, their spring trappability indices in these forests were 3.0, 7.6, nad 5.2/100 trap-nights, while zero in other habitats.

In the pine forests of this zone (*Pinetum cladinoso-callunosum*, *Pinetum vacciniosum*, and *Pinetum hylacomiosum*), the shrub layer can be poor and the field layer poorly diversified, composed mostly of heath, mosses and lichens, ledum, cowberry and bilberry. The trappability of the bank vole, which dominates in these forests, was 2.4, out of a total small mammal trappability of 3.5/100 trap-nights.

Larger deciduous forests of the subzone of mixed forests belong to the *Betuletum dryopterioso-caricosum* and *Alnetum dryopterioso-caricosum* associations. The bank vole trappability in these habitats was 3.9/100 trap-nights, and the total trappability of small mammals was 5.9. In aspen forests (*Tremuleto oxalidosum*) with spruce, *Sorbus aucuparia* and *Frangula alnus* in the undergrowth, and predominantly *Oxalis acetosella* in the herb layer, the trappability of the bank vole was 2.8 and the total trappability of small mammals was 4.8/100 trap-nights. In ash, oak, or alder forests with a rather dense undergrowth made up of hazel, rowan, linden, and buckthorn, where grasses and *Aegopodium podagraria* formed the herb layer, the trappability of the bank vole was 3.3/100 trap-nights.

Farther to the west, in the same zone of deciduous and mixed forests (Sweden), bank voles generally inhabit forests with hazel, aspen, and willow species in the undergrowth (Curry-Lindahl, 1959). Data of Bergstedt (1965) and Hansson (1967) show that bank voles in southern Sweden prefer deciduous forests and alder-ash floodplain forests. Their density there can reach 200 individuals per hectare (Bergstedt, 1965).

Adolf (1972) has analysed bank vole trappability in three different biotopes, in deciduous forests of central and eastern Europe. He found that the highest proportion of bank voles (63% of the small mammal community) was trapped in oak forests, and the lowest (54%) in spruce forests. In peatlands covered with sallows, birches, alders, and pines, and also with dense grass in herb layer, bank voles accounted for 57% of the mammals caught. Popov (1960) analysed vole densities in 23 biotopes of the Volga-Kama region, and distinguished five groups of habitats differing in vole numbers. The most densely populated habitat consisted of linden-oak forests and mixed deciduous forests with an admixture of spruce, well-developed shrub layer, and with grasses in the herb layer. Equally occupied by voles were spruce-fir forests with a large admixture of deciduous trees. The next group, readily occupied by the bank vole, comprises pure or almost pure oak plantations, linden forests, and aspen forests with grass in the well-developed herb layer, as well as deciduous and mixed thickets, and riverside hawthorn scrub. Then there is a group of biotopes permanently occupied by low numbers of the bank voles. It comprises pine forests at different ages, rich in moss, mixed forests dominated by birch, clearings in deciduous forests, and thickets more than 10 years old. The next group includes habitats not readily occupied by the bank vole. These are dry coniferous forests, pine clearings, juniper brushwood, and thickets. The last group of habitats consists of sporadically inhabited biotopes such as open meadows, crop fields, and forest clearings.

Table 3.2
Occurrence of the bank voles in different plant communities of Poland (M. Pucek in litt.)
(arranged in order of vegetation type)

Community type	Trappability index in %
I — Entrophic bog and riverside ecosystems	
Bog alder forests and flood plain forests (*Carici elongatae Alnetum, Circaeo-Alnetum, Fraxino-Ulmetum*)	4.7
Bog willow brush (*Myrico-Salicetum auritae, Salicetum pentadro-cinereae)*	3.0
Red swamps	0.7
Moist meadow communities (*Molinietalia, Caricetalia fuscae*)	1.3
II — Oligotrophic and meso-oligotrophic coniferous and mixed forest ecosystems	
Continental bog pine forest (*Vaccinio uliginosi-Pinetuh)*	3.0
Continental pine-oak forest (*Pino-Quercetum*)	3.8
Continental moist pine forest (*Peucedano-Pinetum, Leucobryo-Pinetum*)	6.4
Coastal dry pine forest (*Empetro-Vaccinietum*)	1.6
Mesooligotrophic oak forest (*Abietum polonicum*)	15.5[1]
Mesooligotrophic oak forest (*Quercetalia robori-petraeae*)	5.6
III — Mesoentrophic and entrophic deciduous forest ecosystems	
Poor Pomeranian beech forest (*Trientali-Fagetum*)	1.6
Rich lowland beech forest (*Melico-Fagetum*)	8.8
Rich mountain beech forest (*Dentario glandulosae-Fagetum*)	3.5
Deciduous oak-hornbeam forest (*Querco-Carpinetum medioeuropaeum*)	6.7
IV — Cropland and buildings in forests	0.9

[1] Only three plots, see the text.

Trappability of the bank vole was also analysed in one of the best preserved forest complexes of lowland Europe — in the Białowieża Forest. Pivovarova (1955) found that the mean trappability was 2.1 voles/100 trap-nights there. According to this author, the distribution of the bank vole in this forest is relatively uniform, and it is difficult to distinguish optimum habitats. However, bank vole numbers were highest in spruce habitats (5/100 trap-nights). In bog alder forest, where vole numbers were most stable, the trappability varied from 2.8 to 3.2/100 trap-nights over three years. In a mixed forest, the numbers of voles trapped per 100 trap-nights were 0.5, 4.0 and 4.3 over successive years. In a deciduous forest, the trappability in two successive years was 4.0 and 1.7. Aulak (1967, 1970) points out, however, that in the Białowieża National Park, bank voles most abundantly occur in rich forest communities such as deciduous forest and floodplain ash forest, where they accounted for 44.7 and 33.5%, respectively, of the total number of small mammals trapped, while only for 14.9% in *Pinetum typicum* forest,

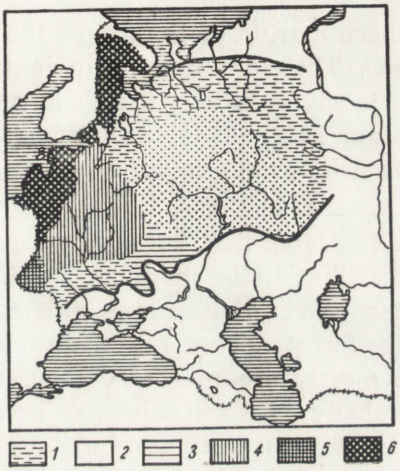

Fig. 3.1. Geographical variability in the maximum number of bank voles trapped in the European part of the USSR (number of animals per 100 trap-nights). After Golikova & Lapin, 1967.
1 — zero voles, 2 — 6 to 15, 3 — 16 to 25, 4 — 26 to 35, 5 — 35 to 55, 6 — more than 55.

Some light on the occurrence of the bank voles in different plant communities can be shed by unpublished data (Pucek M.) collected from nearly throughout Poland over 1963—1971. The highest trappability index was recorded in rich lowland beech forests, where it was 8.8% on the average (Table 3.2). It is worth noticing here that the value of this index was 1.6% in poor Pomeranian beech forests and 3.5% in rich mountain beech forests. In deciduous oak-hornbeam and mixed forests this index was 6.7 nad 5.6%, respectively. Among coinferous forests, a peak trappability index of 6.4% was recorded in a moist pine forest.

Fir forests, though not numerous in Poland, represent an exceptional habitat for the bank vole, with trappability indices of 5.9, 11.6, and 29.1% on three plots, respectively. High trappability was also observed in a bog alder forest and floodplain ash forest (more than 4.7%). The smallest numbers of bank voles were traped on meadows, reed swamps, crop fields, and in buildings situated in forests (1.3, 0.7, and 0.9%), respectively).

At the western border of its range, in the zone of Atlantic oak forests, this species is characteristic of *Quercetum roburi sessiliflorae* (Birkan, 1968).

Closer to the southern margin of the range, the bank vole avoid pure, high coniferous forests. They are most abundant in wet, shady alder and ash-alder forests in river valleys (Bolshakov & Vasilev, 1975), also in wet clearings (Lozan, 1971). This species has not been recorded in very dry, calciphilous oak forests covering southern parts of its range. The same is true of steppes (Kirikov, 1935; Bolshakov & Vasilev, 1975).

This short review indicates that bank voles are present in all forest habitats. But their distribution is characterized by a zonal variability. In northern and eastern parts of its range, this species seems to prefer spruce and pine-spruce forests, as well as shady clearings. In the central part of the range, it mostly occurs in deciduous and mixed forests. In the south it prefers shady and wet biotopes as summer temperatures are high and the land desicates. Optimum habitat conditions for the bank vole occur in the subzone of deciduous forests of Europe where it is the only representative of the genus *Clethrionomys*. It attains the greatest numbers in northern and western regions of the European part of the USSR (Fig. 3.1). The fact that these rodents also inhabit boreal spruce and spruce-fir forests of taiga and the forest-steppe zone to the south provides evidence of their high ecological plasticity.

3.2. Feeding Habits

Zofia GĘBCZYŃSKA

The bank vole is a polyphagous animal, changing the diet according to habitat. This doubtlessly is one of the factors that enabled voles to spread over vast geographical regions differing in climatic and vegetative conditions. The areas inhabited by the bank vole are also characterized by a distinct rhythm of seasonal changes, hence available food resources are subject to similar fluctuations. Moreover, the diet of females may differ from that of males, and it can also be affected by population density. These relationships, digestibility and assimilation of natural food, are documented in this section.

3.2.1 Geographical Changes in the Diet

Bank voles inhabiting taiga forests of the Kola peninsula, thus living at the northern limit of their range, avoid almost all green plant parts, taking lichens instead. The preferred lichens include the genus *Bryopogon* from spruce and pine trees, the genus *Parmelia* from spruces and birches, or, when they are lacking, also *Nephroma arcticum.* This diet is supplemented with berries of *Vaccinium myrtillus,* leaves of trees, fungi, and food of animal origin (Koshkina, 1957).

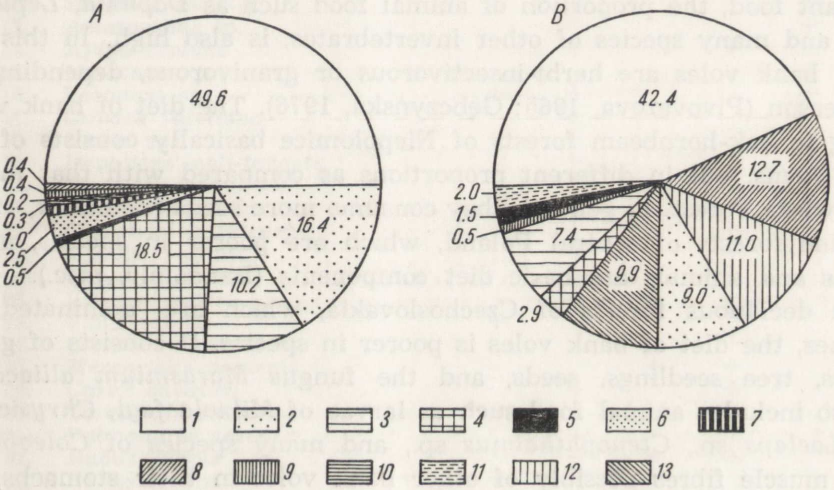

Fig. 3.2. Percentage composition of the diet of *C. glareolus* from the Białowieża Forest (A) and southern Moravia (B).
1 — green parts of herbaceous plants, 2 — animal food, 3 — seed, berries of herbaceous plants, 4 — seeds, fruit of trees, 5 — fungi, 6 — roots, 7 — mosses, 8 — leaves of trees and shrubs, 9 — non-green parts, 10 — pollution, 11 — nonindentified, 12 — bark of trees and shrubs, 13 — parts of flowers.

Under less severe climatic conditions of southern Sweden, bank voles mostly feed on seeds of *Fagus silvatica, Ulmus glabra, Quercus* sp., and *Picea abies,* and also on green parts of herbs. Supplementary food consists of insect larvae, tree bark, fungi, nad berries (Hansson, 1971b).

The diet of *C. glareolus* inhabiting deciduous and mixed forests of central and eastern Europe (European part of the Russian SFSR, Poland, Czechoslovakia) is less variable in different, even very distant regions, but the proportions among particular components of the diet can change greatly (Fig. 3.2). For example, in coniferous forests of the east-European lowland (the regions of Perm, Vologda, and Syktyvkar), the list of food species is very long, changing seasonally (Bashenina, 1968; Petrov, 1974). According to Sviridenko (1940), the basic diet components in this area are green plant parts and seeds, and next buds, bark, and roots. Lapin (1963) also has found that green parts and seeds are basic food items of the bank vole diet.

In oak-hornbeam forests of Białowieża, where the herb layer is rich in species, the food spectrum of bank voles is even larger. In addition to plant food, the proportion of animal food such as *Daphnia, Lepidoptera,* and many species of other invertebrates, is also high. In this habitat, bank voles are herbi-insectivorous or granivorous, depending on the season (Pivovarova, 1965; Gębczyńska, 1976). The diet of bank voles living in oak-hornbeam forests of Niepołomice basically consists of the same items, but in different proportions as compared with that in the Białowieża Forest. In general, they consume more seeds (Zemanek, 1972). In pine forests of central Poland, which are poorer in species, green plants and animals are basic diet components (Bandomir, msc.).

In deciduous forests of Czechoslovakia, which are dominated by beeches, the diet of bank voles is poorer in species. It consists of green plants, tree seedlings, seeds, and the fungus *Marasmium alliaceum.* It also includes animal food such as larvae of *Mikiola fagi, Chrysichloe* sp., *Laelaps* sp., *Ctenophthalmus* sp., and many species of *Coleoptera.* Also muscle fibres possibly of other bank voles in their stomachs, indicates cannibalism (Turček, 1953).

Bank voles inhabiting western parts of their range (British Isles) consume relatively few seeds. According to Watts (1968), even in the years of abundant acorn crops, seeds do not account for more than 16% of the total food consumed. Their diet mostly consists of green plant parts and leaves of trees. Miller (1954) suggests that bank voles occupying the same area can exhibit highly variable diets. It consists of animal food (such as larval *Melanotus rufipes,* larval and adult *Dorcus parallelipipedus*) and also of plant food such as seeds of *Acer pseudoplatanus* and *Fagus silvatica* and as well as fruits.

Changes in the species composition of plants related to climatic differences and site conditions have a major effect on the taxonomic composition of food in different parts of the European continent colonized by the bank vole (Table 3.3). Thus, we can observe differences in the consumption of various food items such as seeds, herbaceous plants,

Table 3.3

Herbaceous plants recorded in the diet of the bank vole in different parts of its range (after: 1 — Bashenina, 1966; 2 — Gębczyńska, 1976; 3 — Zemanek, 1972; 4 — Drożdż, 1966, 5 — Holišova, 1966).

No.	Species	1	2	3	4	5
1.	*Urtica dioica*	+	+			+
2.	*Glechoma* sp.	+				+
3.	*Lamium* sp./*Stachys* sp.	+	+			+
4.	*Ficaria verna*		+			+
5.	*Galium* sp.					+
6.	*Rumex* sp. or *Pericaria* sp.	+				+
7.	*Ranunculus* sp. or *Geranium* sp.	+	+	+		+
8.	*Daucaceae*					+
9	*Gramineae*	+				
10.	*Asperula odorata*		+		+	+
11.	*Gagea lutea*					+
12.	*Stellaria holostea*	+	+			+
13.	*Amaranthus* sp.					+
14.	*Ajuga reptans*		+		+	+
15.	*Medicago* sp.					+
16.	*Veronica* sp.	+	+			+
17.	*Circaea lutetiana*		+			+
18.	*Geum* sp.	+	+			+
19.	*Impatiens noli-tangere*		+			+
20.	*Anemone nemorosa*		+	+	+	
21.	*Oxalis acetosella*	+	+	+	+	
22.	*Galeobdolon luteum*		+		+	
23	*Mycelis muralis*		+	+	+	
24.	*Hepatica nobilis*		+		+	
25.	*Viola silvestris*		+	+	+	
26.	*Viola canina*	+				
27.	*Hieracium murorum*				+	
28.	*Mercurialis perennis*			+	+	
29.	*Carex silvatica*		+		+	
30.	*Carex caespitosa*	+				
31.	*Pulmonaria obscura*		+		+	
32.	*Rubus hirtus*		+	+	+	
33.	*Rubus idaeus*	+				
34.	*Actaea spicata*			+		
35.	*Hedera helix*		+	+		
36.	*Orobus vernus*	+				
37.	*Fragaria vesca*	+	+	+		
38.	*Lathyrus vernus*		+			
39.	*Majanthemum bifolium*	+	+			
40.	*Polygonatum multiflorum*		+			
41.	*Polygonatum officinale*	+				
42.	*Isophyrum thalictroides*		+			
43.	*Luzula* sp.		+			
44.	*Dentaria bulbifera*		+			
45.	*Festuca* sp.		+			
46.	*Sanicula europaea*		+			
47.	*Aegopodium podagraria*	+	+			
48.	*Milium effusum*		+			
49.	*Dryopteris filix mas*		+			
50.	*Polygonum persicaria*		+			
51.	*Polygonum bistorta*	+				
52.	*Athyrium filix femina*		+			
53.	*Paris quadrifolia*	+				
54.	*Draba verna*	+				
55.	*Chrysosplenium alternifolium*	+				

Table 3.3, concluded.

No.	Species	1	2	3	4	5
56.	*Ribes nigrum*	+				
57.	*Filipendula ulmaria*	+				
58.	*Linnaea borealis*	+				
59.	*Rosa cinnamomea*	+				
60.	*Trifolium pratense*	+				
61.	*Epilobium angustifolium*	+				
62.	*Melampyrum pratense*	+				

or lichens from one geographic area to another. Also changes in the composition and proportion of the food of animal origin are significant. In addition to this geographical differentiation, seasonal differences in the plant cover and animal species also greatly affect the diet of the bank vole.

3.2.2. Seasonal Changes in the Diet

In spring, the main component of the *C. glareolus* diet is green plant parts in most of the known habitat types, except for the northern taiga (the Kola peninsula), where lichens predominate the diet, along with berries of the cranberry and crowberry, *Empetrum* sp., leaf-buds of blueberry, sallow, and rowan, and birch catkins. In deciduous forests of Great Britain, the preferred food items consist of *Campanula rotundifolia, Oxalis acetosella, Primula* sp., green leaves of *Quercus robur* and *Rubus* sp., also seeds and invertebrates, e. g. larval *Lepidoptera* (Miller, 1954, Watts, 1968). In deciduous forests of Czechoslovakia, the most important dietary components are the bark of trees, shrubs, and herbaceous plants in early spring, while in mid-spring herbaceous plants account for 95% of the diet. In late spring food of animal origin predominates in 70%. These are mostly annelids, mollusks, arthropods, and small mammals (Holišova, 1966). In the oak-horbeam forests of Niepołomice (Zemanek, 1972) and Białowieża (Gębczyńska, 1976), green food accounts for 40—70% of the diet in spring. Seeds account for 19—55% of the diet in the Niepołomice Forest, while for a very low percentage in the Białowieża Forest. In both of these habitats, the proportion of animal food is high (7 to 21%). Hansson (1971b) also reports that the proportion of this food is particularly high in spring. Food content in the diet is closely related to food abundance, e. g., if the number of accorns laying on the ground is high, they become an important component of bank vole diet (Zemanek, 1972). When seeds are in short supply, the proportion of insects and green plants in the diet increases.

In summer the diet of the bank vole is somewhat different than in spring, largely due to the fact that some food plants have a short growing season, and are replaced by other species. Watts (1968) has observed that on the British Isles the proportion of herbaceous plants declines in summer, and in this time bank voles live on tree leaves, particularly of the privet, spindle tree, and maple. According to this author, also fungi (*Ascomycetes, Basidiomycetes,* and *Mucorales*) are rather commonly foraged upon throughout the year. From May to September they reach a maximum and account for more than 10% of the diet volume. In summer the proportion of *Lumbricidae* increases in food of animal origin (Watts, 1968; Hansson, 1971b). In southern Sweden it has been found that bank voles, which are granivorous there, consume many more herbaceous plants in summer than in any other season (Hansson, 1971b). According to Sviridenko (1951), this is related to the replenishment of water deficiency in the periods of drought. On the Kola peninsula, an important dietary component of during the short summer (end of June, July) is immature berries of *Vaccinium myrtillus*, but at the same time the proportion of tree leaves declines as compared with spring (Koshkina, 1957; Ivanter, 1975). In the Białowieża Forest, the diet of the bank vole consists of 30 species of plants in summer. The proportion of vegetative plant parts declines to 54% of the diet as compared with 68% in spring. But most of the plant diet (62%) consists of the same species in spring and summer (Gębczyńska, 1976). In the Niepołomice Forest (Zemanek, 1972), the proportion of seed and fruit in the diet is four times that in the Białowieża Forest (Gębczyńska, 1976). In poorer habitats of pine forests in central Poland, green plant parts are gradually replaced by food of animal origin during July-September (Bandomir, msc.). Turček (1953) observed a marked increase in the number of seeds in the diet at the end of summer, when the seeds of such preferred herbaceous plants as *Asperula odorata, Mercurialis perennis* and *Galeopsis tetrachit* are abundant. Holišova (1966) also reported that herbaceous plants and leaves of trees and shrubs are most important food items early in summer, while seeds predominate later in summer.

Basic changes in the diet of this rodent occur in autumn, when the proportion of green parts of forbs, grass, and leaves of trees and shrubs drastically declines, while that of seed and fruit increases. Such shifts have been observed in Czechoslovakia, Great Britain, Poland, Sweden, and on the Kola peninsula. In the latter region, these include berries of the dogwood with seeds, cowberries, blueberries as well as various fungi (Koshkina, 1957). In Sweden the proportion of berries in the diet is above 10% in autumn, when the proportion of the fungi also markedly increases (Hansson, 1971b). In the Białowieża Forest, the proportion of seeds in the diet outweighs that of other plant parts (Fig. 3.3). It should be noted, however, that the number of seeds in the diet strongly depends on their supply, and in the years of low seed production they may not represent the basic food item (Zemanek, 1972).

In winter the diet also mostly consists of fruit and seeds of herbs, trees, and shrubs. However, green and wooded plant parts are also included. According to Holišova (1966), underground parts of herbs can

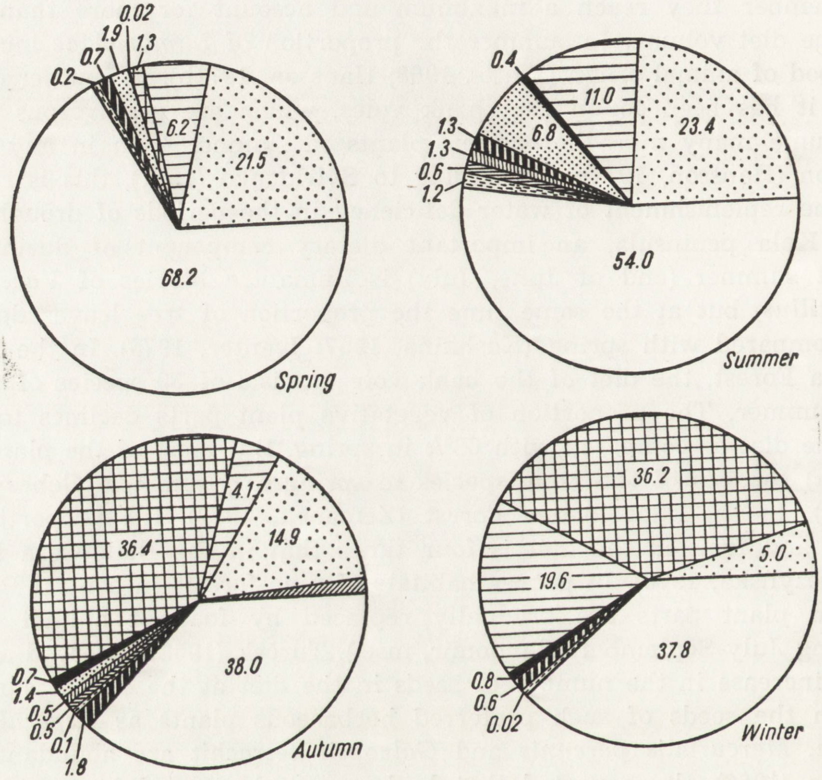

Fig. 3.3. Seasonal variability in the proportion of the diet components of *C. glareolus* from the Białowieża oak-hornbeam (symbols as in Fig. 3.2).

even be a basic dietary component early in winter. Also tree and shrub bark is consumed. Similar data are reported by Zemanek (1972). In the Białowieża Forest, the proportion of seed is 56% of the winter diet, though the amount of green forage does not decline as compared with that in autumn; instead, the proportion of animal food drops significantly to 5% (Gębczyńska, 1976). The winter diet of the bank vole in the Moscow region consists mostly of fallen bark or snow laden branches of the aspen, birch, and pine, the aspen being a clearly preferred species.

In addition, ban voles browse the bark of *Acer platanoides, Corylus avellana, Cytisus ruthenicus,* and *Sambucus racemosa* (Rotshild & Krivosheyev, 1957). Similarly, Curry-Lindahl (1959) emphasises the great importance of bark and branches. Many investigations document the proportional reduction of animal food in winter (e. g. Hansson, 1971b; Zemanek, 1972; Obrtel, 1974; Gębczyńska, 1976).

The diet of the bank vole is characterized by a clear rhythm of seasonal changes. Despite significant differences in the diet due to the variability in environmental conditions, in spring and summer bank voles generally live on green parts of herbaceous plants. In addition, they consume animal food, seed, and fungi. In autumn and winter their diet contains more seed. The proportion of other components is smaller than in spring and summer, and is strongly dependant on available food supply.

Feeding adaptability of the bank vole accounts for the fact that it is a herbivorous animal in spring and summer, while granivorous in autumn and winter. The proportion of animal food can be very high, but it also fluctuates from season to season, reaching a maximum in spring.

3.2.3. Diet Composition in Relation to Sex and Population Density

The diet of the bank vole also depends on sex. In spring and summer, females can use much more animal food than males (Holišova, 1971; Gębczyńska, 1976). According to Watts (1968), females consume more seed and fungi, as compared with males, particularly from September to November.

Significant differences in the diet were found between populations of different densities. The proportion of high-caloric seed is the highest and dominant in the diet of animals living in populations of low densities or in the population recovery phase. High-density populations mostly use green vegetative plant parts and bark, thus energy-poor food. A long-term shortage of appropriate food supply, also with respect to its energy content, can account for a premature inhibition of growth and cessation or reduction of reproduction (Holišova, 1971).

3.2.4. Digestibility and Assimilation of Natural Food

In the studies of energy flow through a small rodent population, it is important to know how much of the energy taken with food is assimilated and how much is recycled in the form of feces and urine. It is thus necessary to determine not only the consumption of food but also its digestibility and energy assimilation. For this purpose, the content of bank vole stomachs was examined, and experiments of food preference were conducted. Experimental animals were supplied with three kinds of diet: concentrated, mixed, and bulky. All these diets were characterized by high digestibility coefficients of all their components. The digestibility coefficients of the dry matter of the forage ranged from 80 to 90%, except for the bulky diet (74 to 76%). The digestibility of crude protein, other extracts and crude fiber varied from about 70 to 97%. Some food energy was lost as partially digested food in the feces, and in the form of urine as partially degraded nitrogen compounds. The size of these losses depends on the amount and energy content of the excreta. Fecal energy losses of animals fed on the protein and mixed diets ranged from 7 to 17% of the energy intake, and the losses with urine from about 3 to 4%. In the case of the bulky diet (herbaceous plants) the losses of energy reached highest values, up to 28% (Drożdż, 1968).

The daily energy intake depends on the kind of forage, its energy content, and on the body size and physiological condition of the animal. The daily consumption in bank voles of an average body weight of 22.8 g was 1.92 g of beech nuts, 2.26 g of mixed forage, and 3.40 g of oat seeds, on the average (Drożdż, 1968). Similarly, under natural conditions these animals consume about 3 g of seed per day (Górecki and Gębczyńska, 1962). This corresponds to 13—15 kcal/day, which is consistent with the energy budget of this species (Górecki, 1968). Subtracting the energy lost in the form of excreta (about 1.67), bank voles assimilate about 11 to 13 kcal per day (Drożdż, 1968).

During pregnancy, the energy demand gradually increases to an average of 23.7 kcal/day/animal at the end of this period. During the lactation period, a drastic increase up to 38.9 kcal/day/animal occurs. The energy requirements in females throughout pregnancy rises by 24%, on the average, while in lactating females by 92% (see section 8.3.1). Food utilization is equal to that in nonbreeding females, and the digestibility coefficent is 88.5% (Kaczmarski, 1966). An increase in energy requirements related to lactating is about 10 kcal of the assimilated energy per gram of weight increment of the young. The energy costs of growth in the nest are low. During the first days of life the young can incorporate into their tissues 60% of the energy intake, 20% at the age of 10—18 days, while less than 5% later (Gębczyński, 1975).

3.2.5. Food Storage

Storing of food by voles for the winter period has been recorded in various parts of their range. The stores are usually small and less diverse than, e. g., those of *Apodemus flavicollis* inhabiting the same areas. Bank voles store food in hollow tree under roots, in bark crevices, under logs, etc. Storing begins in autumn. Hazel nuts (Löhr, 1938; quoted in Ognev, 1950), the lichens *Usnea barbata* and *U. florida,* aspen catkins, maple seeds, and acorns (Sviridenko, 1940; Formozov, 1948; Naumov, 1948), as well as invertebrates e. g. *Mikiola fagi* (Turček, 1953) are commonly stored. In northern coniferous forests, bank voles store cranberries (*Oxycoccus quadripetala*), cowberries, service berries, larch cones, and green grass parts (Ivanter, 1975). Bank vole stores may also contain fallen leaves of the linden, oak maple, and other deciduous trees. These leaves are used in winter not only for food but nest construction and insulation (Ognev, 1950; Turček, 1953).

3.3. Predators

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3.3.1. Proportion of Bank Voles in the Diet of Predators

The bank vole is closely associated with wooded areas. Since many predators prefer cropland and grassland as their hunting grounds, the proportion of these rodents in the diet of avian and mammal predators is not high. The reason for which predators hunt more frequently in open habitats lies not only in greater surface area of these habitats but also in greater numbers of rodents, e. g. common voles living there, and their higher vulnerability to predation in such habitats. The body structure of some predators (e. g. of the long-eared owl) does, however, allow an effective hunting in dense forests (Smeenk, 1972).

The available data indicate that the diet is largely determined by the ratio of open to wooded areas within the hunting area of a predator. The proportion of bank voles is usually higher in the diet of tawny owls having their hunting grounds within forests than in small woods or parks, surrounded with cropland (see Ryszkowski *et al.*, 1971). Even in the diet of the barn owl, the species preferring open areas, the proportion of bank voles markedly varied (from less than 1 to 10%, Czarnecki *et al.,* 1955), depending on whether the hunting grounds of this bird were located within cropland, or bordered on forests. In studies on the diet of predators, usually individuals hunting in forests are not considered as a separate category, thus we present an average proportion of the bank vole in diets of different predators (Table 3.4).

Among the predatory birds and mammals common in Europe, only tawny owls, martens and weasels regularly have in their diet a high proportion of the bank vole (Tab. 3.4). Also foxes and perhaps badgers can consume many bank voles, but the food requirements and the proportion of bank voles in the diet of the latter are not known. Notably, the proportion of bank voles is high in the diet of vipers (Pomianowska-Pilipiuk, 1974), but these are not common predators. Other predators (Table 3.4) feed on bank voles rather occasionally.

Table 3.4.

Proportion of bank voles in the diet of different predators.

Predator species	Per cent bank vole in the diet	Reference[1]	Daily consumption (g/day ind.)	Reference[1]	Biomass of voles consumed (g/day ind.)
Asio otus	1.2	4,11,17,26	35	18	0.4
Strix aluco	16.0	1,7,8,11,17,26	54	18	8 6
Tyto alba	1.0	3,7.9,11,12, 13,15,20,26	57	18	0.6
Buteo sp.	1.0	6,25	85	18	0.8
Lanius excubitor	0	27			
Corvus frugilegus	0	26			
Vulpes vulpes	1.0	16,21	470	18	4.7
Meles meles	<1.0	2,14	700[2]		7.0
Mustela nivalis	9.0	23	30	18	2.7
Mustela putorius	0	16			
Mustela vison	0	10			
Martes sp.	7.0	5,16,24	190	18	13.3
Felis catus	1.0	26	300[2]		3.0
Vipera berus	46.9	22			0.7

[1] 1— Southern (1954), 2 — Andersen (1955), 3 — Czarnecki *et al.* (1955), 4 — Czarnecki (1956), 5 — Lockie (1961), 6 — Sládek (1961), 7 — Cais (1963), 8 — Hagn-Meincke (1967), 9 — Schnurre von (1967), 10 — Gerrel (1968), 11 — Thiollay (1968), 12 — Rybář (1969), 13 — Rothkopf, von (1970), 14 — Skoog (1907), 15 — Ruprecht (1971), 16 — Rzebik-Kowalska (1972), 17 — Smeenk (1972), 18 — Ryszkowski *et al.* (1973), 19 — Schnurre, von & Bethge (1973), 20 — Štasný (1973), 21 — Goszczyński (1974b), 22 — Pomianowska-Pilipiuk (1974), 23 — Erlinge (1975), 24 — Goszczyński (1976), 25 — Truszkowski (1976), 26 — Goszczyński (unpubl.), 27 — Goszczyński & Truszkowski (unpubl.).

[2] Approximate estimate.

There are some doubts concerning the so-called preference for the bank vole by predators. Experiments out-of-doors have shown that such small mammals as *C. glareolus*, *Microtus agrestis* and *Apodemus silvaticus* are caught by weasels without preference (Erlinge, 1975). Tawny owls hunting for bank voles and *A. sylvaticus* occurring at similar densities in wooded areas without shrubs and herbs showed preference for *A. sylvaticus* (Southern and Lowe, 1968). An opposite preference was noted in the pine marten. Common voles and bank voles were much more frequent in their diet than mice, although trapping indicated that mice were most abundant (Lockie, 1961). Also vipers prefer bank voles in the areas where *A. agrarius* is more abundant (Pielowski, 1962; Pomianowska-Pilipiuk, 1974).

Further studies are needed to determine the effect of the hunting method, size of predators, and the mobility of the prey on the diet of predators.

3.3.2. Preference for Bank Voles Differring in Sex, Age and Migratory Status

An analysis of the sex ratio in bank voles preyed upon by owls has shown that these predators do not select for sex. According to Southern and Lowe (1968), the proportion of males in the bank vole population was 57.6%, as compared with 56.5% in the tawny owl diet. Also the results obtained by Simeonov (1971) show that the male to female ratio in the rodents preyed upon by owls is the same. The aviary experiments carried out by Smirin (after Iličev, 1975), demonstrated that long-eared owl hunt more frequently for more active rodents. Although males seem to be more active, as indicated by their higher trappability (Andrzejewski *et al.*, 1967), pregnant and lactating females have to search for food more frequently. Consequently both sexes can be equally available to predators. Predators, however, show preference for some size- or age-classes of the bank vole. Birds of prey hunting by day or by night generally catch the prey moving on the ground surface, thus rodents heavier than an average individual in the population (Goszczyński, 1977). Southern and Lowe (1968), showed no preference for different size classes, but these results do not contradict this as these authors considered only the trappable part of the population. The lack of very small rodents in the diet of owls and birds of prey hunting during day light has also been indicated by Simeonov (1971), Ryszkowski *et al.* (1973), and Goszczyński (1977). Cats also presumably prey on bank voles caught on the surface.

It has been found (Andersen, 1955; Skoog, 1970; Goszczyński, 1972, 1977) that some predatory mammals such as badgers, foxes, and some martens capture many young common voles. Thus it might be expected that they also catch some young bank voles. It should be remembered, however, that digging out the young from their burrows is much more difficult in woodland than in cropland (Skoog, 1970). Probably animals which occasionally eat rodents, for example, wild boars, dig out the young from their burrows.

Such predators as weasels (mostly females), due to their small body sizes, can enter burrows and nests (Erlinge, 1975). In this case it may be suggested that particular age-classes of the prey population are taken in similar proportions. Also the diet of vipers includes young rodents, therefore they can hunt for bank voles in their burrows. It is not known, however, whether different age-classes are preyed upon in proportion to their numbers, as it was not possible to identify the species of the young (adults were identified) found in the diet of vipers (Pomianowska-Pilipiuk, 1974). There is no information on the effect of predation by insectivores on rodents. These animals are abundant and they enter the burrows of rodents, thus may well account for the considerable nesting mortality in the bank vole.

Pielowski (1962) and Pomianowska-Pilipiuk (1974) suggest that most of the bank voles caught by vipers are migrants. The same is suggested with reference to predation by owls in aviary experiments (Metzgar, 1967; Iličev, 1975).

In short, predation on different age-classes of bank voles depends on the number and composition of predators in the habitat, as well as on the processes occurring in prey populations (e. g. increased migrations).

3.3.3. The Rate of Predation on Bank Voles

Territories of predators can consist of a mixture of woodland and cropland habitats, and their densities are usually estimated per unit of such heterogenous areas. To estimate the effect of predators on the bank vole, however, we need information on the number of predators hunting in the wooded areas. For example, if the density of tawny owls in the Turew region has been estimated to be 13.6 individuals/31 km^2, we should take into account that these owls preyed upon bank voles only within an area of about 4 km^2 covered with woods. Therefore, there were 3.4 owls per km^2 of wooded areas. Knowing this figure and also the average biomass of the voles consumed by one predator (Table 3.4), we can estimate the number of rodents consumed (Table 3.5).

Not all the species of predators listed in Table 3.4, have to occur in a given area, but the most important (tawny owls, foxes, weasels, martens) are typical of most habitats. The number of predators and the proportion of the bank vole in their diet can vary. Nevertheless, this table provides an approximate characteristic of the possible consumption. The estimated biomass of the bank voles removed from the population by predators over a year varies between 303 and 809 g/ha. A comparison of these figures with the production of bank vole populations (244 — — 3265 g/ha year), according to different authors quoted in Petrusewicz and Hansson (1975), shows that the potential impact of predators is high. And it should be remembered that bank voles are presumably also reduced by predators not considered here, such as crows, shrews, wild boars, and vipers.

The estimate of the impact of only one predator, the tawny owl, confirms a significant role of predators in reducing bank vole populations. Southern and Lowe (1968) individually marked rodents with ear-tags. Analysing the content of owl pellets they found that tawny owls removed at least 6.8% of the tagged bank voles. This figure underestimates since it was not possible to find all the pellets in the forest. In studies dealing with the effect of tawny owls on a bank vole population living in a small (100-ha) wood, it has been found that these predators consume about 45% of all the voles (Ryszkowski *et al.*, 1971).

Table 3.5

Biomass of bank voles consumed by predators (g/km²).

Predator species	Density of predators (indiv./km²)	Reference[1]	No. of predators per 1 km² of wooded area	Reference[1]	Biomass of voles consumed (g/day /km²)
Asio otus	0.2	13	1.4	13	
	0.06	1	2.0—4.0	7	0.6—1.6
Strix aluco	0.44	13	3.4	13	
			10.0	3	29.2—86 0
Tyto alba	0.25	13	1.9	13	1.1
	0.03	1			
Buteo sp.	0.95	12	7.2	12	5.8
	0.1				
	1.0				
Vulpes vulpes	0.8	13	6.4	13	
	0.3	10	1.5—6.0	9	7.0—30.1
Meles meles	0.2	13	1.4	13	
			0.1—2 0	8	0.7—14.0
Mustela nivalis	3.1—11.2	2	3.1—11.2	2	
			7.0—19.0	6	8.4—51.3
Martes sp.	0.27	13	2.1	13	27.9
	0.1—0.2	4			
	0 1	11			
Felis catus	0.8	13	0.8	13	
	1.3	11	1.3	11	2.4—3.9
					83.1—221.7

[1] 1 — Ferianc (1962), 2 — Southern (1964), 3 — Southern & Lowe (1968), 4 — Nasimovich (1973), 5 — Tomek (1973), 6 — Erlinge (1974) — number of weasels present in the study area, 7 — Iličev (1975), 8 — Sumiński (1975), 9 — Lloyd *et al.* (1976), 10 — Pielowski (1976a), 11 — Pielowski (1976b) — shooting data, 12 — Truszkowski (1976), 13 — Goszczyński (1977).

In the areas where bank voles coexist with fluctuating common vole populations, predators can limit bank vole numbers when the density of the common vole is low (Ryszkowski *et al.*, 1973). When the densities of the common vole are high, almost all predators switch to the "field" diet, and populations of forest rodents, including bank voles, being free from their limiting impact, increase in numbers (Ryszkowski *et al.*, 1973). Such a differentiation of the pressure shows that predators are able to search in an active way for buffer food, when their main food, the bank vole, is scarce.

The impact of predators on bank vole populations inhabiting large forests is unknown. In view of the fact that other prey species occurring in these forests do not undergo such violent fluctuations as common vole populations in agrocoenoses, it is possible that the impact of predators on the bank vole may be more stable.

4. INVERTEBRATES ASSOCIATED WITH THE BANK VOLE

4.1. Arthropod Communities

Ryszard HAITLINGER

The number of arthropod species that permanently, periodically, or occasionally occur on *Clethrionomys glareolus* is enormous and far from being well known, particularly in the case of occasional froms.

There are many papers on this subject for central Europe, including Poland, generally dealing with representatives of a single order or even family (e. g., *Trombiculidae*). They usually contain scarce ecological information, and only some of them broadly discuss relationships among parasites, their hosts, and environmental conditions (Rosicky & Černy, 1956; Mrčiak, 1958, 1963; Daniel, 1957, 1961; Kepka, 1964; Mahnert, 1971a, 1971b; Haitlinger, 1976a, 1976b, 1977c, and others).

The number of arthropod species occurring in nests of the bank vole is even higher and the knowledge of this group is very poor (Mrčiak *et al.*, 1966; Vysotskaya, 1974). But particularly scarce data exist on the entire communities of arthropods associated with the bank vole (Vysotskaya, 1974; Haitlinger, 1977b). Arthropod communities (observed in different years over successive months) occurring on the bank vole are predominated by *Acarina*. Also the number of species is the highest in this order. For example, in the Sowie and Pieniny mountains ranges in southern Poland, where the parasites of this rodent were most intensely studied, *Acarina* can account for even more than 70% of the community (Fig. 4.1). The most abundant species of *Acarina* belong to the family *Trombiculidae* (e. g. in the Pieniny, they account for more than 50% of the arthropod community), but their numbers vary greatly from one area to another. The lowest proportion of the community is represented by *Ixodides* (Fig. 4.1). The number of arthropod species known to be associated with the bank vole in Poland is 142. They consist of 29 species of *Siphonaptera*, 7 species of *Anoplura*, and 106 species of *Acarina* (Tables 4.1 and 4.2). They differ in the degree of their dependence on the host. They can be classified into three biological groups: host dwellers, host-nest dwellers, and nest dwellers. These groups are distinguished according to the criteria given by Vysotskaya (1967) and modified by Haitlinger (1981). The most abundant species on the bank vole belong to the group of host dwellers and host-nest dwellers, but the highest faunal diversity was recorded for the group of nest dwellers (Table 4.2).

4.1.1. The Group of Host Dwellers

In Poland, 14 species of host-dwelling arthropods were noted on bank voles inhabiting the Sowie mountains (Haitlinger, 1977b) and 12 species on bank voles in the Pieniny (Haitlinger, 1974a, 1974b, 1983). Among them, typical of the bank vole are *Laelaps clethrionomydis* and *Polyplax hannswrangeli*. Some of the other species occur only on representatives of the genus *Clethrionomys* (*H. edentula*). Most of them occur only on *Microtidae*, but some are typical of the hosts of other taxonomic groups. The frequency of the occurrence of the latter species of arthropod on the bank vole is likely to correspond to the frequency of contacts with their respective hosts (mostly dead) or with their nests; *Laelaps hilaris*. or *L. agilis* is an example. This happens on rather rare occasions (Haitlinger, 1976b). Two species of the host dwellers; *Hoplopleura edentula* and *L. clethrionomydis,* usually predominate arthropod communitis and play an important part in the community dynamics (Table 4.3).

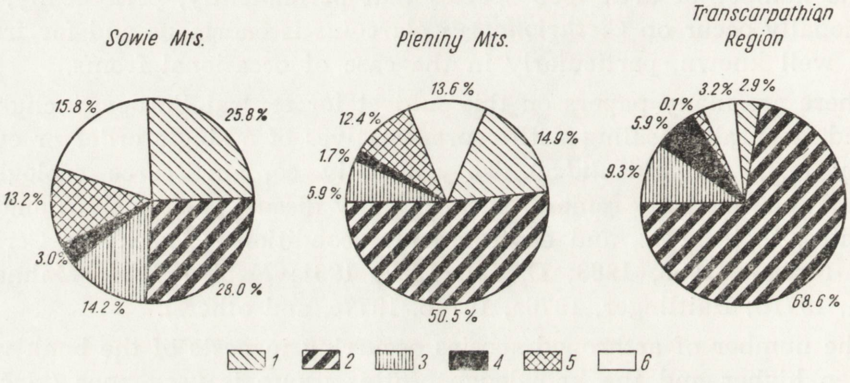


Fig. 4.1. Proportion of six groups in arthropod communities infesting bank voles in different mountain areas.
Sowie Mts. after Haitlinger, 1977; Pieniny Mts. after Haitlinger, 1974a; 1974b, and 1983; Transcarpathian Region after Vysotskaya, 1974, 1 — *Mesostigmata*, 2 — *Trombidiformes*, 3 — *Sarcoptiformes*, 4 — *Ixodides*, 5 — *Anoplura*, 6 — *Siphonaptera*.

Table 4.1

Check-list of the host dwelling and host-nest dwelling arthropods on the bank vole in Poland.

Host-nest dwelling arthropods

Siphonaptera

Ctenophthalmus agyrtes (Hell.)
Ctenophthalmus assimilis (Tasch.)
Ctenophthalmus congener Roths.
Ctenophthalmus uncinatus (Wagn.)
Ctenophthalmus solutus Jord., Roths.
Ctenophthalmus obtusus Jord., Roths.
Ctenophthalmus bisoctodentatus Kolen.
Peromyscopsylla fallax (Roths.)
Peromyscopsylla bidentata (Kolend.)
Peromyscopsylla silvatica (Mein)
Rhadinopsylla pentacantha (Roths.)
Rhadinopsylla integella Jord., Roths.
Megabothris turbidus (Roths.)
Megabothris walkeri (Roths.)
Megabothris rectangulatus (Wahlg.)
Amalareus penicilliger (Grube)
Amalareuls arvicolae Ioff
Palaeopsylla soricis (Dale)
Palaeopsylla similis Dampf
Palaeopsylla steini Jord.
Nosopsyllus fasciatus (Bosc)
Hystrichopsylla talpae (Curtis)
Hystrichopsylla orientalis Smit
Doratopsylla dasycnema (Roths.)
Leptopsylla segnis (Schon.)
Atyphloceras huperum (Jord.)
Monopsyllus sciurorum (Schrank)
Ceratophyllus gallinae (Schrank)
Ceratophyllus garei Roths.

Ixodides

Ixodes ricinus (L.)
Ixodes trianguliceps Bit.
Ixodes apronophorus Schul.
Dermacentor reticulatus (Fabr.)

Acarina

Mesostigmata

Androlaelaps fahrenholzi (Berl.)
Androlaelaps casalis (Berl.)
Eulaelaps stabularis (Koch)
Haemogamasus nidi Mich.
Haemogamasus hirsutus Berl.
Haemogamasus horridus Mich.
Haemogamasus hirsutosimilis Willm.
Myonyssus rossicus Breg.
Hirstionyssus isabellinus (Oud.)
Hirstionyssus sunci Wang
Hirstionyssus soricis Türk

Trombidiformes

Neotrombicula zachvatkini Schlug.
Neotrombicula inopinata (Oud.)
Neotrombicula autumnalis (Shaw)
Neotrombicula talmiensis Sching.
Neotrombicula earis Kepka
Neotrombicula japonica Tan., Kaiwa, Teram., Kag
Neotrombicula nagayoi Sasa, Hay., Sato, Miura, Asah.
Neotrombicula vulgaris Schlug.
Neotrombicula multisetosa Willm.
Cheladonta costulata (Willm.)
Ascoschoengastia latyshevi (Schlug.)
Miyatrombicula muris (Oud.)

Sarcoptiformes

Glycyphagus hypudei (Koch)
Xenoryctes krameri (Mich.)
Xenoryctes punctatus Fain
Orycteroxenus soricis (Oud.)

Host dwelling arthropods

Anoplura

Hoplopleura edentula Fahr.
Hoplopleura acanthopus (Burm.)
Hoplopleura affinis (Burm.)
Polyplax hannswrangeli Eichler
Polyplax borealis Ferris
Polyplax serrata (Burm.)
Polyplax spinigera (Burm.)

Acarina

Mesostigmata

Laelaps clethrionomydis Lange
Laelaps hilaris Koch
Lalaps agilis Koch
Laelaps pavlovskyi Zachv.
Hyperlaelaps microti (Ewing)

Trombidiformes

Radforida lemnina (Koch)
Myobia musculi (Schrank)
Protomyobia claparedei (Poppe)
Amorphacarus elongatus (Poppe)

Sarcoptiformes

Myocoptes japonensis Radf.
Myocoptes musculinus (Koch)
Trichoecius tenax (Mich.)
Listrophorus brevipes Dub.

The occurrence of *H. edentula* in Poland probably corresponds to the distribution of the bank vole (Haitlinger, 1976a; Cais, 1977). In mountain areas, the extent of invasion of bank voles by *H. edentula* ranges from 25% (the Sowie Mountains) to 34% (the Pieniny Mountains, pooled data for two years). The abundance of this parasite undergoes large annual fluctuations (Fig. 4.2). Peak numbers are reached in May, June (Haitlinger, 1974a, 1976a), and in high mountains (the Alps) in July (Mahnert, 1971a). In the other months the number of *H. edentula* varies considerably. There are few literature data on the long-term mean intensity of infestation of bank voles with *H. edentula*. In the Sowie Mountains it was 1.3 (Haitlinger, 1976a), in the Pieniny 2.0 (Haitlinger, 1974a), and in the Alps 1.8 (Mahnert, 1971a). Although this species belongs to the group of dominants, it rarely occurs in large

Table 4.2

Check-list of the nest dwelling arthropods found on the bank vole in Poland.

Acarina

Mesostigmata

Veigaia kochi Tragh.
Veigaia nemorensis (Koch)
Macrocheles glaber (Müll.)
Macrocheles montanus Willm.
Macrocheles muscadomesticae (Scop.)
Macrocheles tridentinus (G et R. Canes.)
Geholaspis longispinosus (Kram.)
Neopodocinum mrciaki Selln.
Holoparasitus excipuliger (Berl.)
Holoparasitus intermedius (Holz.)
Holoparasitus pseudoperforatus (Berl.)
Parasitus kraepelini (Berl.)
Parasitus lunulatus (Müll.)
Parasitus remberti (Oud.)
Parasitus distinctus (Berl.)
Pergamasus alpestris (Berl.)
Pergamasus runciger (Berl.)
Pergamasus longicornis Berl.
Pergamasus crassipes (L.)
Pergamasus quisquiliarum (G. et. R. Canes)
Pergamasus runcatellus Berl.
Pergamasus brevicornis Berl.
Pergamasus septentrionalis (Oud.)
Poecilochirus necrophori Vitzt.
Cyrtolaelaps mucronatus (G. et R. Canes)
Cyrtolaelaps minor Willm.
Euryparasitus emarginatus (Koch)
Hypoaspis sardoa (Berl.)
Hypoaspis heselhausi Oud.
Alloparasitus oblongus (Halb.)
Proctolaelaps pygmaeus (Müll.)
Pachylaelaps furcifer Oud.
Olopachys suecicus Selln.
Platyseius italicus (Berl.)
Ameroseius corbicula (Sowerby)
Typhlodromus meridionalis Berl.
Eviphis ostrinus (Koch)

Trombidiformes

Pygmephorus forcipatus Willm.
Pygmephorus spinosus Kram.
Pygmephorus soricis Krczal
Pygmephorus erlangensis Krczal
Pygmephorus krczali Mahun.
Bakerdania cultrata (Berl.)
Bakerdania bavarica (Krczal)
Bakerdania sellnicki (Krczal)
Bakerdania amplus (Krczal)
Eucheyletia flabellifera (Mich.)
Cheyletus eruditus (Schrank)

Sarcoptiformes

Acarus farris (Oud.)
Acarus siro (L.)
Acotyledon pedispinifer (Nesb.)
Anoetus sapramyzarum (Dufour)
Wichmannia spinifera Mich.
Belba corynopus Hern.
Belba verticillipes Nic.
Nothrus silvestris Nic.
Platynothorus peltifer Koch
Tyrophagus humerosus Oud.
Mycetoglyphus fungivorus Oud.
Bonomoia sphaerocerae Vitzt.

numbers on individual hosts. In the Sowie Mountains, the maximum number of *H. edentula* collected from single bank voles was 68, and more than 30 individuals were collected only four times; in the Alps the maximum was 54 (Mahnert, 1971a).

In the older literature, *H. acanthopus* is quoted as one of the species most frequently infesting the bank vole. The cause was that *H. edentula* and *H. acanthopus* were not distinguished at that time. Probably a large majority of the earlier records of *H. acanthopus* on the bank vole refer to *H. edentula*. But in some parts of Europe, e. g. in Hungary, *H. edentula* are absent from bank voles, instead *H. acanthopus* are noted (Haitlinger, 1973b).

Table 4.3

Check-list of dominant species in arthropod communities associated with the bank vole in different mountains.

	Sowie Mts.	Pieniny Mts.
Eudominants more than 15% of the community	*Neotrombicula zachvatkini*	*Neotrombicula zachvatkini* *Neotrombicula autumnalis*
Dominants 5.1—15% of the community	*Ctenophthalmus agyrtes* *Laelaps clethrionomydis* *Haemogamesus nidi* *Neotrombicula inopinata* *Glycyphagus hypuadei* *Hoplopleura edentula*	*Neotrombicula inopinata* *Glycyphagus hypuadei* *Hoplopleura edentula*
Subdominants 2.1—5% of the community	*Peromyscopsylla bidentata* *Peromyscopsylla silvatica*	*Ctenophthalmus agyrtes* *Megabothris turbidus* *Amalareus penicilliger* *Peromyscopsylla bidentata* *Neotrombicula talmiensis* *Leptotrombidium europaeum* *Laelaps clethrionomydis* *Haemogamasus nidi*

There is much less information on *P. hannswrangeli* and *P. borealis.* In central Europe they occur almost exclusively in mountains, rarely in large numbers. Smetana (1962) found a high mean intensity of infestation with *P. hannswrangeli* in the Tatra Mountains, Czechoslovakia, is 1.9. Cais (1977) rather frequently recorded this parasite on bank voles living in the Polish part of the Tatras. Also *P. borealis,* which is a particularly rare species in Europe, under favourable conditions can be rather numerous on bank voles. In the Polish Tatras, it has been proven to be more abundant than *P. hannswrangeli* (Cais, 1977).

So far there has been no satisfactory explanation for the relationship between the intensity of infestation and habitat type of the bank vole.

In the Alps, *H. edentula* and *P. hannswrangeli* usually occurred on the bank voles inhabiting the subalpine and alpine zones (Mahnert, 1971a). In Polish mountains (the Tatra and Sowie mountains) high numbers of *H. edentula* were noted in different zones (Haitlinger, 1976a; Cais, 1977).

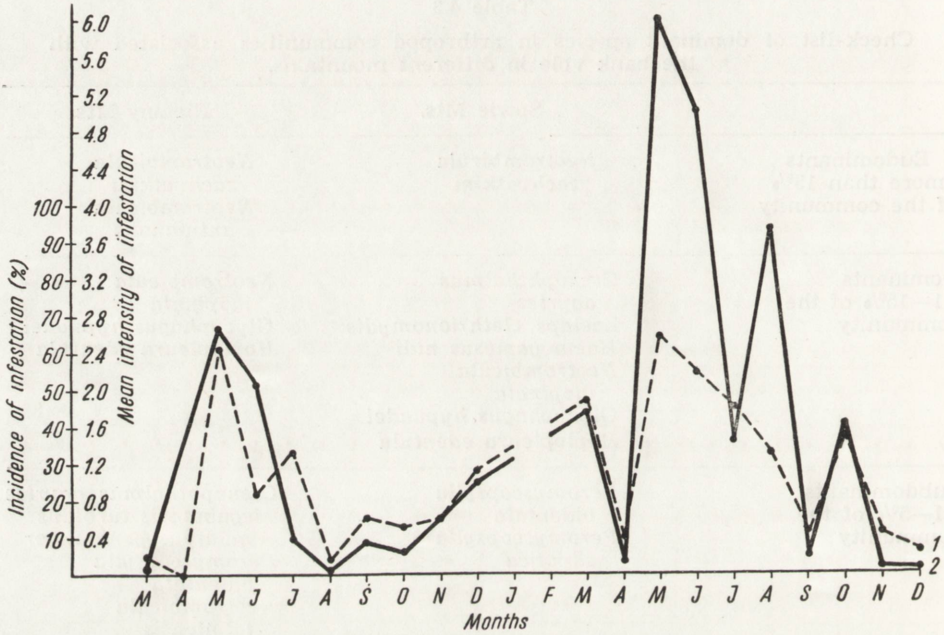


Fig. 4.2. Incidence of infestation (1) and mean intensity of infestation (2) with *Hoplopleura edentula* in a bank vole population in the Sowie Mountains (after Haitlinger, 1976).

To some extent the intensity of infestation depends on the sex of the host. The data are scarce, however, and refer to some months. For example, in the Sowie Mountains the intensity of infestation of bank voles in July and August was 3.3 for females and as much as 8.0 for males. But in May and June no differences were recorded (Haitlinger, 1976a).

In larger mountain ranges, *L. clethrionomydis* is a dominant among host dweller. This parasite of the bank vole also occurs on *Clethrionomys rufocanus* (Sund). and *Microtus gregalis* (Pall.) in some parts of northern Europe and Siberia (Edler, 1968; Edler and Mehl, 1972). In the arthropod community living on bank voles in the Sowie Mountains, *L. clethrionomydis* is the third most numerous. It is abundant only from March to May (Mahnert, 1971b; Haitlinger 1976b) and to a lesser extent also in autumn. In low mountains, this species is sparse; in the Pieniny the mean intensity of infestation for two years was merely 0.55 (Haitlinger, 1983). In high mountains it can be more than 1.0 (Mahnert, 1971b; Haitlinger, 1976b). The abundance of this species in successive months of different years can vary greatly, even by a factor of six. It is rarely numerous on single hosts, the maximum recorded being 62.

The species of the host-dweller group significantly affect the arthropod community dynamics on the bank vole, particularly in mountains areas (the presence of *L. clethrionomydis* and some species of lice). In the Sowie Mountains they account for 26.3% of the community but in the Pieniny only for 16.9% (Haitlinger, 1974a, 1974b, 1976b, 1983).

4.1.2. Nest-host Dweller Group

The nest-host wdeller gropu generally consists of more species than the host wdeller group. For example, in the Sowie Mountains, 33 species were recorded and in the Pieniny 36 species (Haitlinger, 1974a, 1974b, 1977b, in print). *Siphonaptera* are abundantly represented on the bank vole and is more diversified than that on other rodents (Haitlinger, 1971b, 1973a, 1978; Bartkowska, 1973, 1981). At the same time, none of these species is characteristic of the bank vole, and only some are more abundant on the bank vole than on other mammals. Particularly clear difference in the flea fauna occurs between bank voles inhabiting lowland and mountain areas; the latter are dominated by mountain species, and in the Tatra Mountains also by alpine-boreal species (Bartkowska, 1973). The lowland fleas of Poland are dominated by *Ctenophthalmus agyrtes* and *Megabothris turbidus* (Haitlinger, 1977c). In the foothill region and in the mountains, also *Amalareus penicilliger* and *Peromyscopsylla bidentata* are abundant, and in some mountains *P. silvatica* (Haitlinger, 1973a; Bartkowska, 1973; Ryba *et al.*, 1975). Bank voles living in the High Tatra are heavily parasitized with *Megabothris rectangulatus* (Bartkowska, 1973).

Many *Siphonaptera* occur seasonally. They have an important influence on the dynamics of bank vole infestation with arthropods but only during a few (sometimes 1-2) months. For example, out of 15 flea species collected in the Sowie Mountains, only six are abundant throughout the year or in some seasons of the year (Haitlinger, 1975). The reduction in the number of species is coupled with an increase in the intensity of invasion. In spring, nine species were recorded, and the mean infestation intensity was chiefly related to the abundance of only one species, *Ctenophthalmus agyrtes,* which accounted for 62% of the flea community at that time. In summer (July-September), *Peromyscopsylla silvatica* was dominant (56.6% of fleas), and in autumn, when the unmber of species increased to 15, *P. bidentata* (43.1%) (Fig. 4.3). There may be large annual differences in the composition of dominant

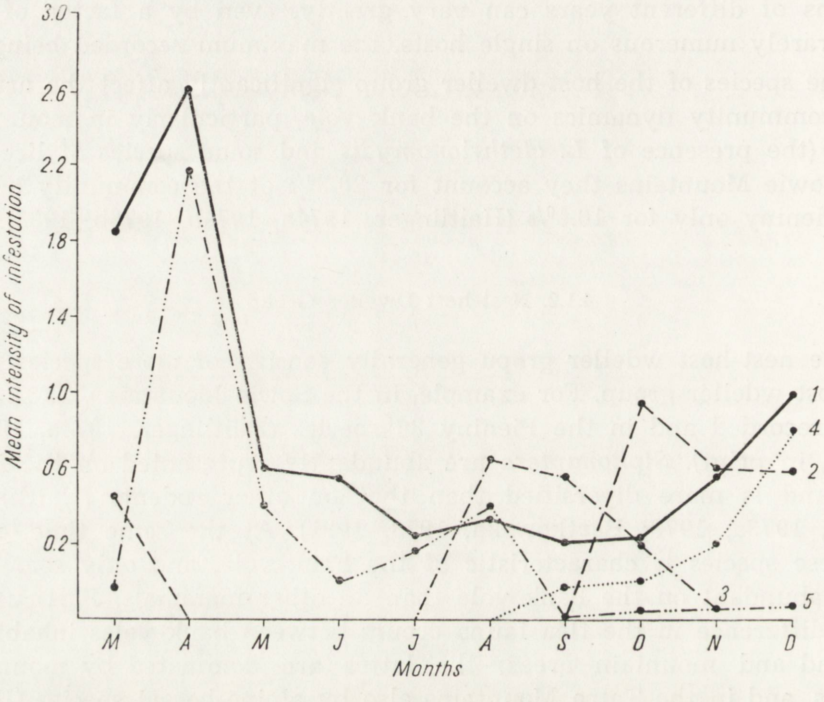


Fig. 4.3. Seasonal changes in the mean intensity of infestation of bank voles by the most common flea species.
1 — *C. agyrtes,* 2 — *P. bidentata,* 3 — *P. silvatica,* 4 — *R. integella,* 5 — *C. congener.*

species. The mean annual intensity of infestation of the bank vole with fleas is not high; in Poland it ranges from 1.0 to 2.0 (Haitlinger, 1971a, 1971b, 1973a, 1974b, 1975, 1978; Bartkowska, 1981). A highest mean value of 2.0 was recorded in urban areas (Haitlinger, 1971a). It is possible that the intensity of infestation of the bank vole declines with altitude. The mean intensity of infestation of the populations living in the western Sudetes and Żywiec Beskids, mostly between 900 and 1500 m above sea level, was 0.87 and 1.04, respectively. For the populations living in the Pieniny and Sowie mountains at an altitude of

300—900 m above sea level, it was 1.41 and 1.58, respectively. In the Western Beskids, the average for bank voles living at very different altitudes was 1.23. Species diversity increases from lowland to mountain areas, but only to about 1000 m above sea level.

Both intensity and extensity of flea infestation can depend on the sex of the host. Generally males are more heaviely parasitized than females (Brinck, 1966; Mahnert, 1972; Brinck-Lindroth, 1968). For example, in the Sowie Mountains the mean annual extensity of infestation of male bank voles with fleas was higher than that of females by 11.7% (Haitlinger, 1975). Also the intensity of infestation was higher for males. But these relations can vary from one month to another (Haitlinger, 1975). The extent and intensity of infestation and also the composition of flea communities vary with the age of the bank vole (George & Corbet, 1959; Ulmanen & Myllymäki, 1971). In Poland, these relationships were analysed for two age groups distinguished by body weight for males and females separately. In the Sowie Mountains, the mean annual intensity of infestation was 1.8 for old and 1.2 for young bank voles; the respective figures in the Pieniny Mountains were 1.7 and 0.9 (Haitlinger, 1974b, 1975). In Poland, the most frequent mites of the nest-host dweller group occurring on the bank vole consist

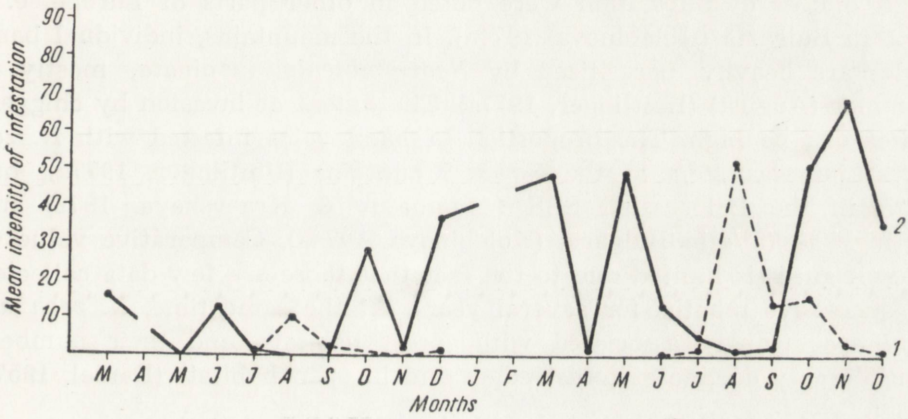


Fig. 4.4. Sasonal changes in the mean intensity of infestation with *Neotrombicula inopinata* (1) and *N. zachvatkini* (2) for bank voles in the Sowie Mountains (after Haitlinger, 1977a).

of *Eulaelaps stabularis, Haemogamasus nidi, Hirstionyssus isabellinus, Neotrombicula zachvatkini, N. inopinata, N. talmiensis, Leptotrombidium europaeum, Glycyphagus hypuadei,* and *Xenoryctes krameri.* Some of them are abundant only in certain regions of Poland (e. g. *N. talmiensis* and *L. europaeum* in south-eastern nad eastern parts). Of all these species. *N. zachvatkini* and *G. hypuadei* have an important effect on the dynamics of arthropod communities in the lowland and mountain areas, as does *N. inopinata* in the mountains. In particular, chigger-mites (*Trombiculidae*) have specific environmental requirements. In forests of Poland there are mass appearances of *Neotrombicula zachvatkini* in spring and summer (Fig. 4.4). In the Sowie Mountains the mean intensity of infestation for two years was 2.0 (Haitlinger, 1977a). Particularly high indices of infestation were noted in other parts of Europe, e. g. 40.1 in Bulgaria (Kolebinova, 1974a). In the mountains, individual bank voles are heavily parasitized by *Neotrombicula inopinata,* mostly in summer (August) (Haitlinger, 1977a). The extent of invasion by chigger-mites can be high. The proportion of bank voles infested with *N. zachvatkini* was 26⁰/₀ in the Sowie Mountains (Haitlinger, 1977a), but 57⁰/₀ in the Belorussian SSR (Arzamasov & Kraevskaya, 1972) and as high as 75⁰/₀ in Bulgaria (Kolebinova, 1974a). Comparative value of these figures is limited due to the fact that there are few data collected in successive months for several years. At the same time, *N. zachvatkini* are strongly associated with forest habitats, and their numbers considerably decline at forest edges and in open habitats (Daniel, 1957).

4.1.3. Nest Dweller Group

This group of arthropods contains the greatest number of species. Occasionally some of them can be found on the host. Their appearance on the host is usually based on phoretic alliances. For example, in the Sowie Mountains, 42 species of this group were recorded from the host, and in the Pieniny, 23 species. Obviously, the number of mite species in the nest itself is much higher (Vysotskaya, 1974). Two species of the family *Parasitidae* are rather often found on bank voles. These are *Parasitus kraepelini* nad *P. lunulatus* and, quite frequently, unidentified deutonymphs of different species (Haitlinger, 1977a). The number of nest dwelling arthropods recorded from the bank vole continue to increase with growing research effort. The total abundance of these mites on bank voles is low and does not account much for fluctuations in the mean intensity of infestation of these rodents by the entire arthropod community.

4.1.4. Seasonal Occurrence of *Acarina*

The occurrence of many mites is seasonal. As a result, there are quantitative and qualitative differences in the infestetion of bank vole populations from month to month (Fig. 4.5). Invasions of arthropods, as measured by the mean intensity of infestation, are highest in spring. This is related to low host numbers at that time and to particularly abundant appearance of some mite species. In the Sowie Mountains, *Mesostigmata* occurring on bank voles were dominated by *L. clethrionomydis* and *H. nidi* in spring and autumn (in May by *H. isabellinus).* The other mites were dominated by *N. zachvatkini* in spring and autumn, and by *N. inopinata* in August and September. This picture can vary in particular years; in some months dominant species can be different. For example, *I. trianguliceps* may be dominant in April, and *G. hypuadei* in addition to *N. zachvatkini* can dominate from August to December (Haitlinger, 1976b, 1977a). The dominant species may be different in particular parts of Poland (mountains) and Europe. These differences can also be seen on adjacent areas. For example, in the submontane zone of the Sowie Mountains, *I. ricinus* and *G. hypuadei* dominated in spring, while *N. zachvatkini* in the montane zone. In summer and autumn *G. hypuadei* dominated in the submontane zone, while *N. inopinata* (summer) and *N. zachvatkini* (autumn) in the montane zone. The highest mean intensity of infestation of the bank vole, that is 13.3 (with the species of the suborder *Mesostigmata)*, was recorded in March (Sowie

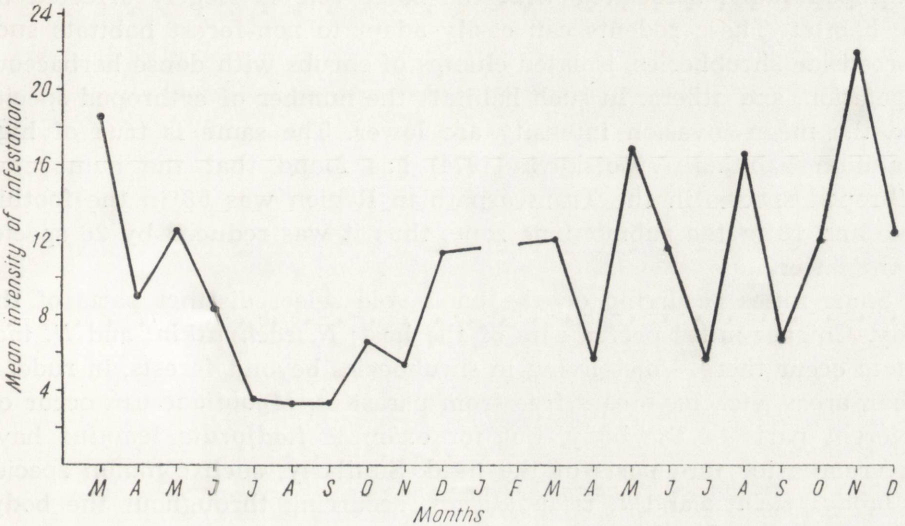


Fig. 4.5. Seasonal changes in the mean intensity of infestation of bank voles with the total arthropod community in the Sowie Mountains (after Haitlinger, 1977b).

Mountains), and minimum numbers in early autumn (0.8 in August, September) (Haitlinger, 1976b).

The peak of mean intensity of invasion by *Trombidiformes* and *Sarcoptiformes* jointly was noted in December (3.8), and in November of 1972, when the infestiation was as high as 18.1. The value of this index is largely influenced by changes in numbers of three species: *N. zachvatkini, G. hypuadei,* and *N. inopinata.* The extent of vole infestation was high in early spring. In the Sowie Mountains in March and April more than 80⁰/₀ of the population was infested with *Mestostigmata* and 60⁰/₀ with *Trombidiformes.* In August and September infestation with *Mesostigmata* considerably declined (Haitlinger, 1976b, 1977a). The arthropod fauna associated with the bank vole is largely affected by the habitat. These rodents can easily adapt to non-forest habitats such as roadside shrubberies, isolated clumps of shrubs with dense herbaceous vegetation, and others. In such habitats the number of arthropod species and the mean invasion intensity are lower. The same is true of high mountain habitats. Vysotskaya (1974) has found that the number of arthropod species in the Transcarpathian Region was 58 in the foothill zone and 18 in the submontane zone, thus it was reduced by 26 species in the latter.

Some mites occurring on the bank vole select distinct parts of the body. Chigger-mites prefer ears of the host; *N. zachvatkini* and *N. inopinata* occur there. Voles living in shrubberies beyond forests, in ruderal urban areas, etc., have ears free from parasites. *Myobiidae* can occur on different parts of the body, but for example *Radfordia lemnina* have preferences for fore parts of the head. Similarly, such common species as *Ixodes ricinus* and *I. trianguliceps,* occurring throughout the body, prefer upper parts of the ears and settle on both sides and the anal region. Most mite species do not show preferences for particular parts of the body.

4.1 5. The Effect of Host Sex and Age on Infestation by Some Mites

The relationship between the rate of infestation and the sex of the host is still unclear. Many factors are probably involved here, and they should be analysed each acarid species separately in successive months of the year. For example, in the Sowie Mountains more of males than females were infested with *I. trianguliceps, I. ricinus, N. zachvatkini,* and *G. hypuadei* over the year. Individual males were more heavily infested with *N. zachvatkini* and *N. inopinata,* while females carried *I. trianguliceps* and *G. hypuadei.* Different relations were observed in various seasons. A higher proportion of females than males was infested with *N. zachvatkini* in autumn and winter (October-December) and in summer (July-September). *G. hypuadei* infested a higher proportion of males than females in all the seasons.

The effect of host age (sometimes measured by host body surface) on the intensity of infestation of bank voles with with mites in not known. Edler (1973) found that subadult bank voles were infested with mites in the highest proportion. Haitlinger (1976b) noticed that the intensity of infestation with *Mesostigmata* in spring (March-June) was highest for the smallest voles. The intensity of infestation of bank voles 80—95 mm long was more than twice as high as that of larger voles. Among the *Mesostigmata* the main parasite of the bank vole in the Sowie Mountains is *L. clethrionomydis,* which is particularly abundant in March. This suggests that this mite is mostly associated with younger (smaller) voles. Similar results were also noted for other mite species. For example, *I. trianguliceps* and *N. inopinata* are most often caught on juvenile males.

4.1.6. Dynamics of Arthropod Communities

Parasitological studies usually consider some selected groups of organisms infesting a host. Studies of whole parasite communities or even ectoparasite communities are extremely rare. Hence the knowledge of the dynamics of arthropod communities on the bank vole is very poor. It is known, however, that more than 80% of the bank voles

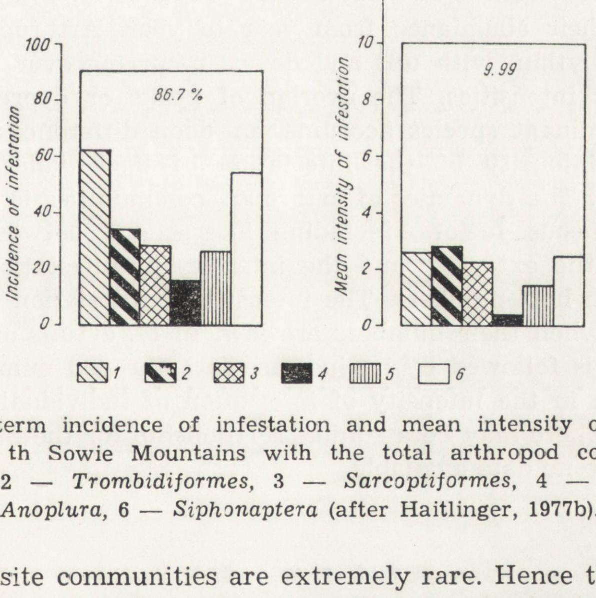


Fig. 4.6. Long-term incidence of infestation and mean intensity of infestation of bank voles in th Sowie Mountains with the total arthropod community: 1 — *Mesostigmata,* 2 — *Trombidiformes,* 3 — *Sarcoptiformes,* 4 — *Ixodides,* 5 — *Anoplura,* 6 — *Siphonaptera* (after Haitlinger, 1977b).

living in best habitats are infested with arthropods (Fig. 4.6). Only in marginal habitats (e. g. in ruderal urban areas) the extent of invasion can be lower (Haitlinger, unpubl. data). In such cases the mean intensity of infestation is also lower. The mean intensity of infestation of bank voles by the entire arthropod community can be compared only for three regione: the Sowie Mountains (Haitlinger, 1977b), the Pieniny Mountains (Haitlinger, 1974a, 1974b, 1983) and the Transcarpathians (Vysotskaya, 1974). There are no comparable data for lowland habitats. In mountain areas the long-term mean intensity of infestation with arthropods of all possible kinds reaches 10.0 (Fig. 4.6) in the Sowie Mountains (Haitlinger, 1977b), 16.6 in the Pieniny (Haitlinger, 1974a, 1974b, 1983), and as much as 67.5 in the Transcarpathian Region (Vysotskaya, 1974). There are clear fluctuations in numbers within and between years. For example, one year in the Sowie Mountains there were two peaks of arthropod numbers on the bank vole, one in March (18.5) and the other in December (11.2), with a low point in August-September (3:3); in the following year four peaks were observed: in March (12.0), May (16.7), August (16.6), and November (22.1), separated by deep depressions in April (5.7), July (5.8), and September (6.9) (Fig. 4.5) (Haitlinger, 1977b). This pattern should be considered as typical in the areas with diversified arthropod communities. It is an effect of rapid monthly changes in numbers of abundant but only seasonally occurring species such as *N. inopinata* and *P. silvatica*, which also markedly change their abundance from year to year. Arthropod dynamics has its own rhythm, with ups and downs recurring over the year but with different intensities. The overlap of peaks or depressions particularly of dominant species accounts for deep differences in both incidence and intensity of the infestation of bank voles within and between years. The dynamics of arthropod communities is regulated by many simultaneous factors, including interactions betwen component species. Both the extensity and the intensity of infestation of rodents also depend on host numbers. The intensity of infestation of individual voles is high when their numbers are low. In *M. arvalis* an increase in host numbers is followed by an increase in arthropod numbers coupled with a decline in the intensity of infestation of individual voles (Haitlinger, 1981). There may be a similar relationship for the bank vole, but so far there are no data available.

4.2. Dynamics of an Ectoparasite-host System

Stefan M. JANION

The adaptations of parasites can be classified into adaptations to their hosts and adaptation to the environment in which their hosts live. Hence, two types of habitats have been distinguished here: a primary habitat, which is the host itself, and a secondary habitat, in which the host occurs. There are many adaptations and interactions in the parasite--host system. Here we will discuss ecological adaptations in ectoparasites (fleas) related to the organization of host populations (rodents), thus the adaptation of parasites to the primary habitat.

Fleas spend varying amounts of time on their hosts, where they feed on their blood, or in the nests of the hosts, where their larval development occurs, except for some species, e. g. *Tunga penetrans* L. (Labunec *et al*., 1966a).

The number of fleas in nests and shelters of the host is very high, exceeding many times the number of hosts (Gershkovich, 1955). It has been found that the removal of all fleas from the fur of rodents at 24-hour intervals on five consecutive days of capture and release, had no noticeable effect on the proportion of rodents infested or on the number of fleas per host. The number of fleas on the hosts and the proportions of particular flea species remained unchanged throughout the removal experiment (Janion, 1962). It may be concluded, therefore, that during these five days rodents were in permanent contact with places of flea occurrence, and that the removal of fleas from the hosts did not reduce their numbers in host nests.

Essentially, host nests are an inexahaustible source of fleas. The number of fleas varies, however, depending on the number of hosts and their activity. High activity of hosts and their frequent leaving the nest account for a greater "attachment" of fleas to host bodies and a prolonged occurrence on them. For this reason, Ioff and Skalon (1954) and subsequently many other authors distinguished an ecotype of "fleas associated with the fur", that is, occurring longer on the host body, and an ecotype of "fleas associated with the nest", that is, spending more time in host nests than on the hosts themselves.

Host life style has an important effect of the infestation by fleas. For example, there are differences in infestation between migrant and resident rodents. The infestation of migrants is lower, and the species composition of fleas on them is different than on residents (Janion, 1960a, 1960b).

It has also been shown that the mobility of hosts related to changes of nests, even within the same site, accounts for changes in the number of fleas on them. For example, moving from one nest to another during the first period of movements gives rise to a decline in the number of fleas in the fur. After a ten-day stay in the new nest, the number of fleas on the host reaches the level from the period preceding the change (Fig. 4.7) (Janion, 1968).

Factors determining the level of saturation of the habitat on the host, that is, affecting the number of fleas on the host, largely depend

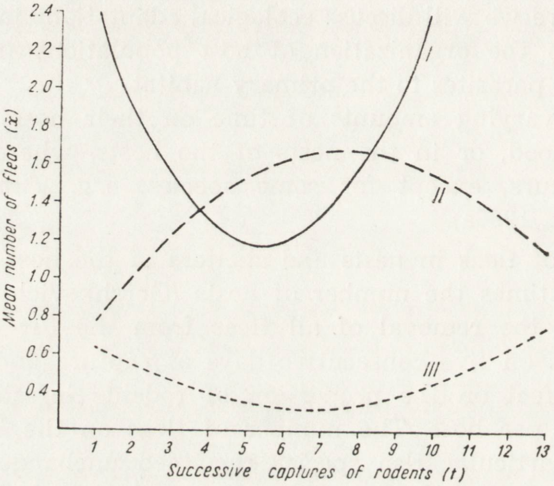


Fig. 4.7. Numbers of fleas on rodents at the continuous capture of fleas (curve II) and at their capture only in the first days of the experiment (curves I and III) (after Janion, 1968).

on the position of the host in the population structure, on the one hand, and on the number of fleas in the host environment, on the other (Janion, 1974). This can be illustrated by changes in the number and composition of fleas over the most lifetime in the wild (Figs. 4.8 and 4.9).

The age of a host, as determined by successive captures on the plot, can be divided into three periods with respect to the structure of infestation with fleas. The first period is when the young rodents leave the nest for the first time in search of food, thus begin to enter traps. At that time they are about 3—4 weeks old. The structure of infestation of these rodents with fleas differs from that in later periods. They are infested only with specific fleas, that is, fleas associated with only one host species. The second period is when the rodents are 4 to 10 weeks old. It is characterized by the appearance of fleas typical of foxes, squirrels, and birds, but not of rodents. In the third period, when rodents are 10 to 18 weeks old, nonspecific fleas do not occur on them, and a lower proportion of rodents is infested as compared with the two preceding periods. It is interesting that the rodents differing by age, that is, by the time of presence on the plot and from which fleas were collected on the same dates and hours of the day, showed age-specific differences in their infestation with fleas. This may imply that the individuals differing by age also differ by the places they visit on the plot, in which they are infested with fleas.

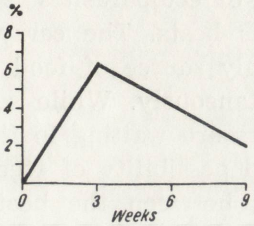


Fig. 4.8. The percentage proportion of nonspecific to specific fleas during August, September, October, November, December, and January (after Janion, 1960b).

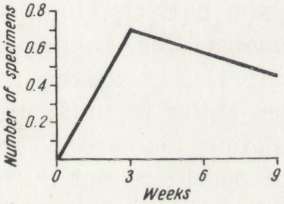


Fig. 4.9. Numbers of nonspecific fleas during August, September, October, November. December, and January (after Janion, 1960b).

The infestation of rodents is also sex-related. Usually males are more heavily infested than females (George & Corbet, 1959; Smith, 1962; Brinck-Lindroth, 1968; Hass, 1969; Ulmanen & Myllymäki; 1971, Peus, 1972; Mahnert, 1972). These authors suggest that the higher infestation of males is related to their higher activity during which they encounter more fleas, as compared with females. This is not a rule, however. Some data indicate that females can be more infested than males, and this depends on age, presence of the young in the nest, etc. (Janion, 1961).

There are also seasonal differences in the infestation of hosts. They are related to seasonal changes in the host population (Ioff & Skalon, 1954; Rosicky, 1957; Skuratowicz, 1964). Other changes in infestation occur when human management causes seasonal disturbances in the habitat of rodents (Czerwińska, 1977).

Changes in the number of hosts, as already noted, are the equivalent of changes in the carrying capacity of flea habitat. An increase in the number of hosts means an increase in available food resources and in the number of nests, in which fleas can reproduce. The opposite is true when the number of hosts decreases. Remarkable changes, both annual and multiannual, in the number of rodents gave rise to the development of specific mechanisms of number regulation in their ectoparasites. As already noted, the number of ectoparasites is many times higher than the actual number of their hosts. The carrying capacity of the host population, which is the only source of food for parasites, is not used by all the parasites simultaneously. While some of them are feeding on the host body, the others are waiting in the habitat of the host for a contact with the host and possibility of feeding. There is a continual circulation of ectoparasites between the host habitat and host body. This process is influenced by the actual structure of the host population, and also by the relation between the size of the host population and flea population (Janion, 1979). In the case when the number of ectoparasites is not significantly higher than the number of their hosts, the distribution of parasites on the hosts is clumped. A certain proportion of the host population remains free from parasites. But when the number of hosts declines in relation to the number of ectoparasites, the distribution of the latter shifts to uniform. The proportion of infested animals in the population increases. The categories of infested rodents, number of parasites per host, and the number of not infested animals depend on the actual structure (organization) of the host population. When the number of hosts continue to decrease in relation to the number of fleas, the rate of the circulation of fleas between the host body and the environment is accelerated. This is the case because the carrying capacity of the host body is limited, and it can "feed" only a limited number of fleas at a time. Staying for a shorter time on the host, fleas suck less blood (Jurkina, 1968). This abbreviation of the host occupancy has serious consequences for female fleas. To reproduce, they need blood not only as food but also as the source of hormones secreted by the host adrenal glands. To get an adequate amount of these hormones, they must spend a sufficiently long time on the host. Otherwise the development of their eggs is inhibited or the eggs undergo resorption (Rotshild & Ford, 1966). Thus, the females that are short of hormones do not lay eggs. The reproduction is inhibited and the size of flea populations is reduced.

This summary of some relationships between rodents and fleas shows that ecological adaptations which evolved in the parasite-host system are highly diversified.

4.3. Ecological Characteristics of Parasitic Worm (Helminth) Communities

Krystyna KISIELEWSKA

4.3.1. General Characteristics of Helminths in Bank Voles

To date, about 80 species of helminths associated with the bank vole have been recorded in the literature over its geographical range. Recent, comprehensive papers concerning taxonomic revision of helminths (mostly nematods) in rodents introduced significant taxonomic changes. A review of these is beyond the scope of this paper and the numerical data given below on the helminth fauna of the bank vole are therefore approximate:

1) 33 species of *Nematoda* (16 genera, 7 families) — 42%
2) 21 species of *Cestoda* (7 genera, 3 families) — 26%
3) 16 species of *Cestoda*-larvae (6 genera, 1 family) — 20%
4) 9 species of *Trematoda* (7 genera, 6 families) — 11%
5) 1 species of *Acanthocephala* — 1%

Thus, the helminth fauna of the bank vole is dominated by nematodes, and their dominance would be even higher (52% of the community) if larval forms of nematodes were eliminated from the calculations, though they are only a taxonomic and not an ecological component of the helminth community.

Most frequently noted in bank voles of at least four European countries are:

Trematoda: *Plagiorchis muris* (Tanabo 1922)
Cestoda: *Catenotaenia pusilla* (Goeze, 1782)
Catenotaenia cricetorum (Kirschenblatt, 1949)
Skrjabinotaenia lobata (Bear, 1925)
Aprostatandrya macrocephala (Douthidt, 1915)
Andrya microti (Erhardova, 1956)
Paranoplecephala brevis (Kirschenblatt, 1938)
Hymenolepsis diminuta (Rudolphi, 1819)

Hymenolepsis horrida (Linstow, 1901)
Rodentolepsis assymetrica (Janicki, 1904)
Nematoda: *Syphacia obvelata* (Rudolphi, 1802)
Aspiculuris tetraptera (Nitzch, 1921)
Heligmosomum costellatum (Dujardin, 1845)
Heligmosomum glareoli (Baylis, 1928)
Heligmosomum polygyrum (Dujardin, 1845)
Heligmosomum halli (Schultz, 1926)
Capillaria muris sylvatici (Diesing, 1851)
Trichocephalus muris (Schrank, 1788)
Mastophorus muris (Gmelin, 1870)
Cestoda (larvae): *Taenia tenuicollis* (Rudolphi, 1819)
Hydatigera taeniaeformis (Batsch, 1758).

These species also occur in other microtins and in murids.

For most of helminths, bank voles are definitive host, being an intermediate host for larval cestodes only. These mature in predatory birds and mammals, the diet of which includes the bank vole.

Developmental cycles of helminths are diversified and include two categories, biohelminths and geohelminths. Biohelminths require at least one intermediate host for the completion of their development, while geohelminths are characterized by so-called "simple" life cycle, that is, without an intermediate host.

Known biohelminth species of the bank vole include: 9 Trematodes, 21 cestodes, 4 nematodes, 1 acanthocephalid, 16 cestode-larvae. The 29 geohelminth species (all *Nematoda*) are: 14 geohelminths (*sensu stricto),* 7 pseudogeohelminths, 8 ageohelminths.

Thus, the helminth fauna of the bank vole is dominated by biohelminths (64%). Then there are geohelminths *s. str.* (17%), ageohelminths (10%), nad pseudogeohelminths (9%).

In this respect, bank voles are closer to insectivorous micromammals than to rodents (Tenora, 1967; Wahl, 1967). The dominance of the parasites reaching the definitive host through the mediation of different invertebrates (myriapods, insects, molluscs) is a good indicator of the richness of the bank vole diet. The helminth fauna of other, more herbaceous, rodents, is dominated by parasites not requiring intermediate hosts.

In bank voles, helminths occupy the stomach, small intestine, large intestine and caecum, while larval nematodes invide the liver, mesentery and body cavity. Gut parasites predominate (64 species, or 80%) for which the bank vole is the definitive host. For larval nematodes (16 species, or 20%), these rodents are intermediate hosts.

Emphasis here is on the ecological (i. e. structural and functional) characteristics of helminthocoenoses living in bank vole populations.

Characteristics of any ecological unit involve: a) a static description, that is, a synthesis of the structure (Kisielewska, 1970), which provides information on which qualitatively different elements are involved, how many they are and in what proportions; and b) a dynamic description, which shows the variability in these elements. The recurrence of changes in time provides evidence for the reality of a given ecological unit and for its homeostasis.

The structure of helminthocoenoses (multispecies parasite communities) associated with the bank vole is characterized by qualitative, quantitative, and spatial relations. Below, the following types of structures will be discussed: (1) taxonomic, (2) biological, (3) topical, (4) spatial, and (5) quantitative.

4.3.2. Taxonomic Structure

The theoretical maximum of associated parasite species is never attained in real host populations as it is limited by an ecological specifity. This is illustrated in Table 4.4, of the alimentary canal helminths of Polish bank voles (Kisielewska, 1970).

Table 4.4.
Helminths of the alimentary canal of Polish bank voles (after Kisielewska, 1968). Number of species is shown

Theoretical maximum for Poland	Helminths	Tape-worms	Nematodes	Trematodes
	19	8	10	1
Białowieża National Park	10	4	5	1[1]
Leśno	6	3	3	—
Mikołajki	8	4	3	1
Ojców	5	2	3	—

[1] Unknown species.

The taxonomic structure of helminths infecting individual bank voles can be largely difersified. All its variants, however, are a combination of the species composition of helminths occurring in a given population of the bank vole (Kisielewska, 1970). The helminthocoenosis of the bank voles in the Białowieża National Park consists of three groups (Table 4.5).

Taxonomic structure involves all the species recorded in the bank voles of the BPN, independent of whether they permanently occur (every month from year to year), or periodically (in some months each year), or sporadically (not every year and in few bank vole individuals).

4.3.3. Biological Structure

Biological structure characterizes a helminthocoenosis with respect to the groups representing various biological and ecological cycles.

Biohelminths. This group eomprises *Cestoda* and *Nematoda*. Among *Cestoda* the following species were recorded: 1. *Catenotaenia pusilla* (intermediate hosts: *Tenebrio molitor, Gliciphagus domesticus, Leptopsylla musculi* (Joyeux & Baer, 1936, 1945).

2. *Hymenolepsis diminuta* (intermediate hosts: *Coleoptera, Lepidoptera, Orthoptera, Siphanoptera, Dermaptera,* and *Myriapoda,* naturaly and experimentaly, infected (Joyeux & Bear, 1936; Skryabin & Mathevossian, 1948; Yamaguti, 1959).

Table 4.5

Taxonomic structure of the helminth community of the Białowieża National Park bank voles (after Kisielewska, 1970).

	Family	Species
Cestoda [1]	*Catenotaeniidae* Spassky, 1950	*Catenotaenia pusilla* (Goeze, 1782)
	Anoplocephalidae Cholodkovsky, 1902	*Paranoplocephala brevis* Kirschenblatt, 1938
	Hymenolepididae Railliet et Henry, 1909	*Hymenolepis diminuta* (Rudolphi, 1819) *Vampirolepis fraterna* (Stiles, 1906)
Nematoda	*Heligmosomatidae* Cram, 1927	*Heligmosomum halli* (Szulc, 1928) *H. glareoli* (Baylis, 1928)
	Capillariidae Neveu-Lemaire, 1936	*Capillaria muris sylvatici* (Diesing. 1851)
	Syphacidae, Skryabin et Šihobalova, 1951	*Syphacia (Syphacia) obvelata* (Rudolphi. 1802)
	Spiruridae Oerley, 1885	*Mastophorus muris* (Gmelin. 1790)
Trematoda		*Trematoda spp.*

[1] Systematics according to Yamaguti (1959).

3. *Vampirolepis fraterna* (intermediate hosts: *Siphanoptera* and *Coleoptera* (Joyeux & Bear, 1936: Skryabin & Mathevossian, 1948; Yamaguti, 1959).

4. *Paranoplocephala brevis* (intermediate host unknown).

Nematoda are represented by: 1. *Mastophorus muris* (intermediate hosts: *Geotrupes stercorosus, Tenebrio molitor, Tinca* sp., and *Ceratophyllus fasciatus).*

Each of these helminths occupies only one of several possible intermediate hosts. Their ontogenetic stage occurring in the external environment (eggs) is a possive element of the biocoenosis (it does not feed or move, it is passively transmitted from the environment to the intermediate host). It is subject only to physico-chemical effects of the environment.

Biohelminths also involve trematodes.

Among geohelminths we can distinguish: Geohelminths *sensu stricto*. For some time their larvae are free-living in the external environment: they take food and undergo successive transformations. In a certain stage of their ontogenesis, these parasites are closely related to the external environment both passively (subject to physico-chemical and biotic factors) and actively (as primary consumers). In the Białowieża National Park these are the nematodes *Heligmosomum halli* and *H. glareoli*.

Pseudogeohelminths. Only eggs of these parasite, resembling spores, occur in the external environment. They are subject to ambient temperature, which can delay or accelerate larval development, thus attainment of the invasive stage. In Białowieża National Park they are represented by the nematode *Capillaria muris sylvatici*.

Ageohelminths. Females lay eggs in the perianal region of the host. These eggs have a delicate cover and contain an already developed larva. Infection generally takes place by autoinvasion or by individual contacts between, hosts omitting, in a sense, the external environment. Forms living beyond the host organism, can survive some time in the microclimate of the body surface or nests of the host. In the Białowieża National Park they are represented by the nematode *Syphacia obvelata*.

4.3.4. Topical Structure

In the alimentary canal of the bank vole provides three habitats or zootopes (Petrusewicz, 1938) for helminths: stomach, small intestine, and caecum (Table 4.6). When an animal is heavily infested, parasites characteristic of the small intestine can also occur in the large intestine. No parasite species restricted to the large intestine were recorded. In most heavily infested bank voles no more than five helminth species were recorded (1—2 species on the average). Moreover, the species composition and the number of species can differ for individual bank voles (Table 4.6).

Table 4.6

Topical distribution of the helminth community in bank voles of Białowieża National Park (after Kisielewska, 1970).

Stomach	Small intestine	Caecum
Capillaria muris sylvatici	*Heligmosomum halli*	*Syphacia obvelata*
Mastophorus muris	*Heligmosomum glareoli*	*Trematoda sp.*
	Catenotaenia pusilla	
	Hymenolepis diminuta	
	Vampirolepis fraterna	
	Paranoplocephala brevis	

4.3.5. Spatial Structure

One of the characteristic features of helminth communities in the bank vole is their topical structure (Kisielewska, 1970). This is the spatial distribution of the community components infecting different habitats (zootopes according to Petrusewicz, 1938), within individual hosts (e.g. in the stomach, small intestine, and caecum).

In the biocoenosis, a territorial unit for a helminth community is not an individual host but the whole host population, representing for parasites a mobile mosaic of habitats. The spatial structure of the helminths communities in a host population involves: 1) the proportion of bank voles infested with particular components of the parasite community (incidence of parasite species), 2) the density of parasites in individual hosts (mean intensity of infestation), and 3) the numerical pattern of distribution of parasites in a number of hosts (aggregations of parasites in different groups of hosts).

Distribution of animals in each habitat can be uniform, random, and clumped. This depends on the type of the habitat (heterogeneous or homogeneous) and on the relationships within animal communities (a tendency to aggregation, antagonistic interactions, etc.).

In this paper, the types of spatial structure of helminth will be analysed for the bank vole populations of the Białowieża National Park (BNP) and other forest bioceonoses of Poland (Kisielewska, 1970). Poisson distributions (Oktaba, 1966; Czechowski *et al.*, 1957) for each parasite species of the bank vole, some parasites (dominant species) have a clumped distribution, while the accessory species are randomly distributed. The latter implies that rare parasites are not involved in organized biocoenotic and structural relationships with the host population (Kisielewska, 1970).

Distribution of parasites which are invasive throughout the year (geohelminths) does not vary with season. The species characterized by a seasonal increase in invasion (biohelminths — in relation to the appearance of invertebrate intermediate hosts, and ageohelminths, the appearance of which is related to the period of bank vole reproduction) show a high degree of aggregation during intensived circulation in the biocoenosis. This implies that only certain groups of bank voles are infested. Voles bearing clumped-distribution parasites fall into three groups: a) non-infested bank vole dominated by young individuals not living long enough to be infested. Most will ultimately be parasitized, b) moderately infested bank voles. This is the most abundant group in bank vole populations, and seems to be the most important for the persistence of the parasitic species. They are not free of parasites, which implies they forage in many places and have a diverse diet. But they are not heavily infested, suggesting a physiological balance in the host-parasite system. The sex ratio and age structure in this group are typical of the whole population. c) heavily infested bank voles (i. e., with a higher intensity of infection that the theoretical maximum). This group involves both young and adult individuals, thus heavy infestation cannot be related to the time of the presence of animals in the biocoenosis. This group seems to consist of the animals most handicapped physiologically or ecologically.

4.3.6. Quantitative Structure

This structure characterizes the quantitative relations among the components (individuals, groups) of a collective unit either by means of absolute values or indices. In a sense, this structure is superior to the qualitative structure which provides description of the set of components of a collective unit. Numerical approaches allow analysis of community structure and dynamics, since numerical relationships are likely to be the most important indication of parasite community inte-

Table 4.7

Synthesis of the helminth community in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

No. of helminth species	Taxonomical groups		Biologial groups		Topical groups	
10	*Cestoda*	4	biohelminths	6	stomach	2
	Nematoda	5	geohelminths	2	small intestine	6
	Trematoda	1	pseudogeohelminths	1	caecum	2
			ageohelminths	1		

Table 4.8

Incidence of intestinal parasite species in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

Parasite species	1953	1954	1955	1956	1957	1958	1961	Total
Catenotaenia pusilla	28.3	28.0	34.4	46.6	27.2	31.8	18.5	30.9
Paranoplocephala brevis	0.3	0.7	2.6	0.9	1.5	—	1.3	1.3
Hymenolepis diminuta	0.9	0.3	0.8	—	—	—	—	0.5
Vampirolepis fraterna	0.3	0.5	1.1	1.9	—	—	—	0.7
Heligmosomum halli	65.8	42.4	65.3	52.3	51.5	63.6	40.9	56.6
Heligmosomum glareoli	1.7	1.2	1.3	0.9	—	—	—	1.2
Capillaria muris sylvatici	30.9	21.4	32.2	17.1	18.8	18.7	19.7	26.4
Mastophorus muris	14.1	3.2	24.9	8.5	9.0	13.6	3.7	13.3
Syphacia obvelata	2.0	10.3	4.4	5.7	4.5	4.5	2.4	4.8
Trematoda spp.	1.4	0.2	0.2	0.9	—	—	—	0.5

gration. Numerical structure of helminth communities is characterized by:

a) Quantitative composition of its structural elements, as expressed in absolute numbers (Table 4.7),

b) Frequency of the degree of infestation of the host population (extent of invasion, Table 4.8),

c) The size of the parasite community or the number of individuals (intensity of invasion, for individual hosts),

d) Density or the number of parasites per unit of space, that is, per individual host within the vole population (Table 4.9),

Table 4.9

Concentration of intestinal parasite species in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

Parasite species and years							For all the years, mean	
1953	1954	1955	1956	1957	1958	1961	Concentration	Intensity
Catenotaenia pusilla								
0.7	0.8	1.0	1.0	0.9	1.0	0.4	0.8	2.7
Paranoplocephala brevis								
0.003	0.009	0.03	0.04	0.02	—	0.01	0.02	1.4
Hymenolepis diminuta								
0.01	0.003	0.01	—	—	—	—	0.008	1.3
Vampirolepis fraterna								
0.003	0.007	0.01	0.03	—	—	—	0.009	1.3
Heligmosomum halli								
2.2	1.1	2.0	2.8	2.4	2.7	3.2	2.4	3.7
Heligmosomum glareoli								
0.02	0.02	0.01	0.03	—	—	—	0.02	1.3
Capillaria muris sylvatici								
5.5	2.1	2.9	8.8	2.3	2.1	1.0	3.5	12.9
Mastophorus muris								
0.4	0.07	0.7	1.8	0.3	0.2	0.1	0.5	3.7
Syphacia obvelata								
1.9	8.2	3.2	4.3	3.2	3.2	0.5	4.1	81.7
Trematoda spp.								
0.001	0.0003	0.0001	0.0005	—	—	—	0.0008	1.5

e) Mean size of parasite aggregations in individual hosts, number of parasites per infested bank voles (Table 4.9).

Frequency, size, and density can be related either to the community as a whole (community indices) or to particular components (indices for particular species of parasites).

These quantitative features of the relations among parasite species (or communities) express: statistically, the probability of the encounter of a parasitized individual per definite number of individuals examined, ecologically, the degree of the infestation of the host population. The sum of the incidence of infestion for particular parasite species in a com-

Table 4.10

Quantitative structure of the helminth community in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

Incidence	Intensity		
	Low	Average	High
Low	*Heligmosomum glareoli* *Paranoplocephala brevis* *Hymenolepis diminuta* *Vampirolepis fraterna*		*Syphacia obvelata*
Moderate		*Catenotaenia pusilla* *Mastophorus muris* *Capillaria muris sylvatici*	
High		*Heligmosomum halli*	

munity is not equal to 100 because the same individual host can be counted several times if it has more than one parasite species.

In the topocoenosis of the bank vole helminths, three numerical categories of components have been distinguished; dominant, influent, and accessory species (Dobrowolski, 1963). BPN is known to carry five rare (extensity 0.5—1.3%) and nonabundant (density 0.008—0.02; mean intensity 1.3—1.5) species. They are considered accessory species. Moreover, one species was frequent and moderately abundant (extensity 56.6%, density 2.4, mean intensity 3.7), one species rather rare and very

Table 4.11

Index of infection calculated for helminth species occurring in the bank vole population of Białowieża National Park (after Kisielewska, 1970).

1953	1954	1955	1956	1957	1958	1961	Total
Heligmosomum halli							
1.5	0.7	1.3	1.6	1.2	1.7	1.6	1.2
Capillaria muris sylvatici							
1.7	0.5	0.9	1.3	0.4	0.4	0.2	1.0
Catenotaenia pusilla							
0.2	0.2	0.3	0.4	0.2	0.4	0.07	0.2
Mastophorus muris							
0.05	0.002	0.2	0.1	0.02	0.03	0.004	0.06
Syphacia obvelata							
0.04	0.8	0.1	0.2	0.1	0.2	0.01	0.2
Heligmosomum glareoli							
0.0003	0.0002	0.0002	0.0003	—	—	—	0.0001
Paranoplocephala brevis							
0.000008	0.0001	0.0008	0.0009	0.0007	—	0.0001	0.0003
Hymenolepis diminuta							
0.0001	0.000006	0.00009	—	—	—	—	0.00004
Vampirolepis fraterna							
0.000008	0.00004	0.0001	0.0003	—	—	—	0.00005

abundant (extensity 2.5%, density 4.1, mean intensity 81.7), and three species moderately frequent and moderately abundant (extensity 13.3—30.9%, density 0.5—3.5, mean intensity 2.7—12.9) (Table 4.10) (Kisielewska, 1970). Lack of a close correlation between the frequency and abundance of these species made it difficult to determine their dominance position. Therefore, the infestation index used by Janion (1968) to estimate the infestation of rodents with fleas was calculated. This index is a product of extensity and intensity. It yields: one dominant, (permanent) component of the community and has the highest infestation index (1.3), three influent species, having an average infestation index (0.2—0.9) and permanently occurring in the community, one seasonal influent species (index 0.1), which appears in the community only during the bank vole breeding season; and five accessory species, with a very low infestation index (0.00009—0.0008), appearing sporadically and irregularly (Table 4.11).

On the basis of the results obtained for the biocoenoses in Poland (Kisielewska, 1970), and using the data of other authors (Rupeš, 1964; Sharpe, 1964; Erhardova, 1958; Mozgovoj *et al.*, 1966; Tenora, 1967a, b), it has been found that the helminth communities living in the alimentary canal have the same general model of the quantitative structure (Table 4.12). This model is characterized by: a) one dominant nematode species of the genus *Heligmosomum,* b) one subdominant species of cestode (most frequently *Catenotaenia pusilla),* and c) accessory species, of the genus *Heligmosomum,* other species of nematodes, and of trematodes. Influent species show the least regularities, especially in their taxonomy.

4.3.7. Seasonal Dynamics of Helminth Community

The preceding data concerned the total sample taken from the field (pooled for several years or seasons). They are static and can be called a synthesis of the community in a biocoenosis (Fig. 4.10). Community dynamics are equally important and may indicate some underlying population control mechanisms.

The structural criterion of each mature community is the balance in proportions among dominant, influent and accessory species. This balance is not static, however. It undergoes changes, but these changes follow some patterns — seasonal cycles correlated with phenological changes in the biocoenosis and with the host population dynamics. A chaotic variability would imply that the community is not an integrated unit.

Structural variability in the parasitocoenoses of the bank vole has

Table 4.12

Frequency of helminths in different bank vole populations (after Kisilewska, 1970).

Present paper 1953—1961. Białowieża National Park	Rupeš (1964), Krčky les 1959—1960	Rupeš (1964), Šarka 1959—1960	Mozgovoj *et al.* (1966), Karelia	Tenora (1967a), Slovakia
		General incidence		
76.4%	60%	63%	62%	75%
		No. of species found		
10	9	6	10	9
		Dominant species		
Heligmosomum halli (N) 57%	*Heligmosomum costellatum* (N) 17%	*Heligmosomum skrjabini* (N) 24% *Heligmosomum polygyrum* (N) 18%	*Heligmosomum costellatum* (N) 44%	*Heligmosomum costellatum* (N) 42% *Hymenolepis horrida* (C) 44%
		Influent species		
Catenotaenia pusilla (C) 31% *Capillaria muris sylvatici* (N) 26% *Mastophorus muris* (N) 13% *Syphacia obvelata* (N) 3%	*Catenotaenia pusilla* (C) 10% *Syphacia obvelata* (N) 8% *Paranoplocephala omphalodes* (C) 8% *Heligmosomum skrjabini* (N) 8%	*Paranoplocephala omphalodes* (C) 7% *Syphacia obvelata* (N) 7% *Heligmosomum costellatum* (N) 6%	*Aprostatandria macrocephala* (C) 7%	*Catenotaenia cricetorum* (C) 8% *Aprostandria macrocephala* (C) 6%
		Accessory species		
Hymenolepis diminuta (C) 0.5% *Vampirolepis fraterna* (C) 0.7% *Paranoplocephala brevis* (C) 1.3% *Heligmosomum glareoli* (N) 1.2% *Trematoda spp.* 0.5%	*Heligmosomum polygyrum* (N) 3% *Capillaria muris sylvatici* (N) 3% *Rodentolepis straminea* (C) 2% *Skrjabinotaenia lobata* (C) 2%	*Capillaria muris sylvatici* (N) 2%	*Paranoplocephala omphalodes* (C) 2% *Catenotaenia pusilla* (C) 2% *Hymenolepis horrida* (C) 2% *Rodentolepis straminea* (C) 1% *Syphacia spp.* (N) 2% *Heligmosomum glareolis* (N) 0.4% *Trichocephalus muris* (N) 0.4%	*Mastophorus muris* (N) 3% *Rodentolepis ampla* (C) 3% *Paranoplocephala dentata* (C) 2% *Heligmosomum polygyrum* (N) 0.3% *Rictularia sp.* (N) 0.3%

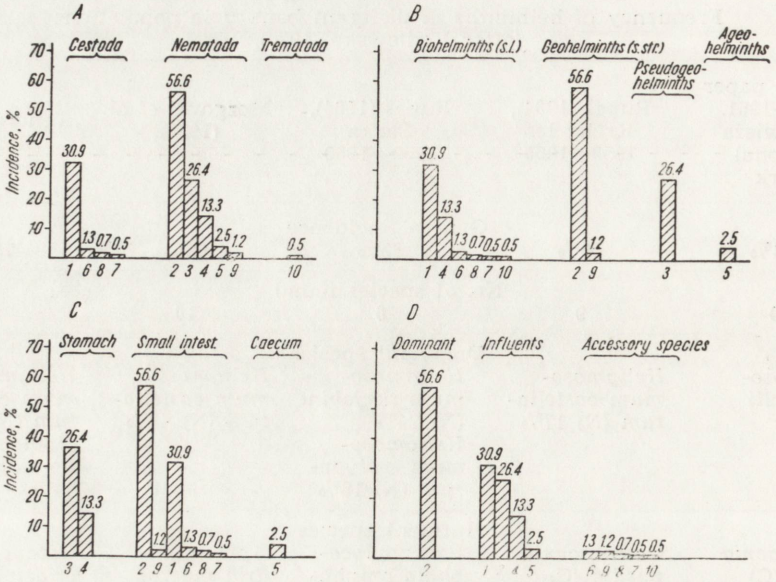


Fig. 4.10. Structure of the intestinal helminth community in the bank vole population of the Białowieża National Park.
1 — *Catenotaenia pusilla*, 2 — *Heligmosomum halli*, 3 — *Capillaria muris sylvatici*, 4 — *Mastophorus muris*, 5 — *Syphacia obvelata*, 6 — *Paranoplocephala brevis*, 7 — *Hymenolepis diminuta*, 8 — *Vampirolepis fraterna*, 9 — *Heligmosomum glareoli*, 10 — *Trematoda* spp. A — taxonomic structure, B — biological structure, C — topical structure, D — quantitative structure.

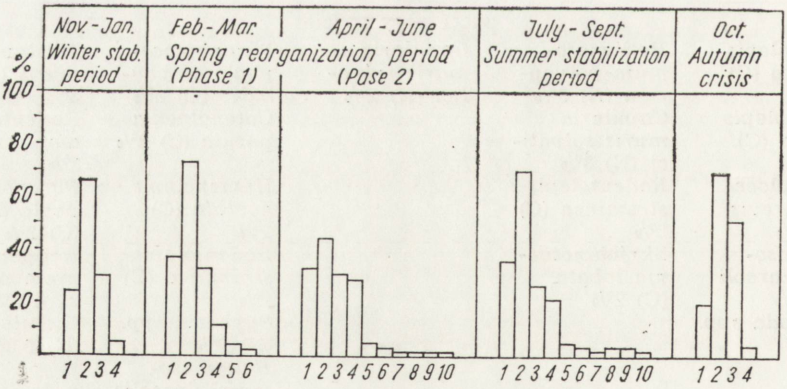


Fig. 4.11. Seasonal changes in the structure of a helminth community of bank vole in the Białowieża National Park.
Explanation see Fig. 4.10.

been analysed from the materials collected in the Białowieża National Park (Kisielewska, 1970). Five periods are distinguished in which helminth communities of the bank vole differ in structure over the annual cycle (Fig. 4.11).

Winter Balance (November-January)

In this period helminth communities consist of one dominant and three influent species; there are no seasonal influents and accessory species; and the dominant is much more abundant than influent species. The bank vole population is stable except for random mortality, which approximates one third of the summer mortality (Gliwicz *et al.*, 1968).

Spring Reorganization (Phase 1: February-March)

The acute differentiation in numbers between the dominant and influent species continues. A seasonal influent appears as a result of intensified sexual contacts among individual bank voles. Also accessory species, mostly biohelminths, appear. Bank voles switch to low energy content diet (Górecki & Gębczyńska, 1962), resulting in drastic increases of their daily activity (Grodziński, 1963). Sexual maturity intensifies this activity (Kubik, 1965). Invertebrates appear and become the prey of these actively foraging rodents.

Spring Reorganization (Phase 2: April-June)

The number of accessory species increases, and seasonal influents become more abundant. At the same time, the difference in abundance between dominant and influent species is reduced. Young voles appear en masse and become infested as a result of their contacts with the biocoenosis. The new generation of bank voles disturbs the numerical structure of the population, thus the structure of the parasite community.

Summer Balance (July-September)

The parasite community in the Białowieża National Park attains its theoretical maximum and comprises one dominant, four influent, and five accessory species, each with clear differences in abundance. Young bank vole mass abundance cease to disturb the numerical relations in the parasite community.

Autumn Begins (October)

Accessory species and the seasonal influents disappear, leaving only the four most abundant species, one of which predominates. Autumnal helminth community changes relate to bank vole population shifts (Kubik, 1965) as overwintered individuals and some current adults die out. This results in drasting decline in species and abundance of helminths previously occupying the oldest voles. These observations at BNP compare favourably with data from other places (Kisielewska, 1970b).

	Dominants	Influents	Accessory species
Spring			
Białowieża National Park	3	2	5
Mikołajki	2	1	5
Summer			
Białowieża National Park	1	4	5
Leśno	1	4	1
Autumn			
Białowieża National Park	1	3	—
Ojców	1	3	—

Mechanisms Organizing Helminth Communities

In each ecological unit there are direct processes and interactions (among individuals) and indirect ones (environmental), which together determine the structure and function of a community.

If a species can exist in a given biocoenosis, its numbers are determined by environmental and intrabiocoenotic mechanisms. And so, individual bank voles, particularly those moderately infested, never have all the niches within the biotope (alimentary canal) saturated with parasites. Co-occurrence of parasite species in single hosts has been analysed (Tarwid, 1960, Kisielewska, 1970). Three groups of parasites have been distinguished: a) co-occurring more frequently than indicated by the random distribution (protective species), b) indifferent to each other (random co-occurrence), and c) avoiding each other (antagonistic species). Two species illustrate the interacting complexities possible: *Heligmosomum halli* (a nematode) and *Catenotaenia pusilla* (a tape-worm), both witin the small intestine. In all the biocoenoses studied these two species showed suggested mutually protective relationships. At the same time, correlation tables suggest inverse numerical occurrences such that the more the nematodes, the fewer the tape-worms, and conversely. Thus, the index of co-occurrence shows that these are concurrent species, while the correlation of numbers says that they are antagonistic, or, at least, that they limit numbers of each other. This apparent inconsistency is a result of two mechanisms determining numbers of the two species. One mechanism acts within individual hosts (in an idiohostal community), and is competition. Both species occupy the same habitat, though their ecological niches are not identical. *H. halli* feed on erythrocytes, while *C. pusilla* on the intestinal content They may compete, however, for space. The other mechanism acts within the whole biocoenosis. The common source of infection with the two species is plant litter and low vegetation, where occur free-living nematode larvae and also acarids — the intermediate hosts of *C. pusilla*. Hence, the chance of bank vole infestation with the two parasites simultaneously is greater than random. Two mechanisms clash here: intracoenotic antagonism and biocoenotic convergence, the latter being more effective.

Clumped distribution of the bank vole parasite in population can be explained by physiologically or ecologically. Physiological reasons involve, e. g. individual differences in the host resistence to the infection with various parasites. Due to these differences, some individuals are not parasitized as a result of an inherited or acquired resistance, while other individuals are more heavily infested than at random, though the chances of infestation are presumably equal for all individuals. Ecological reasons lie in uneven chances of contact with the source of infection for different groups of population members. This may be due to differences in lifestyle; differential foraging positions or times. Different voles may occupy different ecological niches, or have different search ranges. It seems that ecological relationships are ultimately of basic importance, though the role of individual resistance cannot be excluded (there are no data available for the bank vole resistance).

Thus, the mechanisms determining the clumped distribution of parasites in the host population are contained in the structure of this population, and indirectly in environmental interactions.

The mechanism shaping numerical relations in parasite community is intracoenotic selfregulation and biocoenotic regulation.

The dominance of individual species in parasite communities is determined by: a) ecological valence of the species in a biocoenosis, the "efficiency" of the ways of circulation, determining the chances of encounter with a host, and b) its physiological vitality due to which it could eliminate or reduce the abundance of competing species during the community formation.

Related species have the same integration plane, or largely overlapping niches. They do not tolerate each other, though the same type of their circulation in the biocoenosis theoretically creates identical chances of the host infection. For example, among nematodes of the genus *Heligmosomum* only one species becomes dominant in a community. The other members of this genus are reduced to the role of accessory species (Kisielewska, in press.). The dominance structure is the result of a scramble competition (for space, food, etc).

Unrelated species but living in the same biotopes (but occupying different niches) can be dominants or influents in a synthostal community, but they limit numbers of each other in individual hosts (e. g. the already quoted nematode *H. halli* and the tape-worm *C. pusilla*).

The abundance of the species that have no competitors in their tope is maitained at the level determined by environmental conditions of the biocoenosis (e. g. the nematode *Syphacia obvelata,* which is a seasonal influent with a highly clumped distribution, living in the caecum) strongly depends on the dynamics of the host population.

Among the accessory species, some belong to this group as a result of heavy competition with related species, and other because the ways of their circulation in the biocoenosis do not coincide with typical foraging sites and the diet of the host species (casual accessory species). In the former case, intrabiocoenotic competition is the regulatory mechanism, while in the latter case regulation goes through the biocoenosis.

5. NUMBERS: THE CONCEPT AND DEFINITIONS

5.1. Numbers and the Number of Discrete Individuals, Turnover

Kazimierz PETRUSEWICZ

Numbers (*N*), also called densities, have been defined as the number of individuals per unit area at a given time (at the time of sampling). These terms also refer to the number of individuals per sample, or, sometimes, to the number of individuals in the population independent of the size of the area occupied by this population. For animals of the size of the bank vole, numbers (*N*) are usually defined as the number of individuals per hectare.

Numbers of bank voles, like any other species, fluctuate in time. There are seasonal (phenological) changes in numbers and annual changes. I shall discuss them in more detail in section 7.1.

The graph of numbers (*N*) on the time axis is a characteristic curve called the curve of population dynamics (Figs. 5.1, 7.1, 7.2). The curve on Figure 5.1 illustrates seasonal changes in population dynamics.

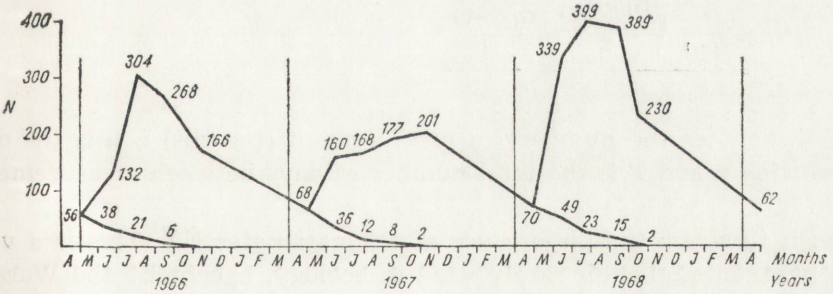


Fig. 5.1. Population dynamics (*N*) of the bank vole on a 4-ha island (from Petrusewicz *et al.*, 1971).

Numbers (*N*) are a basic ecological parameter. In populations containing different categories of individuals (males and females, young and adults, pregnant and lactating females, light and heavy individuals, etc.), numbers are the starting point in calculating other ecological parameters. Thus, in the next section (5.2) I discuss the methods of estimating numbers and their reliability.

Knowing population dynamics in one or more localities over the year or several years, we may be interested in mean numbers (N) per year, or per growing season versus winter period, or per any other period of time. Mean density has been defined (Petrusewicz, 1966b; Petrusewicz & Macfadyen, 1970) as

$$\bar{N}_a = \frac{l}{k}\sum_{i=1}^{i=k} N_i \qquad 5.1$$

where k is the number of measurements (records) and N_i denotes successive population numbers. Note that records should be distributed more or less evenly in time. It is frequently the case that we have many records over the growing season, when N_i is high, and few records in winter (e. g. for technical reasons), when N_i is low, and, consequently, the average value will be overestimated. This issue is analysed in detail by Petrusewicz & Macfadyen (1970), who pointed out that the calculated unweighted average value can be twice the weighted average value (see Fig. 5.2). The best way to avoid this error is to calculate the area under the curve of population dynamics. This can easily be done by summing the areas of figures between successive measurements (Fig. 5.2). Obviously, in this way we will get the value of $\bar{N}T$, where $\bar{N}$ is an average number over time T. The weighted average can be calculated from the formula

$$\bar{N} = \frac{\sum_{i=1}^{i=k}\left(\frac{N_i+N_{i+1}}{2}\right)(t_{i+l}-t_i)}{T}$$

where N_i denotes the numbers in measurement (records) i, t_i is the date of measuring i, and T is the total number of days between measurements i and k.

I wish to stress the importance of the parameter $\bar{N}T$. This is a very useful parameter, though rarely used in ecology, except by the Warsaw School of Ecology (Petrusewicz *et al.*, 1969, 1971; Petrusewicz & Macfadyen, 1970). The value of $\bar{N}T$ indicates the number of individual-days in period T. Therefore, this is the number of individuals that exert a pressure on the environment through their consumption of food, or this is the mass of individuals available for predators; this is also the number of reproducing individuals. The parameter $\bar{N}T$ provides a more comprehensive characteristic of the population than $\bar{N}$.

But neither average numbers, $\bar{N}$, nor the number of individual-days,

$\bar{N}T$, nor the curve of population dynamics characterize the number of individuals present in time T. If, for example, there were 10 individuals at time T_1 and 25 individuals at time, T_2, this might be a result of the input (birth, immigration) of 15 individuals, with no elimination (death, emigration), or of the input of 30 and elimination of 15 individuals, or even the input of 100 individuals and elimination of 75. The real number individuals (ν) present in the population over the study period T is given by the formula

$$\nu + N_o = \nu_r \qquad 5.2$$

where N_o is the initial number, and ν_r is the number of individuals born. The total balance of the number of individuals over time T can be calculated as

$$N_T = N_o + \nu_r - \nu E \qquad 5.3$$

where N_T is the number of individuals present in the population in time T, N_o is the initial number of individuals, and νE is elimination (death, emigration). This formula can also be written

$$\nu_r = N_T - N_o + \nu E = \Delta N + \nu E \qquad 5.4$$

The number of individuals born (ν_r) represents population production expressed in the number of individuals.

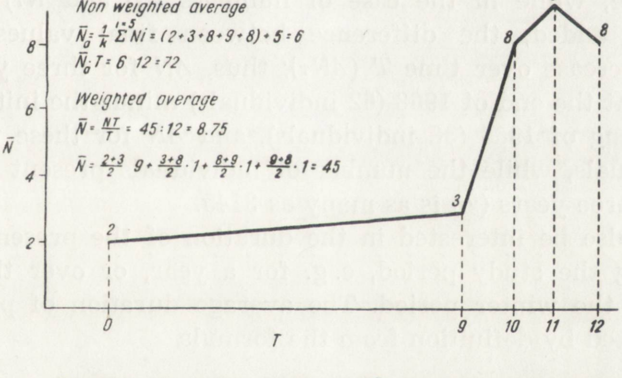


Fig. 5.2. Average numbers ($\bar{N}$) properly averaged.

For a short time periad, usually $\nu_r = \Delta N + \nu E$, but for a longer period, e. g. for a year, or for a reproductive period, N differs little from elimination so that we can write

$$\nu_r \approx \nu E \qquad 5.5$$

I will illustrate this relationship using the data from Crab Apple island on lake Bełdan (Mazuria, Poland), which is inhabited by the most thoroughly studied free-living population of the bank vole. The data calculated from Petrusewicz *et al.* (1971) show the individual budget from April to April (biological year for the bank vole) over three years (Table 5.1).

Table 5.1

Annual balance (April to April) of individuals in the bank vole population on Crab Apple island over three years (after Petrusewicz *et al.*, 1971).

	$\nu_r = N_T - N_o + \nu E = \Delta N + \nu E$
1966	$1048 = 68-58+1038 = 10 + 1038$
1967	$1090 = 70-68+1088 = 2 + 1088$
1968	$1011 = 62-70+1019 = -8 + 1019$
1966—68	$3149 = 62-58+3145 = 4 + 3145$
Average/year	$1049 = 66-65+1048 = 1 + 1048$

As it can be seen from this table, the difference between the initial and final numbers over a year equals to 0.2—1% of the elimination, while the average for three years equals to 0.01% of the elimination. Thus, I do not make a great error if I omit the term ΔN in formula (5.4) and use formula (5.5) instead.

It should be noted that the values of ν_r and νE can be added for any period of time, while in the case of numbers (N_i and N_T) only final values can be added; the difference between final values gives an increase or decrease over time T (ΔN_T); thus, ΔN for three years is the final number at the end of 1968 (62 individuals) minus the initial number at the beginning of 1966 (58 individuals), and ΔN for these three years is +4 individuals, while the number of individuals present in this population for three years (ν_r) is as many as 3145.

One may also be interested in the duration of the presence of individuals during the study period, e. g. for a year, or over the growing season versus the winter period. The average duration of presence (t') can be calculated by definition from the formula

$$\bar{t}' = -\frac{1}{v}\sum_{i=1}^{i=\nu} \cdot t_i \qquad 5.6$$

Note that the duration of presence over time T does not equal the length of life: this is the length of life but only in the study period T, e.g. from April to April; the duration of presence of the animals entering their next reproductive season after winter is considered only by April (for the period April-April); hence, the average duration of life is a little longer than the average duration of presence.

An interesting parameter is

$$\nu\bar{t}' = \sum_{i=1}^{i=\nu} \cdot t_i$$

Obviously, $\nu\bar{t}'$ is the number of individual-days over time T. I have indicated above that $\bar{N}T$ is also the number of individual-days in time T (Petrusewicz, 1966b; Petrusewicz & Macfadyen 1970), thus

$$\bar{N}T = \nu\bar{t}' \qquad 5.7$$

This equation can be of great importance as the parameter T can be arbitrarily selected, parameter $\bar{N}$ can be relatively easily found empirically, while the number of individuals (ν) and the time of presence ($\bar{t}'$) are much more dificult to determine empirically. Thus, if we have one of these parameters, we can easily calculate the other one from equation 5.7. This equation, however, should be used cautiously; e. g. it is usually impossible to calculate ν_r because $\bar{N}$ and $\bar{t}'$ are calculated for individuals that surived until the so-called trappable age.

Let me note that ν: $\bar{N}$ says how many times average numbers have been exchanged over time T, this is turnover as expressed by the number of individuals (Θ_N) (Petrusewicz, 1966b).

$$\Theta_N = \frac{\nu}{\bar{N}} = \frac{T}{\bar{t}} \qquad 5.8$$

And if T is a unit time (e. g. a year) and this unit is used as a measure of $\bar{t}'$, we will get

$$\Theta_N = \frac{1}{\bar{t}'} \qquad 5.9$$

Individual turnover (Θ_N) is similar to but not identical with biomass turnover. We will discuss differences between these two concepts in Chapter 8 after discussing biomass turnover.

Equation 5.7 shows that numbers (standing crop) depend on both the number of individuals and the time of their presence: $\bar{N} = \nu\bar{t}'/T$. Two examples illustrate this.

A removal experiment was carried out in the Kampinos Forest (Andrzejewski & Wrocławek, 1962). As a result of intense trapping, a 4-ha "rodent vacuum" was created. Then the recolonization of this vacuum was observed. It has been shown that the immigration rate was not higher than in the other, undisturbed area. However, more rodents settled there and the duration of settlement increased. As a result, numbers of animals on the experimental plot rapidly increased to the level characteristic of adjacent areas. This increase in numbers was due to the increase in the time of presence ($\bar{t}'$), and not due to the increase in the number of immigrants (ν_{im}).

Another example: in most cases both in the field and in the controlled laboratory experiments the number of young is lower than the number of adults. This results from the fact that a young individual (arbitrarily, up to seven weeks old) can be present at most seven weeks, and then it becomes adult; as an adult it can be present for 18 months.

5.2. Numbers — Methods of Assessment

Henryka CHEŁKOWSKA & Jacek GOSZCZYŃSKI

5.2.1. Capture Techniques

The methods for the assessment of bank vole numbers do not differ from those applied for number estimation of other small rodents. Thus we will only enumerate them here, and indicate what additional information we can get using these methods, without going deep into their advantages and shortcomings. Those interested in the technique of calculations or in the comparison of various methods are referred to Smith *et al.* (1975).

The cases when numbers or density can be determined by the removal of all or almost all individuals living in a given area are rare and limited to isolated populations, e. g. on islands (Andrzejewski *et al.*, 1967; Gliwicz *et al.*, 1968), artificially isolated (Gębczyńska, 1966), or confined. Long-term trapping from open areas can lead to the so-called complete removal, despite disturbance caused by immigrants, but the extent of the "vacuum" produced is not exactly known (Andrzejewski & Wrocławek, 1962; Kozakiewicz, 1976).

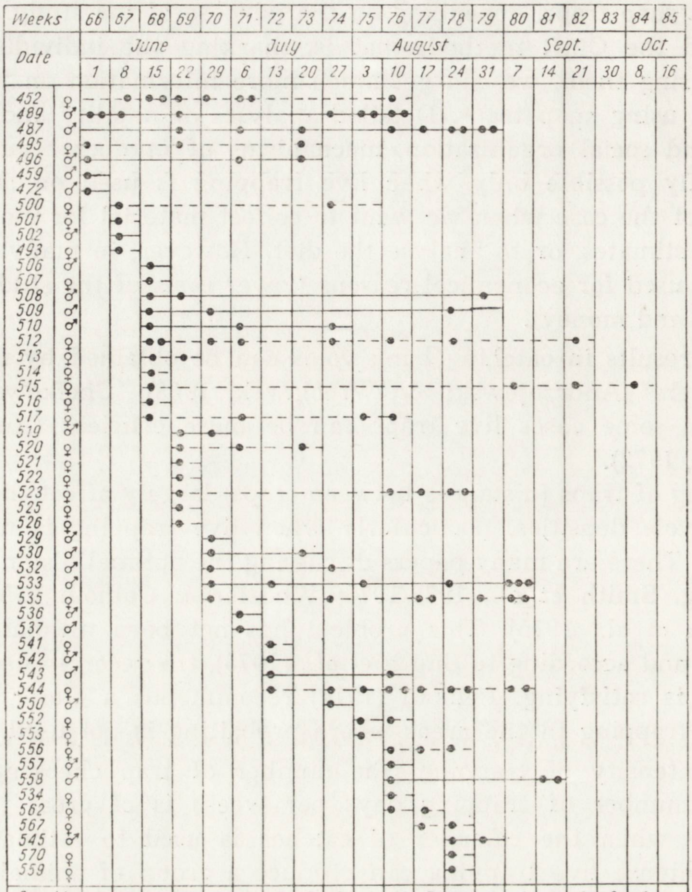
Indirect methods such as tracking on snow provide only rough approximations of vole numbers as the activity of these animals on the surface of snow cover largely depends on weather and snow quality (Rotshild, 1959). Strongly ramified burrow systems of the bank vole do not allow the application of flooding (Truszkowski, personal communication). For these reasons we estimate numbers from samples of individuals caught in a given location. Most frequently, bank voles are caught on sampling areas or on trap-lines with a specific configuration of live or snap traps, depending on the purpose of the study. Using live traps and the CMR method, that is, marking the individuals caught and releasing them, we can get much more information on the population than using snap traps. Detailed analyses of natality and mortality, spatial and social organization, mechanisms of number regulation, etc. are usually possible only when live trapping is used on study plots. This is not the case when we want to collect material for mortality and natality estimates, or to analyse the diet. However, in many cases snap traps are used for economical reasons (lower costs of the study in terms of labour and money).

Good results in catching bank voles can be obtained by using cones or cylinders (Andrzejewski & Wrocławek, 1963); Chełkowska, 1967), though in some cases live traps can be more efficient (Andrzejewski & Rajska, 1972).

Spacing of traps (distances between traps) largely affect the estimates of bank vole densities, particularly when live trapping is used (Tanaka, 1966). There are many papers discussing the optimal distance between traps (e. g. Smith *et al.*, 1969/1970; Wheeler & Calhoun, 1967: quoted by Smith *et al.*, 1975). This problem has not been ultimately solved, however, and according to Smith *et al.*, (1975), the recently used distance of 15 m is satisfying. Pelikàn (1974) recommends a closer spacing to intensify trapping in the areas where prebaiting is not used.

The intensity of trapping (the number of trap checking per day, and the number of trapping days per week) is of great importance, especially when the calender of catches is used to estimate density. A very intense live trapping can produce a group of animals excluded from their normal life in the population, and "living" in traps, that is, recaptured immediately after release (Andrzejewski *et al.*, 1967). In addition, these animals block the access to the trap for other individuals. When trapping is carried out at excessively long time intervals, the animals present for a short time in the area cannot be trapped. This may be the case of young individuals, which show higher migration and mortality rates than adults. According to some authors, the presence of trap-shy individuals in the population can account for some errors in density estimates (Kikkawa, 1964; Bailey, 1968; Andrzejewski *et al.*, 1971). These errors can be reduced by using the calendar of catches or analysing not only current catches at a given time but also the earlier and the subsequent catches (Fig. 5.3).

The rate of capture is greatly affected by the number of traps per point or station (Andrzejewski *et al.*, 1966). Most frequently one or two traps are used per point, though on transects more traps per point would be needed to ensure a high rate of catches.



Weeks		66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Date		June					July				August					Sept.				Oct.	
		1	8	15	22	29	6	13	20	27	3	10	17	24	31	7	14	21	30	8	16
Caught		5	6	12	13	9	9	5	5	8	6	14	7	11	4	4	1	2	0	1	
Present	Males	5	4	7	7	11	11	11	10	9	6	8	5	6	5	2	1	0	0	0	
	Females	2	5	10	13	9	9	11	10	8	9	11	8	9	4	4	2	2	1	1	
	Total	7	9	17	20	20	20	22	20	17	15	19	13	15	9	6	3	2	1	1	
New			4	11	7	5	2	4	0	1	2	5	1	3	0	0	0	0	0	0	
Disappeared		2	3	4	5	2	2	2	4	4	1	7	1	6	3	3	1	1	0	1	
c-mice			3	4	4	1	2	2	0	1	1	2	0	2	0	0	0	0	0	0	

Fig 5.3. Calendar of catches (modified from Petrusewicz and Andrzejewski, 1962). Dots represent catches, the line connecting the dots — duration of trap presence in the study areas. Horizontal data: Life history of an individual. Points indicating captures can be replaced with numbers indicating the location of trapping points (e. g. A1, A2, B7, etc.) which allows determination of the area covered by individual animals. Weight and increase in weight are obtained for each time period. Length of stay (*t'*), average distance between catches (= reciprocal of real trappability), etc. can also be calculated. Vertical data: the situation at a given moment e. g. how many individuals were caught, how many are known to be present (number of lines depicts the number of individuals present on a given day), how many were newly caught, how many males or females, how many migrants, how many disappeared, etc.

Baiting obviously increases the rate of capture (Andrzejewski & Wrocławek, 1963; Tanton, 1969; and others), and facilitates the subsequent estimation of the number of animals living in the area (Gentry *et al.*, 1971), but at the same time it accounts for the concentration of animals at the edge of the study plot, and disturbs the spatial organization of the population by increasing the carrying capacity of this area (Pelikàn, 1974). The additional food can change population dynamics in the case of live-trapping (Gentry, 1968; Smith, 1971), and it increases the distance from which animals are trapped when snap traps are used.

5.2.2. Study Plots

So far study plots of various sizes have been used. The most widely applied method has been Standard Minimum (Grodziński *et al.*, 1966). It was used in the IBP studies on the productivity of small mammal populations (Pucek & Ryszkowski, 1970). The uniform method of capture (the plot of a side length of 225 m, with a network of traps 15 m apart, a fixed time of baiting and trapping) allows a comparison between different populations and ecosystems. A plot of this size ensures rapid capture of all animals, and a sufficiently large material to estimate ecological parameters (e. g. reproductive rate, age structure of the population, etc.). At the same time, it covers at least several individual home ranges, which allows an alternate application of the removal and *CMR* techniques.

According to many authors, however, the size of the Standard Minimum limits its application. The reasons are that setting and checking traps on such an area is labour consuming, and frequently it is difficult to find a homogeneous habitat of this size. Many authors argue that similar results can be obtained using smaller areas (Myllymäki, *et al.*, 1971; Pelikán, 1971; Zejda & Holišova, 1971). On smaller plots (less than 1 ha), however, estimates of the number of resident individuals are more biased (Chełkowska & Ryszkowski, 1966). It is also difficult to calculate the number of individuals in the study area, particularly if there is no baiting. This is related to a lower rate of capture and some disturbances during the capture (Pelikán, 1974; Hansson, 1975). In addition, density estimates based on individual home ranges can be misleading due to a high mobility of rodents (Adamczyk & Ryszkowski, 1968; Tanton, 1969; Ryszkowski, 1971) if the plot is too small.

But if we do not want to catch a large number of animals, and instead are interested in quick results at low costs, small plots seem best. For these reasons they are frequently used. In Scandinavia, the Small Quadrat method is used to predict rodent numbers (Myllymäki *et al.*, 1971; Hansson, 1974a). In this method the study plot is reduced to a quadrat 15 m per side, with three snap traps in each corner. A modified Standard Minimum method (with a reduced surface area) was used by Hansson (1975) and Ryszkowski *et al.* (1973). Also Pelikán (1974) used small plots.

As plots of different sizes are used, a comparison of the results obtained seems badly needed. Hansson (1975) has done this for the Small Quadrat and Standard Minimum. He developed regression equations for particular species that allow density estimates from small quadrats.

When captured animals are removed from a plot, the simplest way of estimating numbers is to divide the number of individuals caught by the plot size. As the duration of the trapping period significantly influences the results, usually a linear regression is used to estimate the number of animals on the plot (De Lury, 1947; Hayne, 1949), or the maximum likelihood method proposed by Janion *et al.* (1968) that allows estimation of an average probability of capture. This method of calculation makes it possible to estimate the total number of individuals without removing them for many days.

When live trapping, the number of animals can be estimated by means of the calendar of catches (Blair, 1951; Davis, 1955; Adams, 1959; Petrusewicz & Andrzejewski, 1962). Due to the interpolation of date to the periods between catches (Fig. 5.3), this method enables us to determine the composition of the population at any time instant or time period, and to follow the fates of individual animals.

Also, a curvilinear regression can be used (Tanaka & Kanamori, 1967). The densities estimated in this way are of relative character, and they can be used for the analysis of population dynamics of the bank vole, comparison of numbers in different ecosystems, etc., thus when we want to record time and habitat-related changes.

5.2.3. Trapping Range

It is known, however, that the area from which the animals are trapped is larger than the area covered with traps. Animals caught on the plot consist of individuals spending all their time within the plot (obviously, if the plot is large enough to cover an average home range), and of the animals only partly active within the plot (Calhoun & Casby, 1958), as well as migrants. If baiting is used, residents from beyond the plot and probably more migrants are captured (Pelikán *et al.*, 1964; Chełkowska & Ryszkowski, 1967). Influx of animals into the plot leads to the so-called edge effect, which is revealed by increased catches of traps located at the plot edge.

Thus, to get an absolute estimate of density, it is necessary to calculate range of trapping. It seems that the methods of rejecting the outer line of traps, and using only the inner square of traps for density estimation (Adamczyk & Ryszkowski, 1968; Pelikán, 1969) are now considered as relative methods. More promising are the methods based on estimating the size of the area from which animals are removed by the traps.

Some authors suggest that a belt of the width equal to the average diameter of the home range or at least to the half of it should be added to the plot area (Dice, 1938; Pelikán, 1974). Such estimates raise some reservations. For example, they should be preceded by gathering information on the average distance covered by individuals, and this parameter is not easier to determine than density itself. The methods for estimating the range of the influence exerted by the trapping area given by Hansson (1969b) and Smith *et al.* (1969, 1970) are based on delimitation of the so-called inner square within which the distribution of catches per traps is homogeneous. Smith *et al.* (1969, 1970) compare the frequency of catches for each belt of traps. Usually the highest frequency of catches was recorded in the first belt of traps; it decreased towards the centre of the plot until a stable level was reached. According to Smith *et al.* (1969/1970), the breadth of the boundary area, that is, the zone with increased catches, should be added to the area of the study plot. Hansson (1969b) calculated the range of the influence exerted by the plot assuming that the ratio of the number of animals caught on the whole sampling area to the size of this area increased by the boundary zone equals the ratio of the number of animals caught in the inner square to the size of this square. The inner square in this method was determined according to Pelikán (1969).

To estimate the trapping range American workers propose the use of assessment lines on which animals are caught when the catches on the basal plot are completed. Cumulating the catches from the end of such a line and analysing the shape of the curve, it is possible to find the boundaries of the complete removal and the range of the incomplete removal (Smith *et al.*, 1971). Assessment lines are also recommended to determine the range of the plot when the CMR method is used (Nabkolz, 1973 quoted by Smith *et al.*, 1975; Swift and Stenhorst, 1976). These last authors use assessment lines to determine the ratio of marked to unmarked individuals at different distances from the plot.

The range of the influence of the plot can also be estimated by using coloured baits prepared according Holišova's (1968) method, which after capture of animals, are detected in alimentary canals of rodents (Ryszkowski, 1971). Using this method, Ryszkowski estimated the number of animals in the central and peripheral parts of the plot. To determine the range of removal, he assumed that both the whole plot and the central part (inner quadrat) are visited by individuals from identical distances. An average distance of removal estimated in this way is higher than that obtained by the Hansson method (Ryszkowski, 1971). This method can also be used *in vivo* as coloured baits can be identified in faeces of rodents (Goszczyński, 1971).

5.2.4. Methods for Estimating Densities

The concepts of absolute and relative numbers are widely known in ecology. Absolute numbers can be characterized as the number of individuals per unit area, while the relative numbers denote the number of individuals recorded by means of comparable methods with no possibility to relate these numbers to the size of the area from which the animals were captured. Absolute numbers are needed in the studies of productivity, trophic relations, and determination of population indices. Relative numbers are used for all other estimates that need not be particularly accurate. First of all they are of comparable value.

Trap-lines. To estimate relative numbers, the method of "trap-lines" can be used. In this method traps are evenly spaced along lines, the number of traps per point being constant. It is difficult to capture all the animals when this method is used (Calhoun, 1949; Hansson, 1967b). Without calculating the total number of animals occurring in the area crossed by the line, the comparison of results from different lines can be misleading. Though this method is easy to apply, it is not possible to get absolute density estimates from the lines alone, when no additional estimates of the range of animal activity are available (Brandt, 1962). Even lines with variable distances between traps do not allow the calculation of home ranges because the number of rodents caught is disproportionately high in places of trap concentration (Hansson, 1974b). Hence results obtained from trap-lines are often expressed in terms of the number of individuals per trap per day. Obviously, these are relative estimates and to get comparable results for different habitats or years, the trap-lines should be standardized, that is, the number of capture points, the number and the type of traps, time of exposure, bait, etc. should be identical for various capture series. Although there are statistics allowing analysis of material collected from non-standardized lines (Linn & Downton, 1975), they can lead to errors. Moreover, results obtained by Ryszkowski (1971), who found that bank voles are more mobile in spring, when densities are low, than in autumn, show that the trap line method is likely to obliterate seasonal differences in population dynamics. Obviously, the results also depend on weather during trapping (Sidorowicz, 1960). Nikitina (1958, 1961b), who compared results from trap lines with those from plots for marked animals, found that number indices from lines are markedly less variable than the actual population density. Russian researchers, however, have for many years used mostly capture lines as the best method to get a quick characteristic of different habitats with respect to their rodent populations. Due to the standardized baiting, traps, and trap spacing, the results are comparable, and are presented in terms of the number of animals caugth per 100 trap-days (Kučeruk, 1963; Popov, 1966).

Attempts to estimate absolute numbers (N) from transects are presented by Smith *et al.*, (1971) and Kaufman *et al.*, (1971). They captured rodents from the census line first, and then from the assesment line. When one census line is used, the assesment line should cross it at an acute angle, and the capture period should be short (Smith *et al.*, 1971). Although this cross line method is simple, and small areas can be sampled, its application is limited because of the variability of enviromental conditions and a rapid immigration of animals (see Smith *et al.*, 1975). An attempt was made to overcome these difficulties by simultaneous application of several cross lines (Kaufman *et al.*, 1971), and calculating a joint density. In practice, the lines were grouped in an octagon, according to the recommendations of Wheeler & Calhoun (1968), and for estimating the range, a line of traps crossing this octagon was used. The results obtained, however, are not unequivocal (Gentry *et al.*, 1971b; Kaufman *et al.*, 1971), since immigration of animals into the octagon made it impossible to estimate the range (Gentry *et al.*, 1971b).

This review of the methods applied, though incomplete, may provide a basis for selection of the best one in view of the study purpose and time/financial limits. We do not suggest any choice but we postulate that the authors should describe in detail the methods they use so that future results on vole densities in various habitats and years may be compared with greater reliability.

6. ECOLOGICAL STRUCTURE OF THE POPULATION

6.1. Sex Ratio

Gabriela BUJALSKA

Sex ratio, the mechanisms of its formation, variability of its range, and significance to the population dynamics have frequently been theoretically analysed, but less frequently studied empirically.

Theoretical bases for the concept of the evolution of optimal sex ratio in diploid animals with sexual reproduction were developed by Fisher (1959). According to his theory, the optimal sex ratio in steady-state populations should approximate 50 : 50.

This hypothesis was tested by means of the mathematical modelling of empirical data for *Microtus ochrogaster* and. *M. pennsylvanicus* populations (Myers & Krebs, 1971). The effect on sex ratio of differences in recruitment rate, survival, trappability, and individual growth between males and females was analysed. The conclusion was that despite all these differences sex ratio should be 1 : 1, as predicted by Fisher.

It is not difficult to find some deviations from the "ideal" sex ratio frequently recorded in rodent populations (e. g. Pelikán, 1965, 1970; Kalela & Oksala 1966; Kalela, 1971; Myllymäki, 1975, 1977; Adamczewska-Andrzejewska & Nabagło, 1977; Hansson, 1978, and others).

According to the phases of individual development, sex ratios have been classified into primary (at the time of conception), secondary (at birth), tertiary (soon after living the nest), and quaternary (in reproducing animals) (Kalela & Oksala, 1966; Pianka, 1974). In practice, however, it is frequently difficult to differentiate the tertiary and quaternary sex ratios (in the case of animals for which the time of leaving the nest is unknown). Therefore, in free-living populations we can determine the sex ratio for immature and mature individuals. But most often only the sex ratio of all the males and females in the population as a whole is examined.

Sex ratio in the bank vole has not been thoroughly analysed. This paper presents a review of the literature on this subject, and also emphasize gaps in our knowledge of the sex ratio in the bank vole relative to published data for other rodents. At the present state of knowledge it is difficult to postulate a synthesis of this issue, or to show relationships between the processes of sex ratio formation and other processes determining population dynamics.

As the primary sex ratio has not been studied in the bank vole at all, I shall start this review with the secondary sex ratio.

6.1.1. Secondary Sex Ratio

Secondary sex ratio in the bank vole was studied by Buchalczyk (1970) under laboratory conditions. Among newborn animals there were 656 males and 636 females. Litters in which some young died consisted of 195 males and 184 females. The observed prevalence of males is not statistically significant, thus the secondary sex ratio is 1 : 1.

Similar results were obtained by Kalela and Oksala (1966) for *C. glareolus* and *C. rufocanus*. In the latter species males accounted for 49.6% of 256 embryos. Also Zejda (1967) examined sex ratios in embryos prior to birth, and found that the proportion of males was 53%.

The estimated data for an island population of the bank vole (Bujalska, 1981b) show that the proportion of males at birth can vary from 44.4 to 72.0%, with an average of 54.7%. A particularly high predominance of males occurred in cohort K_3 (born in the second half of the breeding season) in 1967 and 1968, the respective values being 70.1 and 72.0%. In the other seven cases that were analysed, the uper limit of male proportion did not exceed 59.0%. These values, calculated on the assumption that the number of young decreased exponentially in the period from birth to an age of about three months, can contain some error. However, the thesis that the secondary sex ratio can vary seems reasonable. Even more so since the secondary sex ratio greatly deviates from 1 : 1 in *Myopus schisticolor* (Kalela & Oksala, 1966).

6.1.2. Tertiary Sex Ratio

The tertiary sex ratio is generally determined for immature individuals. Interesting data on this issue are presented by Kalela (1971) for a population of *C. rufocanus* living in Finnish Lapland. He analysed sex ratios for immature and mature animals in successive months from May to September and in different phases of the population cycle over 15 years. In July the sex ratio for immature individuals was 1:1 (47% males), while in August males significantly predominated (64.9%), while in September their numbers fell (55.4%) but remained statistically significant.

Males predominance among immature individuals of an island bank vole population was observed in June-July of 1975 and in June-September of 1977 (Bujalska, 1981b). In June, July, and September of 1975 the proportions of males were 53.3, 55.5, nad 49.6%, respectively, and in 1977 the respective figures were 82.1, 60.6, and 66.2%. Thus in 1975, the sex ratio in immature voles was rather stable and near 1:1, while in 1977 the proportion of males tended to decrease. In 1976, when the population was very low, the sex ratio in July (data for June are lacking) was characterized by a smaller proportion of males (44.9%), while in September this proportion was more equalized (49.1%). It can thus be suggested that a higher proportion of males among immature individuals occurs at higher population densities.

Kalela (1971), who analysed the effect of population factors on sex ratio in *C. rufocanus*, found that males predominated in August and September (61.6%) during years of high population densities. In the years of low population densities the proportion of males in the same months was 53.6% and thus not statistically different from the 50:50 ratio. These consistent results for *C. glareolus* and *C. rufocanus* imply that this pattern may also occur in other representatives of this genus.

6.1.3. Quaternary Sex Ratio

Quaternary sex ratio, that is, in mature individuals, was studied by Kalela (1971) with reference to seasonal changes and population dynamics of the bank vole. The sex ratio of adults was 1:1 late in May and in June (51.9% males) and also in July (50.5% males), and then the proportion of males declined in August and September (35.2 and 28.0%, respectively).

Regression of the number of mature males and females on the total trappable population of an island showed that the female curve was always higher than that of males and the sex ratio declined (Bujalska, in print.).

In years of a high *C. rufocanus* population density, the proportion of males among adult individuals was lower in August and September (28.7%) and equalized in May-July (50.4% males). In low population density years, sex ratio was 50:50 in both May-July (54.8%) and August-September (48.9% males).

Overwintered voles were usually (in 17 out of 30 cases analysed) predominated by females in April, that is, when formed the reproducing stock of the population. This female predominance already occurred in the autumn of the preceding year, thus did not result from differences in winter mortality between males and females (Bujalska, in print).

It seems that the sex ratio in mature, thus capable of reproduction, individuals is particularly important to population dynamics. In this respect the analysis of sex ratio in immature voles would be less important. It would characterize, however, the relations in the "reserve" that they represent for the reproducing part of the population. This reserve accounts for the maintenance of the sex ratio observed in the adult population.

6.1.4. Sex Ratio in Selected Age Classes

Another type of analysis was done by Ivanter (1975) on the basis of long-term data for a bank vole population inhabiting north-western regions of the USSR. He analysed the sex ratio in overwintered voles and in the current-year cohorts recruited into the population early and late in successive months of the year (Table 6.1). At first the proportion of males in overwintered animals was high, and it gradually declined after May. Current-year cohorts were usually predominated by males in the early months of their lives. In older cohorts the proportion of males gradually dropped, while in younger cohorts the sex ratio was 1:1 from the time when they accounted for more than 90% of the population (from October to January of the following year).

Table 6.1.
Percentage of males in three categories of bank voles in 1958—1972 (after Ivanter, 1975).

Month	Category of individuals		
	Overwintered	Current-cohorts	
		Early	Late
March	60.0	—	—
April	62.5	—	—
May	68.7[1]	100	—
June	62.4[1]	65.1[1]	—
July	58.5[1]	66.5[1]	55.4
August	49.0	62.9[1]	59.9[1]
September	11.1	31.7[1]	60.3[1]
October	—	20.0[1]	54.3
November	—	—	48.3
December	—	—	53.3
January	—	—	50.0
February	—	—	—
Mean	58.7[1]	60.5[1]	57.3[1]

[1] Denotes statistically significant deviation from 50:50.

Moreover, Ivanter (1975) found that the proportion of males of the early current year-cohort tended to increase with increasing population density in spring (from 56.2% at the beginning to 66.7% later on). He suggests that this may be explained by a higher number of males born to overwintered animals in response to the high population density. The predominance of males among overwintered voles was noted in the years of average population densities, and among the cohorts later recruited to the population in the years of low and average population densities in spring (Table 6.2). Instead, the sex ratio in the spring and autumn generations of an island bank vole population (Bujalska, 1981b) rarely deviated from the 1:1 ratio (Table 6.3), suggesting that these deviations are independent of the population density.

Table 6.2.

Percentage of males in three categories of bank voles at various population numbers (after Ivanter. 1975).

Population numbers	Category of individuals		
	Overwintered	Current-year cohorts	
		Early	Late
Low spring numbers and rapid increase until autumn	54.7	56.2[1]	56.7[1]
Intermediate spring numbers and moderate increase until autumn	62.4[1]	61.7[1]	57.5[1]
High spring numbers and slow increase until autumn	57.8	66.7[1]	55.0

[1] Denotes statistically significant deviation from 50:50.

Table 6.3.

Mean male : female ratio ($\bar{z}$) in spring and autumn generations of the bank vole (after Bujalska, 1981b).

Year	Generation			
	Spring		Autumn	
	$\bar{z}$	95% confidence limits	$\bar{z}$	95% confidence limits
1966	1.0407	0.9801—1.1013	0.8662	0.3289—1.4035
1967	1.2855	1.1298—1.4412	1.4266	1.2442—1.6090
1968	1.1221	0.9736—1.2706	0.8607	0.5418—1.1796
1969	—	—	0.9328	0.8363—1.0293
1970	0.9683	0.8255—1.1511	0.5342	0.5204—0.5480
1972	0.9123	0.8060—1.0196	1.0245	0.9272—1.1218
1975	0.8362	0.7806—0.8916	0.8690	0.6143—1.1237
1976	0.5995	0.4822—0.7168	0.9340	0.8153—1.0527
1977	1.1366	0.8704—1.4028	0.9704	0.7314—1.2094

6.1.5. Total Sex Ratio

As indicated above, sex ratios for different categories of individuals can vary. In some cases males predominate, in some others females. To understand the role of this variation, it may be important to know whether it intensifies in the population considered as a whole, or the differences compensate for each other.

There is a statistically significant tendency of diminished departure of sex ratio from 1:1 with increasing population numbers (Bujalska, 1981b) (Fig. 6.1), and this may suggest the occurrence of some compensatory processes at the population level. A similar relationship was found for *Microtus arvalis* (Bujalska, 1981a). It is thus possible that the 1:1 sex ratio can be established only when the population numbers reach some critical level.

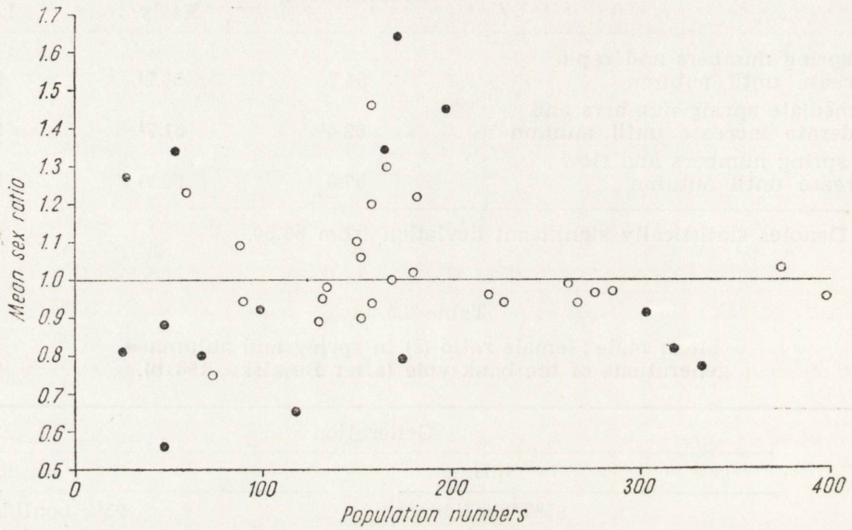


Fig. 6.1. Mean values and 95% confidence limits for sex ratio in various censuses versus population density of the bank vole.
Open circles — 95% confidence limits include 1.0, closed circles — 95% confidence limits do not include 1.0 (after Bujalska, 1981b).

It is worth reviewing the total sex ratio found by other authors for different populations. In a population of *C. rufocanus* (Kalela, 1971) it was 1:1, ranging from 47.9% males in September to 52.6% males in August (statistically insignificant differences), though there were seasonal changes in this ratio for immature and mature individuals. The same pattern was observed in different phases of the population cycle.

Despite significant differences in sex ratio of immature or of mature individuals, the total sex ratio approximated 1:1, ranging from 49.8 to 51.1% males (insignificant deviation).

Similarly interpreted data by Ivanter (1975) on seasonal changes in the sex ratio of the bank vole show a total predominance of males approximate from March to September, thus in the breeding season, while from Oct. to Dec. the sex ratio is about 1:1. In view of the mechanisms of sex ratio formation in the population, it would be interesting to know whether this is a functional regularity or merely a methodological artifact due to a higher mobility of males during the breeding season, thus the possible overestimation of their number.

Also Zejda (1967) found an equal sex ratio in a bank vole population before the breeding season (51.8% males). In April males predominated (61.0%), this being the case by the end of that month (62.5%). In the following months, overwintered voles were predominated by females and the current year voles by males.

Similarly, Bergstedt (1965) observed the predominance of males in a bank vole population in spring, while females predominated in summer. Hansson (1978), however, noted an equal sex ratio in three bank vole populations inhabiting southern, central, and northern Sweden during 1971—1975 (the only exception being females predominance in an increasing population in central Sweden in 1973).

6.1.6. Discussion

The above results of the studies on sex ratio in the bank vole show that it may differ for particular vole categories. These differences generally compensate for each other so that the resultant sex ratio in the population does not deviate from 1:1. In view of this fact we should know whether it is the result of a simple mathematical relationship due to the size of the analysed vole categories, or an effect of intrapopulation processes. Many data show that the equalizing of sex ratio occurs as a result of population mechanisms, namely, differentiated recruitment and mortality of males and females being members of different vole categories, generally age groups. To prove this, we should recognize the causal relation between recruitment and survival for males and females of successive cohorts or generations.

The deviation from the 1:1 sex ratio predicted by Fisher's theory, though generally not occurring in the bank vole populations, is rather common in populations of other species such as *Microtus arvalis* or *Myopus schisticolor*. This may be related to different strategies of number regulation in the populations of these species. An increase in the density of bank vole populations is limited due to the decline in reproduction. Among other things, this is related to sex ratio establishment among mature voles through their territorial tendency, thus independent of the population numbers. In populations producing outbreaks (e. g. *Microtus arvalis* populations), reproduction is reduced at much higher densities than in other populations. Hence, an unlimited maturing of voles is observed in these populations (Adamczewska-Andrzejewska *et al.*, 1979; Bujalska, 1981a).

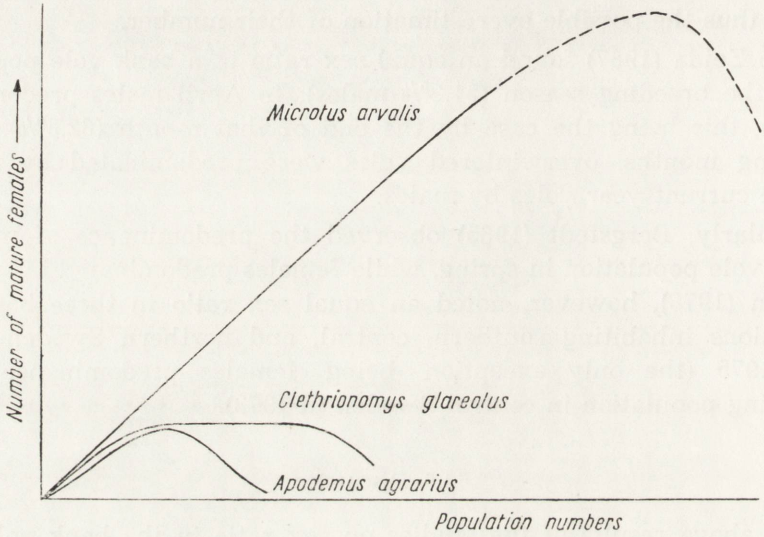


Fig. 6.2. Three curves describing relations between the number of adult females and population density (after Bujalska, 1981a).

As an illustration of changes in the number of mature individuals with changes in population densities of different species, we may quote the results obtained for *C. glareolus*, *Apodemus agrarius*, and *M. arvalis*. These species are characterized by different critical density values above which sexual maturity is delayed (Bujalska, 1981a, 1981b) (Fig. 6.2). There are differences in the rate of this process between males and females, which determine sex ratio in mature individuals at a given population density. These differences can be due to a differential "sensitivity" of males and females to a tolerable number of encounters with other individuals of the same sex. They may also be related to usually differential spatial requirements of reproducing males and females. Consequently, the sex ratio among immature individuals would depend on the number of males and females born, rate of their recruitment to the mature population and on their mortality. An analysis of the behaviour of this population "reserve" can provide information on the ways of compensation for the deviation from 1:1 the sex ratio in the entire population.

Using this approach, the categories of mature and immature individuals would be the axis of the structural division of the population, and the analysis of sex ratio in the cohorts making up these two categories would seem to be one of the most promising ways of obtaining insight into the mechanisms underlying the variablility of sex ratio in the population.

6.2. Age Structure

Joanna GLIWICZ

The age structure of a population at any given moment is the result of birth rate and death rate prior to this moment. It can be modified by migrations if there are differences in migratory tendencies among particular age classes. In turn, the age structure itself largely determines future birth rate and death rate. Therefore, knowing age structure, we can reconstruct some processes that have occurred in the population in the immediate past and also predict some future changes in its population dynamics. Consequently, it is not surprising that much attention is paid to this element in population studies.

It is not easy, however, to study age structure, especially in the wild. We can use one of two basic methods, but each of them serves slightly different purposes. Studying a poorly known population, we can use morphological and anatomical indices which vary with age and do not depend much on the condition of the animal. A critical review of such indices is given by Pucek & Lowe (1975) (see also section 2). The best indices of age in the bank vole are changes in the length of the roots of M_1 (Wasilewski, 1952; Pucek & Zejda, 1968) and changes in weight of the eye lens (Lord, 1959; Adamczewska-Andrzejewska, 1971). But to collect the material for calculating these indices, it is necessary to kill animals, and this is inconsistent with *CMR* methodology. Thus the age of living animals is determined from such indices as body weight or tail length, when their growth with age is known. These are very rough indices, however.

Another way of determining the age structure, but for a little different purpose, is based on the known population dynamics.

Under natural conditions such information can only be obtained by frequent recaptures of marked individuals. Knowing the approximate time of birth of each individual (in practice rather of a group of individuals — a cohort — which are assumed to be born at the same time), we can assess the age structure of the population at any time.

6.2.1. Changes in Age Structure

To characterize in the most general way changes in the age structure of bank vole populations it should be remembered that (1) these animals reproduce only in a breeding season of about six months (mid-March of early April to late September) and (2) they bear many litters throughout the breeding period. Moreover, the turnover is so high in bank vole populations (low mean life span) that the difference in age among animals usually is not greater than one year, rarely 18 months.

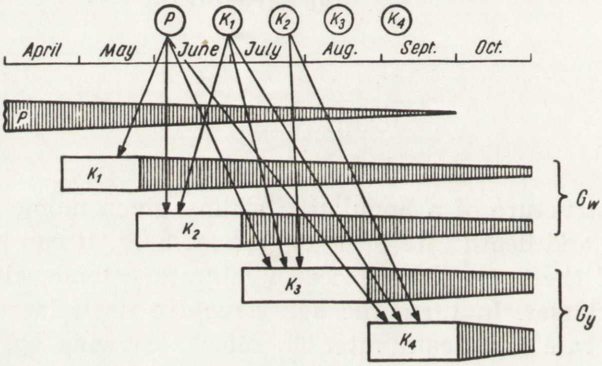


Fig. 6.3. Development of age structure over the breeding period. An island population, Poland.

P — overwintered individuals, K_1—K_4 — subsequent cohorts over the year. Arrows indicate the progeny of each cohort; G_w — spring generation, G_y — autumn generation.

The age structure of bank vole populations becomes completely changed over the six months of the breeding period. On the basis of the most general characteristics it may be stated that the bank vole population will be the oldest, that is, the mean age of individual voles in it will be the highest, in early spring, when it comprises only adults born in the preceding breeding period (overwintered). It will be the youngest immediately after the period of intense breeding, that is, when the number of the young is high and most of the overwintered voles have died. This is usually the case in summer or early autumn.

The sequence of changes in the age structure over the breeding period can be exemplified for an island bank vole population censused by the

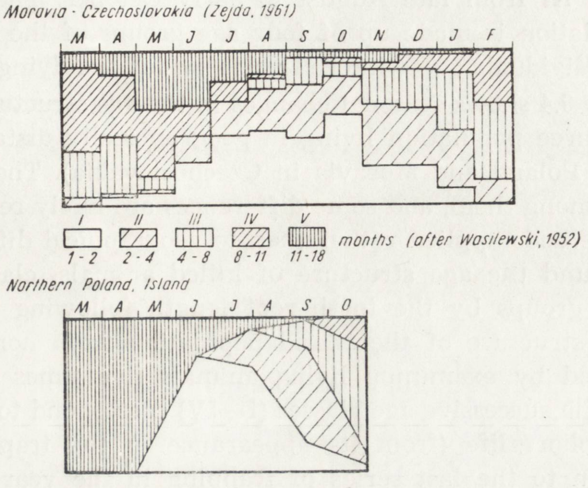


Fig. 6.4. Age structure of different bank vole populations. For explanations see the text.

CMR method (Fig. 6.3). Five age groups entering this population at different times of the season are distinguished. They consist of overwintered animals (K_0), and successive cohorts of the current-year animals (K_1—K_4)*. The first generation of the young (K_1) is born by overwintered animals in April-May and they become independent (enter the trappable population) in June. The next cohort (K_2) is born by overwintered and rapidly maturing K_1 voles in the period from the end of May to late July. Cohort K_2, in turn, gives birth, together with overwintered voles and cohort K_1, to cohort K_3 from July through August, and to cohort K_4 from late August to early October. Therefore, in autumn the population is made up of four age groups of the current-year voles and of individuals overwintered voles, which are dying out.

Figure 6.4 shows seasonal changes in the age structure of the trappable part of three population living in geographically distant areas (Sweden, northern Poland and Moravia in Czechoslovakia). There are great similarities among them, and some differences are likely related to differences in the methods applied rather than to geographical differentiation. Zejda (1961) found the age structure of killed animals, classifying them into five age groups by the tooth root length following Wasilewski (1952). The age structure of the island population from northern Poland was determined by examining living animals five times over the breeding period. The successive age classes (I—IV) correspond to successive periods in the cohort life (from its appearance in the trappable part of the population to the last series of trapping in the year of its birth). The graph of the age structure of the bank vole population in Sweden was drawn on the basis of body weight data in the population studied by Bergstedt (1965), and three weight classes are distinguished. Therefore, we can track only similarities in Figure 6.4 but not differences in the age structure of these three populations.

6.2.2. Generation-related Differences in the Fates of Even-aged Individuals

The effect of age structure on population dynamics and production increases with growing variability of such parameters as reproduction (e. g. maturing, litter size), mortality, and rate of individual growth between particular age classes. Changes in these population and individual parameters are described in other sections (changes in growth rate — section 2.3, reproduction — section 7.2, mortality — section 7.3). It is known, however, that the general characteristics of changes in

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* These cohorts are distinguished in an arbitrary way, based on the dates of successive series of trapping. All young voles captured for the first time during one of the trapping series are considered as a single cohort; the period of their birth determined along with the mean date of birth. Detailed descriptions of the history of cohorts, their characteristics, and the way of distinguishing them are given by Bujalska *et al.* (1968) and Gliwicz *et al.* (1968).

these parameters do not refer to all even-aged individuals in the population to the same degree as there are generation-related differences in individual growth and development.

The four bank vole cohorts distinguished above and which were born in the same breeding season, can be grouped in two essentially different categories: the spring generation comprising voles born in the first half of the breeding period (K_1 and K_2), and the autumn generation (K_3 and K_4). Some authors (Bobek, 1969; Zejda, 1971) have distinguished three generations, considering individuals born in midsummer as a separate group, but I will recognize two generations to enhance the contrast between their characteristics.

Bank voles born in the first half of summer grow faster than those born later. They reach maturity and reproduce in the year of their birth, in contrast to the voles from the autumn generation (Schwarz *et al.*, 1964; Bergstedt, 1965; Bujalska *et al.*, 1967; Gliwicz *et al.*, 1968; Kaikusalo, 1972; Zejda, 1971). As a result of intense growth, maturation, and reproduction their metabolism is much higher. According to Schwarz *et al.* (1964) and some others this may account for their higher mortality. Hence, the "duty" of more successfully surviving the winter and reconstructing the population in the next year would rest on the individuals born in autumn (Schwarz *et al.*, 1964; Kaikusalo, 1972). This view has not been supported, however, by the results obtained, for example, for an island bank vole population studied in Poland. Those results show that the autumn generation often survives worse than does the spring generation, and it usually does not form the bulk of overwintered animals (Gliwicz, *et al.*, 1968; Petrusewicz *et al.*, 1971; Bujalska, 1975a; Gliwicz, 1975; 1976). This discrepancy in views on the role of the autumn generation in bank vole populations may be related to climatic differences between the study areas. It may be expected that the additional energy expenditures for intense maturing and reproduction excessively burden the voles of the spring generation living under severe climatic conditions, thus already having high energy requirements and increased metabolism. For this reason they may live a shorter life and die during their first autumn in those areas. In the areas with less severe climate, the survival of the two generations follows a different pattern.

6.2.3. Age Structure in Overwintered Animals

Because individuals of the two generations differ in their characteristics, it is important to know their proportions in the population. The best time to ascertain this is at the end of the breeding period (end of October), when the youngest individuals have become independent. In this way we have access to the age structure of the population entering the winter period, and, at the same time, the age structure of overwintered animals, since it is generally agreed that winter mortality is independent of age. (see section 7.2). This simplified picture of age structure, with only two groups considered, is a very important population characteristic, which allows conclusions on population dynamics from knowledge of the possible fates of individuals belonging to these groups, and which enables comparison of different populations or the same population in different years.

For example, the age structure of the island bank vole population discussed above was markedly different in autumn (October) for two successive years (Fig. 6.4). Analogous differences occurred in the age structure of overwintered animals (Fig. 6.5). In the spring of 1967, the voles of the preceding spring generation accounted for 93% of the overwintered animals, leaving only 7% for the autumn generation. The respective figures in the spring of 1968 were 43 and 57%. What can be said from this about past and future fates of the population? In 1966, the net production (number born minus nestling mortality) in spring must have been much higher than in autumn. This difference was probably even greater than indicated by the age structure in autumn or spring of the following year because the voles born in spring, being older, were subject for a longer time to the action of different mortality factors. Therefore, in 1967, the group of overwintered animals was rela-

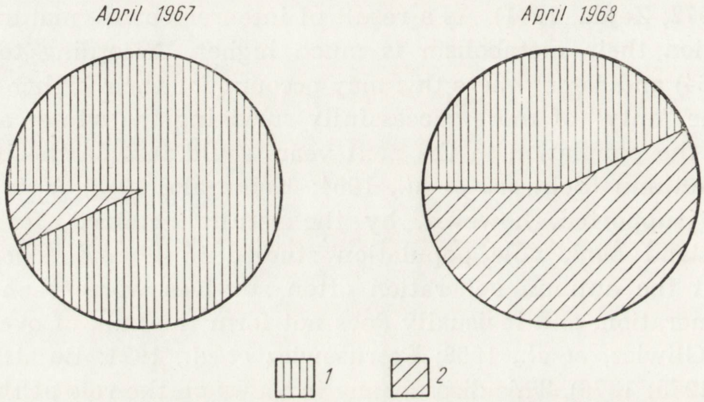


Fig. 6.5. Age structure of overwintered bank voles in the spring of 1967 and 1968 after a high population peak in 1966 and a low population peak in 1967 (island population).
1 — spring generation of previous year, 2 — autumn generation of previous year.

tively uniform (with a small admixture of autumn generation). It consisted mostly of individuals that reproduced in 1966. Moreover, most of these voles were born and grew under similar climatic and habitat conditions, characteristic of the first half of the breeding season. Finally, it may be suggested that the social hierarchy was relatively well developed among those individuals because a large number of them reached independence simultaneously, and tried to find their places in the spatial and social structure of the population at approximately the same time. Such situations should enhance a strong dominance structure. In turn, in 1967, the spring generation increased slower than in 1966, thus more or less at the same rate as the autumn generation. Recruitment of young must have been similar for these two generations. The population of overwintered animals in the spring of the following year was, however, more diversified. It comprised individuals that had reproduced the preceding year as well as individuals just reaching maturity. It is probable that social relationships among them were less antagonistic. As a result, the overwintered animals survived better in 1968 (Gliwicz, 1975) and their offspring survived better as well (Bujalska, 1975a). This generated higher population numbers in that breeding season, to a different age structure, and thus changes in other population parameters.

Cyclic changes in the age structure of overwintered animals in bank vole populations, and the effects of these changes on population dynamics have also been recorded by Zejda (1967) and Pucek & Pucek (in litt.). Also Hansson (1969a) observed that in the year of a high population density, the overwintered animals were youngest, while in the year of a low population density they were oldest (more than half were recruited from the first spring litters of the preceding season). All these observations suggest that the population age structure can be a component of intrapopulation mechanisms of number regulation, thus determining population level.

6.3. Spatial Organization of the Population

Maria MAZURKIEWICZ

According to Naumov (1956), bank voles live singly or in families, and spatial structure of their populations as well as forms of individual interactions are realized through a system of home ranges. A general characteristic of the spatial organization of the population can, therefore, be obtained by examining dynamic changes in the size of home ranges for individuals of different categories.

The home range was defined by Burt (1943) as the space surrounding a permanent dwelling of the animal, where it is searching for food, breeding, rearing the young. An individual inhabiting a relatively stable home range over its life span becomes familiar with it, and due to this it can find food easily and without large losses of energy, or a shelter from predators and adverse weather. The interest of ecologists in home ranges of small mammals, including bank voles, arose partly from the fact that there is a relationship between the size of home ranges as a species-specific characteristic determining spatial organization of the population and other aspects of population organization (Brown, 1966; Bujalska, 1970, 1973, 1975a; Rajska-Jurgiel, 1976) its dynamics (Merkova, 1955; Naumov, 1956; Ryszkowski, 1962; Kulicke, 1962; Nikitina & Merkova, 1963; Koshkina, 1967; Kučera, 1968; Zejda & Pelikán, 1969; Mazurkiewicz, 1971), also competition (Andrzejewski & Olszewski, 1963a; Andrzejewski *et al.*, 1964; Aristova, 1970) and epizootic disease (Karaseva, 1956).

In studies on the size of home ranges, methods are a difficult issue. The same methods are used for bank voles as for other species of cryptic small mammals. Difficulties concern the reliability of the information collected and with data processing method. Information on the size of home ranges, as the basic element of the spatial structure, can be collected by direct observation of animals or traces left by them, but most frequently the materials obtained from trapping by the *CMR* method are used for this purpose. In contrast to direct observations, which allow data collecting for only a small number of individuals, the *CMR* method provides information on almost all animals living in a given area. Another advantage of the *CMR* technique over direct observations lies in the fact that it also provides data on other population parameters (e. g. number dynamics, age and sex structure), thus it allows the observation of changes in spatial organization with reference to these parameters.

6.3.1. Characteristics of Home Ranges

Home range size. The size of a home range can be estimated from information on the places in which individual animals were trapped. As there are many methods differing in their approach to the estimation of home range size, they will be reviewed below. In general, they can be classified into cartographic and statistical methods.

The cartographic methods use the data collected to construct ts early as possible an exact distribution of the points at which individual animals were caught to determine the size of their home ranges. For example, this group of methods is represented by the so-called "Minimum Area" technique (Dalke & Sime, 1938; Mohr, 1947). It determines the surface area of the convex polygon containing all the points at which an animal was trapped.

Statistical methods determine the mean size of a home range by analysing the way in which the animal moves within it. Included here is the method of the greatest or the mean distance covered by an individual over the study period (Chitty, 1973; Godfrey, 1954; Brown, 1956) as a measure of the home range radius, or the method developed by Wierzbowska (1972), based on the relationship between the probability of visiting particular trapping points by an individual and the size of its home range. Also the concept of a centre of individual activity as the geometric centre of all the points of capture of an individual and changes in the probability of its capture with increasing distance from the centre (Hayne, 1949) prompted development of a theoretical model of the home range. Dice and Clark (1953) assumed in this model

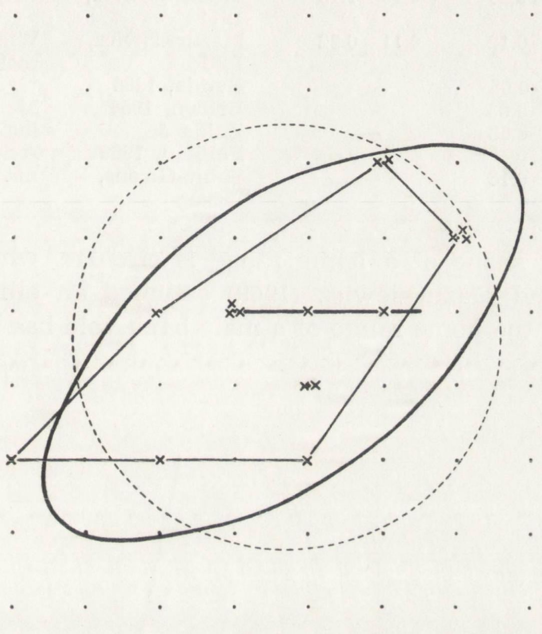


Fig. 6.6. Home range of male 127, as calculated by different methods. · — trapping points, x — points of effective capture, home range size in ha: polygon — 0.27, ellipse — 0.55, circle — 0.64, Wierzbowska's method — 0.32, mean distance as a radius — 0.04.

Table 6.4.
The size of home ranges (in ha) in summer as estimated by different authors.

Males	Females	Young males + females	Author	Method of estimation
0.9	0.09—0.28	0.08—0.23	Aristova, 1970	not specified
0.89—1.1	0.05—0.14	0.07—0.20	Nikitina & Merkova, 1963	not specified
0.10—0.45	0.02—0.25	0.01—0.33	Naumov, 1951	"
0.01—0.23	0.08—0.15	0.01—0.24	Golikova, 1958	"
0.20—0.88	0.16—0.56	0.12—0.84	Koshkina *et al.* 1972	"
2.00—2.20	0.19—0.32	0.10—0.25	Nikitina, 1961a	"
0.77—1.39	0.13—0.20	0.13—1.18	Mazurkiewicz, 1971	elliptic model
0.12—0.25	0.11—0.12	0.11—0.22	Mazurkiewicz, 1981	Wierzbowska's method (1972)
0.30—0.50	0.05	—	Radda, 1968	"Minimum Area"
0.08—0.70	0.07—0.63	—	Brown, 1956	Manville's method
0.02—0.48	0.02—0.63	—	Zejda & Pelikán, 1969	inclusive boundary strip
0.02—0.16	0.01—0.18	—	Saint-Girons, 1960a	not specified

that the general shape of a home range is circular, while Jennrich & Turner (1969) and Mazurkiewicz (1969) assumed an elliptical shape.

For example, the home range of a male bank vole has been calculated

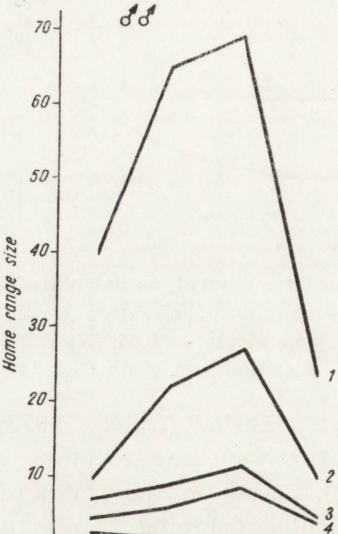


Fig. 6.7. Seasonal changes in home ranges as calculated by different methods (1 = 225 m²).
1 — circle method, 2 — elliptic model, 2 — "Minimum area", 4 — Wierzbowska's method, 5 — mean distance.

using the methods listed above and by the mean distance covered over a two-week period. The results vary from 0.04 to 0.64 ha (Fig. 6.6). Therefore, the choice of the method, which strongly depends on author's views of space utilization by an animal, anticipates the results, this being frequently the case in ecology. There are many literature data on the size of home ranges for the bank vole, and they differ markedly because different methods were used (Table 6.4). Thus, absolute values of home range sizes should be considered as rough approximations. It seems, however, that the analysis of changes in the size of home ranges with time is not significantly affected by the methods used. This is shown in Figure 6.7 illustrating seasonal changes in the mean size of home ranges for males of an island bank vole population, as calculated by the methods discussed (Mazurkiewicz, unpublished data). Except for the mean distance method, which was insensitive, all the other methods show similar trends in changes of the size of home ranges, though at different mean levels.

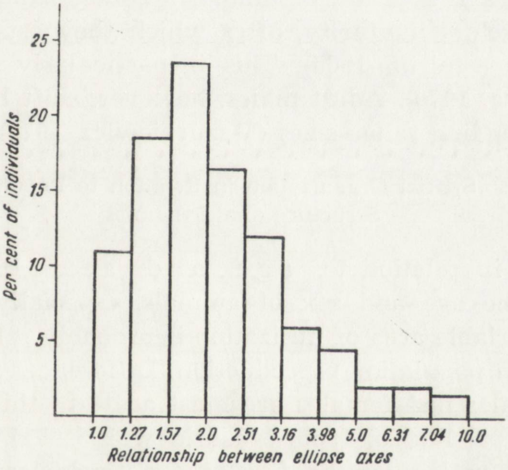


Fig. 6.8. Distribution of individual bank voles in relation to the degree of elongation of their home ranges.

Home range shape. Many data show that home ranges of the bank vole are frequently elongated, and the animals follow run along preferred paths (Tanaka, 1953; Mohr, 1965; Mazurkiewicz, 1971). Also maps of bank vole home ranges published in many papers to analyze their size (Naumov, 1951; Karaseva, 1956; and others) concur. Such a parameter as shape makes it possible to examine the effect of environmental, biocoenotic, or intrapopulation factors inhibiting some directions of animal movements and enhancing others. Characteristics of the shapes of individual home ranges can be obtained using the elliptical model for estimating home range size. Such an analysis exist for more than 1000 bank voles of an island population (Fig. 6.8) (Mazurkiewicz, 1971), and for bank voles living in an open population (Mazurkiewicz, 1969) in order to eliminate the possible effect of the limited surface area of the island. In both cases, the shape of home ranges was elongated (the mean elongation expressed as the ratio of the ellipse axes was 2.5—3.6).

Duration of home ranges. In addition to the size and shape, the general characteristic of a home range should also include its existence in space and time. Duration influences the estimate of the home range size (if the home range is shifted during the study area, its size will be overestimated), as well as processes occurring in the population (see section on migrations). Usually, it is assumed that bank voles are characterized by a high site tenacity, and differences in the size of home ranges result from their seasonal shrinkage or extension (Naumov, 1951; Nikitina, 1970; Koshkina *et al.*, 1972). Site tenacity may thus depend on age and sex of animals. Young bank voles are highly mobile until reaching maturity, after which they establish and attache to home ranges (Smirin, 1965). This is particularly the case of adult females (Aristova, 1970). Adult males, however, shift home ranges while reducing or extending range sizes (Mazurkiewicz, 1971).

6.3.2. Spatial Organization in Relation to Population Structure and Dynamics

Home range in relation to age and sex. Home range size is a function of the age and sex of animals, especially in overwintered animals. This variable area of utilization is probably related to their most important role in population reproduction. Differences in the home range size between males nad females are most acute in this group (Manville, 1949; Brown, 1965; Radda, 1968; Mazurkiewicz, 1971). The home ranges of overwintered males can be five to ten times larger than those of females (Naumov, 1951; Nikitina & Merkova, 1963). Also the degree of their elongation may be different. Males have very long ranges with an axis ratio of 3.0—3.6, while for females this ratio is 2.1—2.4 (Mazurkiewicz, 1971). Differences in both the size and the shape of home ranges between males and females primarily result from their differential space utilization. Home ranges of females are better delimited and they do not overlap (Naumov, 1951; Ilyenko & Zubchaninova, 1963; Aristova, 1970; Bujalska, 1970). The distribution of home ranges of adult females is related to reproduction and the need for securing adequate food supply (Bujalska, 1973). Instead, the home ranges of males largely overlap. Differences in the size of home ranges between males and females can also be observed in even-aged groups of voles born in the current year, but they are not so drastic as in the case of overwintered animals (Naumov, 1951; Mazurkiewicz, 1971).

Seasonal changes. Changes in population numbers from spring through autumn are accompanied by changes in the spatial organization of the population. In spring, when the population is made up only of overwintered animals, males occupy large and long home ranges located in several directions according to the location of female home ranges (Mazurkiewicz, 1971). A high mobility of males at that time (Smirin, 1965; Zejda & Pelikán, 1969) increases the frequency of contacts with females. Naumov (1951) found that males cover home ranges of several adult females, though two adult males have never been caught in the home range of the same female at the same time. Females have small, isolated home ranges and are less mobile (Radda, 1968), particularly during gestation and lactation (Nikitina & Merkova, 1963).

The position of generations entering the population from June to October within the spatial structure of this population depends on many factors. The most important seem to be the actual composition and density of the population at the time of the appearance of a new cohort, the abundance of this cohort and its role in reproduction (Naumov, 1951; Bock, 1972). In an island bank vole population a relationship has been found for males between the sequence of their recruitment to the population and the size of their home ranges (Mazurkiewicz, 1971; Andrzejewski & Mazurkiewicz, 1976). The later a cohort was recruited, the smaller were home ranges of males. Home ranges of females belonging to different cohorts were similar. Also Bujalska (1970, 1973) found for the same population that the home ranges of mature and immature females do not differ in size. However, according to Naumov (1951), home ranges of adult and subadult females are 1.5 to 2 times larger than those of young females. In new cohorts as in overwintered animals, the home ranges of males are larger than those of females (Fig. 6.9). The shape of individual home ranges in particular cohorts shows irregular changes with time and it tends to "round out" from spring to autumn (Mazurkiewicz, 1971).

After the breeding season, such features as age and maturity of population members and their participation in reproduction have less effect on the spatial structure of the population. Consequently, in autumn a decline is observed in the differentiation of the size of home ranges between cohorts and of the two sexes. The smallest home ranges occur in winter (Saint-Girons, 1960a; 1961; Ilyenko & Zubchaninova, 1963; Nikitina & Merkova, 1963) when bank voles are most sedentary. At the end of winter, prior to the breeding season, individual home ranges are increasing (Ilyenko & Zubchaninova, 1963).

Spatial distribution of individual voles. In the literature there are data indicating that individual bank voles tend to occur in aggregations because of habitat heterogeneity (Bock, 1972) or interspecific competition (Naumov, 1948; Larina, 1957; Turček, 1960; Krylov, 1975). Differences in the size of home ranges related to the age and time of recruitment of individual bank voles to the population (Naumov, 1948; Mazurkiewicz, 1971) show that there are some spatial relationships among individuals of different age-classes. This is also indicated by differences in the distribution of individual voles in an island population with reference to the population density and the proportion of young animals (Mazurkiewicz, 1981). A clumped distribution is observed in this population in spring at low density (about 20 voles/ha). This is an effect of a high activity of males on the island, which occupy large widely overlapping home ranges at that time. Mature females, however, are rather evenly distributed (Bujalska, 1970). A tendency towards

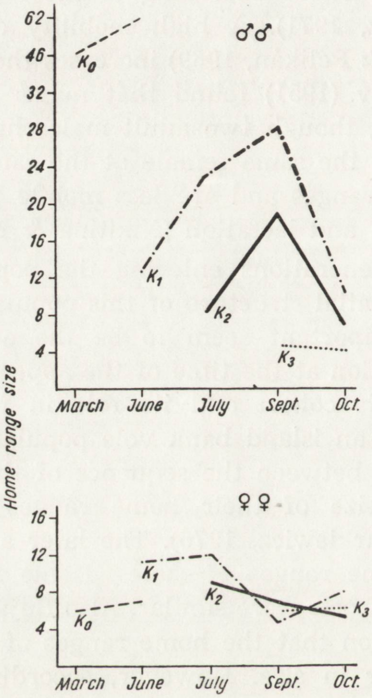


Fig. 6.9. Seasonal changes in the size of home ranges of different generations (1 = 225 m²).

clumping at low population densities of the bank vole was also observed by Krylov (1975). In summer and autumn the general character of the distribution of individuals in the population depends on the proportion of young voles in it. Bujalska (1970), who analysed the distribution of mature and immature females, found that the latter had a clumped distribution. Also the general analysis of the distribution of bank voles on the island shows that the clumped distribution occurs when the youngest individuals are several times more abundant than adults (Fig. 6.10).

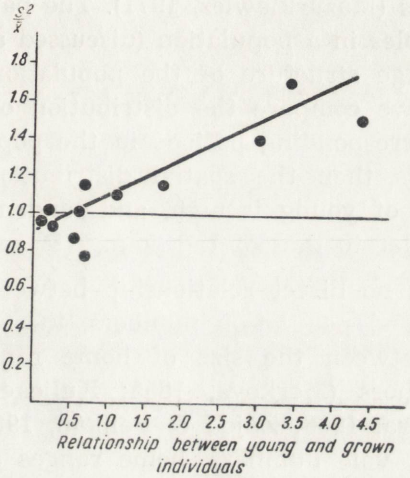


Fig. 6.10. A relationship between the degree of clumping and the proportion of young individuals in the population ($r = 0.871$, $p > 0.001$).

Therefore, in addition to the environmental factors mentioned above, the age and sex structure of the population importantly determines the distribution of bank voles.

6.3.3. Vole Numbers in Relation to Spatial Organization of the Population

Patterns of number dynamics in bank vole populations vary from year to year, and as a result, population numbers can be high or low (see section on population dynamics). Let us try to see whether and to what degree the spatial structure of the population varies in the years of differing population numbers.

It seems that some features of the spatial structure do not depend on the total population size, thus they are constant to some degree. One of these features is the differentiation of home ranges between males and females. Males always take larger home ranges than females in the years of both peak numbers and low numbers (Zejda & Pelikán, 1969; Mazurkiewicz, 1971; Andrzejewski & Mazurkiewicz, 1976). Also the relationship between the time of the recruitment of a cohort to the population and the size of individual home ranges in males holds at any population density. Also males from late cohorts have smaller home ranges than males from early cohorts (Mazurkiewicz, 1971; Andrzejewski & Mazurkiewicz, 1976). A decrease in the mean size of home renges in autumn, as well as its differentiation between different cohorts and between males and females are observed in both declining and increasing populations (Mazurkiewicz, 1971). The pattern of distribution of individual bank voles in a population (discussed above) seems mostly determined by the age structure of the population. This is indicated by the fact that if we compare the distribution of voles in different years but for the corresponding periods in the populations life and at similar density levels, then the spatial distribution will be clumped when the proportion of young is high, and random when the proportion of adults is similar to that of the young (Mazurkiewicz, 1981).

Although there is no direct relationship between many features of spatial organization and population numbers, there is, however, a general relationship between the size of home ranges and population numbers. Many authors (Merkova, 1955; Kulicke, 1962; Nikitina & Merkova, 1963; Kučera, 1968; Zejda & Pelikán, 1969) have found that in the years of high vole numbers, home ranges are smaller than in the years of low numbers. An analysis of the mean size of bank vole home ranges in the years of population peaks and depressions for the island population yielded similar results (Mazurkiewicz, 1981). Home range size is also influenced by the available food supply since bank voles search smaller areas in rich vs poor habitats (Golikova, 1958; Bovet, 1962; Nikitina & Merkova, 1953). It is known that the food abundance is one of the basic factors determining bank vole numbers (see section on habitat preference); an experimental increase in food supply for the island bank vole population was followed by a several-fold increase in numbers, as compared with numbers at natural food supply (Andrzejewski, 1975; Bujalska, 1975a), and, at the same time, home ranges were reduced in size (Andrzejewski & Mazurkiewicz, 1976; Bujalska, 1975b).

These data clearly indicate that we may speak about interrelatedness of food resources, population numbers, and spatial organization of the population (as expressed by the size of home ranges, the most easy measured parameter). There is a question, however, whether changes in the available food resources affect the population size through modifying its spatial structure, or whether the character of the spatial structure is an effect of the population numbers, which is directly determined by the available food supply. In the first case the increase in food resources accounts for a decrease in the area covered by animals in search of food (an adequate food supply can be found within a smaller area). As a result, agonistic interactions among mature females may be reduced and, consequently, more females may have chances to reproduce than in the case when food resources are scarce (Bujalska, 1975b). A high birth rate and high infant survival result in a significant increase in numbers (Bujalska, 1975a). In the second case, abundant food supply has a direct effect on population numbers through a positive effect on the condition of animals (Andrzejewski, 1975) and their low mortality (Bujalska, 1975a, 1975b). The increase in population density intensifies agonistic intraspecific interactions and, as a result, leads to a reduction of the area they search. Both possibilities seem to be equally probable in the light of the data presented above. It is also possible that both are realized at the same time. The considerations presented above on the role of the spatial structure in the life of the population and individual animals are schematically illustrated in Figure 6.1.1.

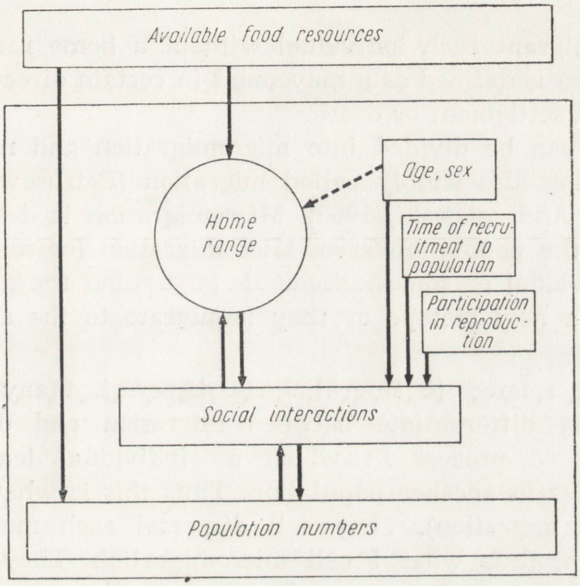


Fig. 6.11. Possible effects of ecological factors on the size of home ranges.

6.4. Residents and Migrants in the Population

Kazimierz PETRUSEWICZ

6.4.1. Concepts Related to Residency and Migration

The problems of migration and residency have prompted much controversy about the terminology and the essence of this issue. Therefore, I shall start by discussing the concepts and the relevant terminology.

I call a migrant each individual without a home range at a given time. Migration is defined as a movement in certain direction or without direction until settlement or death.

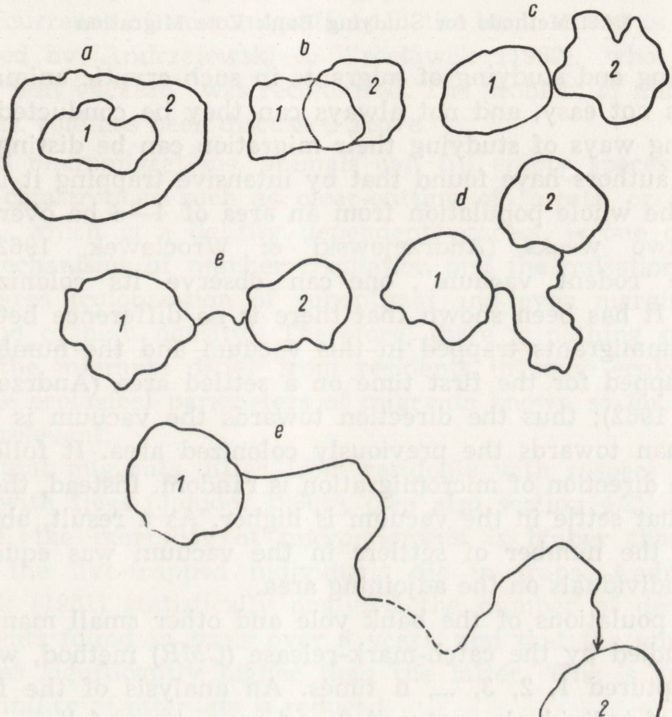
Migration can be divided into micromigration and macromigration, the latter being also simply called migration (Petrusewicz & Andrzejewski, 1962; Andrzejewski, 1963). Micromigration is defined as movement within the population area. Micromigration (or migration) occurs when an individual or some individuals go beyond the population area, and colonize a new biotope or they immigrate to the area of another population.

A concept related to migration is dispersal. Many authors (e. g. Lidicker, 1975) differentiate between migration and dispersal. They call migration a process in which an individual leaves its population or settles in another population. Thus this is what I call macromigration (or migration). They call dispersal each movement within the population, thus what I call micromigration. They use the term "vagrants" for micromigrants, and call them "homeless travelers". It seems that when I speak about micromigration and migration (macromigration), there is no need to distinguish migration and dispersal as a process. Micromigration usually has no direction or it may occur in many directions. Interpopulation migration can have a direction — searching for a new area (Naumov, 1969), or it can have no or many directions (e. g. sparrows in autumn, according to Pinowski, 1965).

In this paper I will call dispersion the result of migration, that is, distribution. By contrast, the process of movement in search of new areas, I will call migration. Obviously, the terms migration and dispersion can be used as synonyms. Then the term dispersion will have a double meaning: the process of dispersal movements (migration, as proposed here) and its result, distribution.

Macromigration, that is, leaving the area of the population and settling within the area of another population, has not been described for the bank vole so far. It is obvious that for longer periods of time macromigration is a logical postulate. The island we have studied on a lake had to be colonized at some time in the past; this was a macromigration — settling in a new habitat. However, there are no literature data on macromigration, therefore I will discuss only micromigration.

I have defined micromigration as the process of movement beyond



Fg. 6.12. Changes in the area and migration. 1 — original area, 2 — new area. Explanations see text.

the population area till settlement in a new area (or death). But there is no a clear-cut boundary between the change of the area and migration (Fig. 6.12). The cases *a*, *b*, and *c* in Figure 6.12. I will certainly consider as a change in the area without migration, while *e* is a micromigration. But there is a certain doubt in cases *c* and *d*. Surely the old area has been left and a new area has been colonized. But if this new area was within an hour or a day, is this still a migration? This question cannot be answered satisfactorily. Besides, I have no data on the distance of bank vole migrations. These issues will be discussed in more detail in the next subsection.

To end these preliminary remarks, I wish to emphasize that the tendency to migrate need not be genetically determined. There are many data (Naumov, 1956; Andrzejewski & Wrocławek, 1962; Petrusewicz & Andrzejewski, 1962; Andrzejewski, 1963), indicating that a migrating individual become settled and a settled individual became a migrant.

6.4.2. Methods for Studying Bank Vole Migration

Recognizing and studying of migrants in such cryptic animals as the bank vole is not easy, and not always can they be conducted directly. The following ways of studying their migration can be distinguished:

1. Many authors have found that by intensive trapping it is possible to remove the whole population from an area of 4—6 ha over a period of about two weeks (Andrzejewski & Wrocławek, 1962). Then, creating the "rodent vacuum", one can observe its colonization by immigrants. It has been shown that there is no difference between the number of immigrants trapped in this vacuum and the number of individuals trapped for the first time on a settled area (Andrzejewski & Wrocławek, 1962); thus the direction towards the vacuum is not more attractive than towards the previously colonized area. It follows from this that the direction of micromigration is random. Instead, the number of rodents that settle in the vacuum is higher. As a result, about three weeks later the number of settlers in the vacuum was equal to the number of individuals on the adjoining area.

2. When poulations of the bank vole and other small mammals are intensely studied by the catch-mark-release (*CMR*) method, we get individuals captured 1, 2, 3, ..., n times. An analysis of the frequency distribution of individuals captured 2 and more times follows an exponential curve. Individuals captured only once do not fit the exponential curve (Andrzejewski & Wierzbowska, 1961; Wierzbowska & Petrusewicz, 1963). They are clearly more abundant. It may be suggested that the individuals trapped 2 and more times are residents. Among the individuals caught only once there are residents with a short time of presence and also migrants, that is, individuals only passing through the study area, so cannot be recaptured (Wierzbowska & Petrusewicz, 1963).

6.4.3. Ecological Effects of Micromigration

Ecological effects of micromigration are important and of different kinds. In the first place one should consider the intrapopulation dispersal: individuals born in any place need not live in this place, but they disperse over the population area. This enhances gene exchange.

In my view, each species must have passive or active means of dispersal (migration and micromigration). The ability to disperse is a necessary condition for permanent existence of each population. Even sessile organisms must have a possibility of dispersal. This is clearly shown in the study on periphyton (Pieczyńska, 1964). Periphytic organisms, are by definition, sessile. Nevertheless, a smaller or larger part of individuals, depending on waving, float in water and then resettle.

The occurrence of micromigrations in the bank vole was conclusively documented by Andrzejewski & Wrocławek (1962), who found that a 4-ha "rodent vacuum" was recolonized. The problem of micromigration in the bank vole has been discussed above.

Due to micromigrations, animals can fill empty spaces created by different catastrophes such as clear-cutting of forests, or local floods. Migration, which is a density dependent process, is one of the more precise mechanisms of number regulation and the pulsation of the population area (colonization of suboptimal and even marginal habitats in a period of high density). Therefore, there is nothing surprising in the fact the migrants differ from residents in some ecological traits. Among the ecological parameters of migrants known so far, the following seem relevant:

First, that migrants differ from residents with respect to their infestation with fleas (Janion, 1960b), (see also section 4.2).

Second, the mortality of micromigrants is higher than residents. Some of the live-trapped individuals die in traps. Andrzejewski & Wrocławek (1961) statistically analysed the number of dead migrants and residents found in traps over 6 years, and that the number of the former was significantly higher than the latter. This is an indication that the vitality of migrants is reduced.

Finally it has been shown that micromigrants are more vulnerable to predation than residents. Pielowski (1962) found that most of the bank voles recorded in the diet of vipers were migrants (see section 3.3).

The increased mortality of migrants suggests that immigration — as expressed by numbers entering an area — should be lower than emigration i. e., numbers leaving the area. Although this has not been empirically confirmed, it appears to be a logical consequence of the increased mortality of migrants as compared with residents. Thus, not all emigrants will have time to become residents, some of them wiil die during migration. As a result, the number of immigrants will be lower than emigrants, especially if one considers a sufficiently large area to exclude immigration into an particularly suitable area.

To some degree it is possible to determine the number of immigrants

(Fig. 6.13), however, it is unable to determine the number of emigrants. Using the calendar of captures one can estimate the number of individuals disapearing from the study area. It is not known, however, how many of them died and how many emigrated. For this reason the number of individuals that disappeared is often called elimination (mortality),

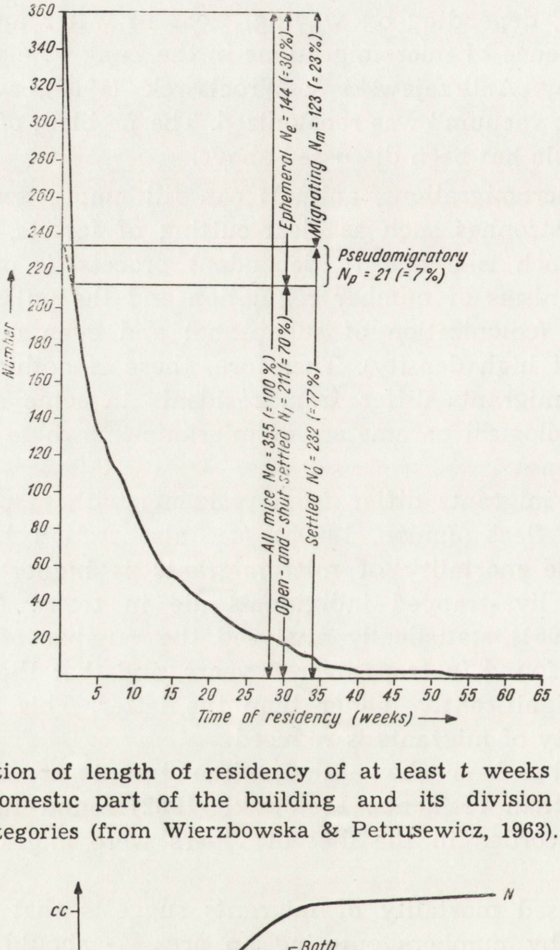


Fig. 6.13. Distribution of length of residency of at least *t* weeks in a population of mice in the domestic part of the building and its division into ecological categories (from Wierzbowska & Petrusewicz, 1963).

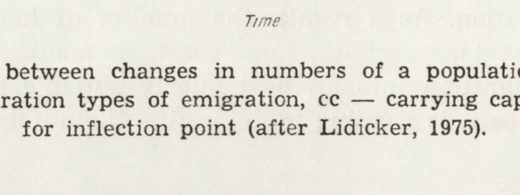


Fig. 6.14. Relation between changes in numbers of a population and both saturation and pre-saturation types of emigration, cc — carrying capacity, ip — stands for inflection point (after Lidicker, 1975).

though some of them could emigrate. A statement is justified for the study area ("an individual disappeared from this area") but the extrapolation of study area parameters to the whole population can be misleading. Some individuals that disappeared from the study area (10.0 ha, 1.7 ha, 2 ha, 4 ha, 6 ha) could establish a home range in another part of the same population.

Macromigration has a much greater influence on population numbers. This is a loss from the population. The size of macromigration for most species cannot be estimated, thus mortality and macromigration are frequently combined and called gross mortality. When macromigration occurs, it can account for a large part of elimination and, together with mortality, determine population numbers.

Lidicker (1975) distinguished pre-saturation dispersal (migration) and saturation dispersal. This seems an important distinction, and the difference in ecological consequences deduced by Lidicker is convincing (Fig. 6.14). Among more important ecological consequences quoted by Lidicker there are: (1) individuals taking part in pre-saturation emigration are in a good condition; these are not weak animals driven away as is the case during saturation emigration; (2) pre-saturation migration prevents overcrowding in the place of birth. In the bank vole, this migration begins in spring, thus long before peak numbers are reached (see above).

In many studies carried out at the Institute of Ecology PAS, particularly in papers by Andrzejewski (1963) and Kozakiewicz (in litt.), it hat been found that:

- micromigration in the bank vole occurs throughout the year (thus there is also a pre-saturation migration);
- it differs in intensity depending on the population density (saturation migration); since the highest population densities occur in autumn (September-October), the largest migration is observed at that times;
- migrants consist largely of 4—6 week old animals (Kozakiewicz, 1976);
- the body weight of migrants is lower than residents of the same age classes (Kozakiewicz, in litt.); this can be explained by their being driven away by stronger animals (saturation migration), or by the deterioration of their condition during migration;
- the mortality of migrants is higher (Andrzejewski & Wrocławek, 1961), and they are more vulnerable to predation (Pielowski, 1962).

It is thus clear that migrations have important effects of different kinds on population functioning.

6.5. Social Organization

Joanna GLIWICZ & Ewa RAJSKA-JURGIEL

6.5.1. Methods of study

The study of the social structure, e. g. of interactions among population members, in rodent populations is methodologically difficult. The best method, successfully used by workers dealing with primates, large predators and ungulates, is direct observation. But the application of this method to the studies of small, generally non-colonial rodents which are mostly nocturnal is very limited. In fact, in can successfully be used only in laboratory populations, but in that case we study social relations among individuals living in densities that differ from natural ones. This is true of spatial structure, food availability, etc., and all these factors may substantially modify social organization. For this reason the most reliable results on social organization in rodents have been obtained for laboratory populations of rats and house mice (e. g. Calhoun, 1952, 1956; Petrusewicz, 1957, 1960, 1966b; Crowcroft, 1966), since for these animals, laboratory conditions deviate little from natural conditions. All these studies have shown that social organization in rodent populations has an important effect on many population processes such as birth rate, death rate, or migrations. Consequently, the knowledge of the social organization in the population is necessary for understanding the mechanisms of population functioning.

Direct observation allows recognition of the type of encounters among individual animals. These encounters may be tolerant or aggressive, resulting in a fight or an escape of attacked animal; escape of both or mixed variants of these behaviours. Thus, to get a general picture of social ogranization in the population through direct observations, it is necessary to develop a system of classification that would allow a transition from subjective statements to numerical estimates for the entire group. Nearly every investigator applies a different classification of the encounters observed. The direct laboratory observations of the social structure for the genus *Clethrionomys* were conducted by Johst (1967), Mihok (1976) and Skirrow (1969).

As such observations are labour-consuming and somewhat subjective, it is interesting to note Kock & Rohn's (1971) finding that in laboratory populations of *C. glareolus* and *Lemmus lemmus* there is a close inverse relationship between the rank in the social hierarchy and the intensity of activity wheel running by individuals.

The method of direct observation of individual interactions in free-living population has been used on very rare occasions. The best results were obtained by means of a noctovisor (Andrzejewski & Olszewski, 1963b), but only a small part of the population can be observed in this way.

The largest number of data on the social organization of free-living populations has been obtained by persistent live-trapping. This method allows only indirect conclusions concerning individual interactions, on the basis of differences in the parameters that can be determined as a result of frequent trapping. For example, it has been found that the trappability of individual voles indicates their social rank (Gliwicz, 1970; Watts, 1970a; Andrzejewski & Rajska, 1972), and that there is a close relationship between the trappability of individual voles and the size of their home ranges, occupancy of better microhabitats, and sometimes the rhythm of activity (Andrzejewski, Petrusewicz & Waszkiewicz-Gliwicz, 1967). Thus, each of these characteristics is also closely correlated with the social rank of an individual.

The most recent method for recording intraspecific contacts in the field is the application of two-compartment traps, which allows the observation of the sequence of capture of two animals. Frequently, this method is modified in such a way that an animal of known characteristics is put to one of the two compartments, and the animal caught aftewards is noted (Kalinowska, 1971); Kołodziej *et. al.,* 1972). This method is based on the assumption that since some individuals enter the trap and other do not, is a result of their mutual tolerance, avoidance, or attraction.

6.5.2. General Characteristics of Social Organization

Intraspecific contacts in the bank vole populations are much more frequent than in populations of co-occurring species, e. g. *Apodemus flavicollis* (Turček, 1960; Andrzejewski & Olszewski, 1963a; Kalinowska, 1971). For example, Kalinowska (1971) has found that the traps already containing one bank vole are more frequently visited by another bank vole than are empty traps or traps containing *A. flavicollis.* At the same time, traps with *A. flavicollis* were much less often visited by individuals of both the same and other species than indicated by a random distribution of events. Similarly, Rajska-Jurgiel (1976) recorded many more visits to the traps with bank voles than to empty traps. This suggests that social bonds are strongly developed in these rodents, thus intraspecific relationships should have a significant effect on demographic processes in the population. Additionally, studies on bank vole populations inhabiting a large forest site and a 4-ha island showed that social organization is more pronounced and that avoidance or attraction is stronger in the isolated island population than in the open population (Rajska-Jurgiel, 1976).

The development of social organization arranges contacts among population members by establishing the norms of response to each other (Rajska-Jurgiel, 1976). The rank of an individual in a social organization depends on its physiological features such as age, sex, etc., thus it is based on the primary differentiation of individuals, which accounts for more or less permanent secondary differentiation among population members (Łomnicki, 1978).

6.5.3. Social Rank in Relation to Age

Social rank of individual animals in bank vole populations largely depends on age. The subordinate position of young individuals in relation to the adults was noticed by all authors studying social organization. Andrzejewski & Olszewski (1963a), who observed individual interactions at feeders, have noticed that adults were feeding long enough to become satisfied (chasing or tolerating other individuals), while young individuals spent little time at the feeders, each time taking a few grains and running away to the nearest shelter to eat them. They were frequently harassed by adults.

Rajska-Jurgiel (1976) pointed out that young individuals were caught in traps with adults less frequently than by chance, especially when a male was in the double trap first. The subordinate position of the young is reflected in their low trappability in baited live-traps. Such a trap is an attractive requisite, and for this reason it is quickly occupied by the dominant, older individuals (Gliwicz, 1970; Andrzejewski & Rajska, 1972). This thesis is consistent with the results of experiments carried out by Watts (1970a), in which the trappability of young individuals increased after the removal of adult males from the population; similary the age of voles trapped for the first time was lower in the experimental population, as compared with the control.

In the island population of the bank vole, different population indices were estimated separately for each cohort. It has been shown that members of successive cohorts established home ranges of decreasing mean sizes (Mazurkiewicz, 1971) and in deteriorating microhabitats (Bock, 1972). These are features that, as noted above, are correlated with rank in the social hierarchy. This provides a basis for an hypothesis that the rank of individuals in the social hierarchy is determined by their age or, strictly speaking, by the sequence of their recruitment into the breeding population (Gliwicz, 1979). By mid-summer, the overwintered animals (K_0) are dominants, and the young born early in spring (K_1) are co-dominants, to become dominants when the overwintered animals die out. The members of the two last cohorts (K_3 and K_4) have the lowest rank in the population. When recruited into the population, they occupy the smallest home ranges and are forced to the poorest (driest) microhabitas. This pattern of social hierarchy is maintained to the end of the breeding season.

It is possible that this relationship between social rank and age is particularly clear in isolated populations, where migration is not possible. In open populations the social rank of an individual depends on the time of its residence in the population.

6.5.4. Social Rank in Relation to Maturity

Young, immature individuals of both sexes, form aggregations in the population (their home ranges have clumped distribution), and they are often caught together in two-compartment traps, suggesting that they are mutually tolerant (Naumov, 1951; Bujalska, 1970; Mazurkiewicz, 1971; Rajska-Jurgiel, 1976). In a dense population of the common vole (*Microtus arvalis*), young individuals can establish a common, group home range during the breeding season, which shows that they are not aggressive (Chełkowska, 1978). It is possible that a similar phenomenon also occurs in the bank vole population before sexual maturity is reached and dispersal takes place.

The time when males reach sexual maturity seems to depend only on their age, thus older males, with a high social rank, are also mature individuals, while subdominant males are younger and immature. Contrastingly attainment of maturity by females depends not only on their age but also on the establishment of exclusive or nearly exclusive home ranges (Kalela, 1957; Koshkina, 1965; Bujalska, 1970; Mihok, 1976). As Bujalska (1970) has shown, a young female which has contacts with too many mature females cannot reach maturity. As a result, home ranges of mature females have a character of territories, and they tend to be evenly dispersed. Interactions among mature females kept under laboratory conditions are aggressive (Mihok, 1976), but we may expect that in the wild encounters between mature females are rare because of behavioural mechanisms isolating mature females in space. Rajska-Jurgiel (1976) found that mature females are less frequently captured in two-compartment traps with other mature females already present in them than indicated by the random distribution of capture. In a free-living bank vole population experimentally supplied with additional food, where population members probably became more tolerant of their conspecifics (this can be inferred from a significant increase in the overlap of their home ranges), mature females continued to maintain evenly spaced and only slightly overlapping home ranges (Bujalska, 1975b; Andrzejewski & Mazurkiewicz, 1976).

Territorial mature females have a higher social rank than immature females. This is indicated by both, direct observations (Kock & Rohn, 1971; Mihok, 1976) and indirect indices such as a higher trappability of mature females. But the maturity-related social hierarchy in females is also strongly correlated with their age structure, since females born in early spring and in summer, when the population density is low, have a greater chance of establishing a home range (a prerequisite of maturity) than do females born in late summer and autumn, when the density of the population is high. As a result, in an island population under study, most of the mature females were represented by overwintered animals and by members of the first spring cohort, while females born in late summer and in autumn did not reach maturity in the year of their birth (Bujalska *et al.*, 1968).

6.5.5 Social Rank of Migrants

According to many ecologists, individuals of a low social rank in their native populations become migrants* (Andrzejewski & Wrocławek, 1962; Lidicker, 1975 — saturation dispersal; Łomnicki, 1978). Thus, these are likely to be subdominant mature and maturing males, also females that reached the age of maturity but failed to establish a home range-territory, etc.

Therefore, an experiment was done to get information on the social position that can be reached by immigrants in an established population. Alien individuals were released into organized laboratory and free-living populations, and their fates were followed either by direct observations or by means of some indices of social rank, such as trappability or running in an exercise wheel. Classic studies of this type were carried out on laboratory populations of white mice (Andrzejewski *et al.*, 1963; Walkowa, 1964). Similar experiments with laboratory populations of the bank vole were conducted by Kock & Rohn (1971), and with free-living bank vole populations by Kołodziej *et al.* (1972) and Rajska-Jurgiel (1976). The conclusions were the same in all cases. Independent of their age, sex, and breeding condition, all individuals entering an organized po-

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* This mostly concerns emigration stimulated by social organization and not emigration forced by a drastic deterioration of habitat conditions (e. g. flood) or seasonal migrations; the fates of emigrants, however, is the same in all cases.

pulation had the lowest rank in the social hierarchy, corresponding to the rank of the youngest independent individuals in this population. They lost fights, occupied the worst nest boxes, had low trappability avoided two-compartment traps with individuals of the local population inside, and frequently ran the wheel. It has also been shown that the introduced individuals readily occurred together (they entered the two-compartment traps with individuals of the same category), which is similar to the already noted clumping of young, subordinate individuals, noted previously.

These results show that the social rank of immigrants is low, and this concurs with theoretical predictions based on classic papers concerning the development of social organization in the population (see a review in Allee *et al.*, 1958). According to these predictions (1) residents holding an area for a long time and defending it against intruders easily win, and (2) the outcome of fight for dominance heavily depends on the earlier experience of animals. Immigrants are always intruders in established populations, and, in addition, they held a very low social eank in their own population. The immigrant's chance of surviving and establishing a home-range and of its possible rise in social hierarchy depends, according to the authors quoted above, on the density of the local population (in relation to resources available), on social relations in this population (the level of aggregation), and on the number of immigrants. Also the phenological time of immigration can be important.

6.5.6. Social Organization in the Annual Cycle

The differentiation of population members discussed so far concerns the breeding season. In most of the free-living populations under study, trapping was carried out from early spring (March, April) to late autumn (October, November). It has also been stated that the clear differentiation in trappability, size and shape of home ranges, and in spatial distribution of individuals occurred only in spring and summer while disappearing almost completely in autumn, independent of the age of maturity of individual animals (Gliwicz, 1970; Mazurkiewicz, 1971; Andrzejewski & Rajska, 1972; Rajska-Jurgiel, 1976). This is related to the termination of breeding, and probably implies that at the beginning of winter, social organization of the population changes, individual interactions are less severe, mechanisms that isolate individuals crumble, and the aggression level in the population declines. A conspicuous effect of this situation may be the formation of large winter aggregations of the bank vole (Naumov, 1951; West, 1977), which may account for a reduction in energy expenditures and mortality of the population, particularly in the areas and years characterized by severe winters.

In early spring, when reproductive activity is resumed, social hierarchy is re-established. This process is accompanied by an increase in aggression. At least in this way Chitty & Phipps (1966) explain the increased mortality of overwintered animals observed during March in *Microtus agrestis* populations, and also occurring in the bank vole. The increase in the level of aggression can reflect the fact that animals which were largely differentiated in the preceding breeding season, become similar to each other in winter. As a result, all overwintered animals are of similar body weight (Bujalska & Gliwicz, 1968, 1972) and all are mature. Development of social hierarchy among similar individuals is a very difficult process (Shilov *et al.*, 1974; Gliwicz, 1975, 1979).

6.5.7. Conclusions: the Effect of Social Organization on Demographic Processes

Reproduction. As was shown in the section dealing with the reproduction, avoidance among mature and maturing females gives rise to competition for space among them and to the limitation of the number of females that can reproduce.

Survival. Disturbances in social hierarchy of the population account for an increased mortality. This has been confirmed in many laboratory studies (Petrusewicz, 1966b, 1978) and also in the studies on free-living bank vole populations (Chitty & Phipps, 1966; Gliwicz, 1975). It is unclear, however, to what extent the length of life depends on the social rank of individual animals. It seems that in the case of a drastic deterioration of environmental conditions, the chance of surviving will depend an the social rank, thus on the size of home ranges, on the quality of the microhabitat occupied, etc. Such a relationship between social rank and survival under extreme environmental conditions was obtained by Warnock (1965) for a laboratory population of *Microtus pennsylvanicus,* deprived of water nad shelters. But in open populations, a decline in numbers under such conditions is likely to be achieved through an increased emigration.

Migrations. Social organization in rodent populations plays an important part in number regulation through migrations. It stimulates emigration and also accounts for difficulties in the establishing of homes by immigrants. This has been confirmed for the bank vole in many field studies (Andrzejewski & Wrocławek, 1961, 1962; Pielowski, 1962; Adamczyk & Ryszkowski, 1965; Rajska-Jurgiel, 1976).

6.6. Organization of the Population

Kazimierz PETRUSEWICZ

In the section on structure and organization of the population, symptoms of the organization of bank vole populations are presented. When describing the elements of population organization (spatial distribution, sex ratio, age structure, etc.), I indicated that different elements of population organization have an effect on the size of this population. This is understandable because each individual lives in the environment which comprises abiotic factors, the ecosystem and the population itself (Fig. 6.15). Thus, the bank vole population is a part of the habitat of each individual member of this population, the population being something more than the sum of individuals of a given species. Due to relationships and interactions among conspecifics living in the same area, a certain system is created as a whole, that is, the population.

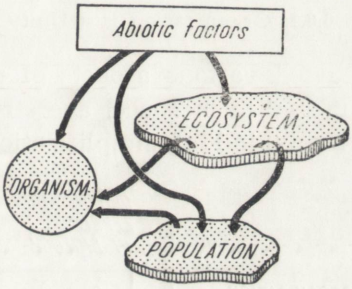

Fig. 6.15. Individual organisms are influenced by the abiotic environment, biocoenosis and population; the character of the population depends on the ecosystem and climatic factors (after Petrusewicz, 1978).

To explain what the concept of population wholeness means, I must refer the reader to the controversy between the advocates of the holistic and reductionistic approach to biological studies. Reductionists say that all living processes can be explained by reducing them to the molecular level, thus through physical and chemical processes. Holists (for a detailed discussion see Dobzhansky, 1961; Jacob, 1973; Urbanek, 1973; Kunicki-Goldfinger, 1976; after Petrusewicz, 1978) argue that there are qualitatively different levels of biological processes (Fig. 6.16) and the properties of a higher level cannot be totally explained on the basis of even a complete knowledge of the lower levels.

According to the holistic approach, and this whole monograph is written from this point of view, even a complete knowledge of individual organisms cannot explain all the properties of life at the population level. Interrelationships, interactions of different kinds form from the population an integron: an integrated system. Not all properties of this integron can be explained by properties of individual animals. They are the product of interactions among individuals and between individuals and their habitat. The integron (system in cybernetic terminology), that is, population in this case, influences, in turn, population members, as already indicated when particular elements of population organization were discussed. The effect of population on individual animals is no longer questioned. Now I am going to show some general features of the population as a system.

6.6.1. Organization is a Unity

I have already discussed various aspects of population organization, such as the organization of life in space, age structure, sex ratio, social structure, etc. This was a kind of simplification, which is useful for description and sometimes necessary in the process of research. In the process of investigation it is convenient and sometimes necessary to distinguish various aspects of population organization. It is impossible to study everything at one time. It should be remembered, however, that population is a unity, a whole. Particular manifestations of organization are interdependent and interrelated. One aspect of organization influences another one and also depends on it. All elements of population organization, whether sex ratio, age structure, or genetic structure, are realized in space. All aspects of organization operate on a definite

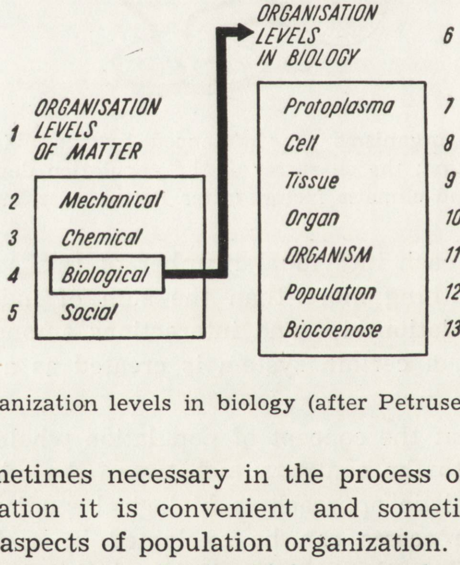

Fig. 6.16. Organization levels in biology (after Petrusewicz, 1978).

number of individuals, they depend either on the total number of individuals in the population, or on the number of individuals in the closest vicinity, that is on density. The probability that a certain symptom of life will always reveal itself depends on the number of individuals and on their distribution in the habitat. In turn, the character and frequency of the occurrence of a certain aspect of life influences the distribution and survival of different individuals, accounting for the development of a specific sex ratio, age structure, or genetic and morphological structures. As a result, the elements of population organization are interdependent, organization works as the resultant, as a whole.

Obviously, this does not contradict the fact that the importance of particular aspects of organization to population functioning and its future fates can vary.

6.6.2. Diversity and Inequality of Population Elements

Describing the elements of population organization, emphasis on the diversity of individuals or their groups is being put. It seems that as a rule the effect of organization on population numbers, or, more precisely, the mechanism of this effect creates different conditions for various population components (individual animals or certain categories of individuals), and gives them different chances. This seems to be a common and general regularity in the functioning of each population. It also seems that the basic regulatory mechanism of the effect of population organization on its numbers does not go through a simple increase in mortality or reproduction, or probability of the survival of all individuals, but just through creating different chances for individuals of different categories with respect to population organization, such as migrant — resident, dominant — subdominant, a member of the group — not a member, individuals in aggregations — individuals beyond aggregations, etc. Inequality, or simply diversity of population members is a basis for population organization.

6.6.3. Relative Persistency of Population Organization

The ecological organization of the population can have a certain inertia, the ability to persist for some time. Each "population curve" provides an indication of this. Let us assume that in an overcrowded population, say at the highest point between *A* and *B* in Figure 6.17, population organization enhances mortality, reduces reproduction and the survival of newborn. Then the population declines. Also the following situation is possible: the symptoms of overcrowding can occur at a lower density than that in the "valley" of the curve of population dynamics, say at the point *C* as compared with *E* in Figure 6.17, and the population numbers decline. Time point *B* indicates on the descending line the state (density *N*) at which at point *A* numbers increased.

The property of population organization due to which it can persist unchanged is extremely important. If the organization directly and without delay changed in response to environmental effects, it would be merely the instrument of adaptation. It would not be possible to figure out the mechanism of modifying these environmental influences by population organization. Population organization develops under certain external ecological conditions (environment and biocoenosis), the action of which can be modified by the previously established organization, and is created by the ecological situation in the preceeding period. Due to this relative inertia, population organization can be not only the mechanism of adaptation but also it can modify environmental effects, and in this way influence processes determinig changes in numbers.

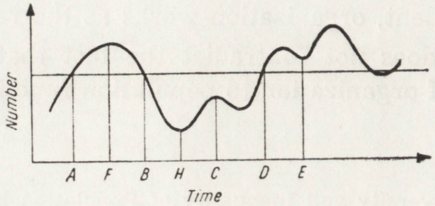

Fig. 6.17. A hypothetical curve of population dynamics. At the same density there is an increase at points *A* and *D*, and a decrease at *B*. Symptoms of overcrowding can occur even at *C*, where the density is lower than in the "valley" *E* (after Petrusewicz, 1968).

7. DYNAMICS AND REGULATION OF THE POPULATION

7.1. Patterns of Population Dynamics

Kazimierz PETRUSEWICZ

Population dynamics, that is, changes in the number of individuals with time, sums birth rate, death rate, emigration, and immigration. Emigration and immigration have been discussed above (section 6.4). Population dynamics of the bank vole seem to depend on emigration and immigration under some special circumstances. I do not know about macroimmigration or macroemigration of the bank vole. Macroimmigration in the bank vole is only a logical postulate: this widely distributed species must have expanded into new areas. Population dynamics of this species greatly depend on the birth rate and death which will be discussed in more detail below (section 7.2 and 7.3). Here, in this introduction to the section on population dynamics I will present only necessary general ideas.

Bank voles breed during the growing season (for details see section 7.2).

The biological year of the bank vole lasts from one spring to another, in England, for example, from March to March, and in Poland from April to April. In Poland, April is the time of minimum numbers in most cases, as on young are born in autumn, winter and spring, and the animals are only dying out. This lowest standing crop — the number of individuals starting breeding and as a result ensuring the continuity of the population — is usually called the basic stock. In April mating begins, the first pregnant females appear, and the first young are born (this will be discussed in detail in section 7.2). As the birth rate is higher than the death rate, the population increases rapidly, raeching a peak in July-October, as is shown in Figures 7.1, 7.2 and 5.1 (Andrzejewski, 1963; Petrusewicz *et al.*, 1971; Gliwicz, 1975; Bujalska, 1975b). Then the population declines until April resulting in a sinusoid-like pattern shown in Figures 7.1, 7.2, and 5.1.

Bank voles live in well-balanced populations. A more detailed analysis was made for 31 populations. A total of 139 maximum/minimum ratios were calculated, and an average of 4.7 was obtained. One max/min ratio was higher than 60, two were higher than 20, and three ratios exceeded 10. Peak numbers most frequently exceeded the spring minimum about 5—6 times. Generally, populations of forest rodents are much more stable than the populations living in open habitats such as meadows, steppes, or semi-desert (Golley *et al.*, 1975b). But even among forest populations, the bank vole population seems to be more stable than populations of other rodents associated with forests.

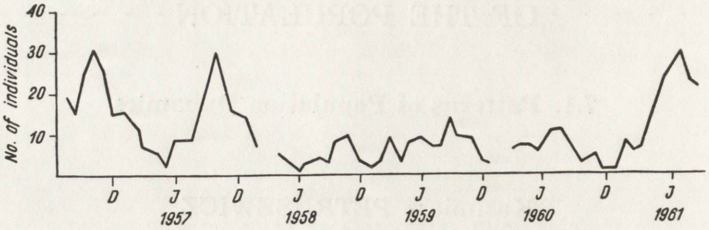

Fig. 7.1. Population dynamics of bank voles in the Kampinos Forest. Average numbers per month per 4 ha are given.
D — December, J — June (after Andrzejewski, 1963).

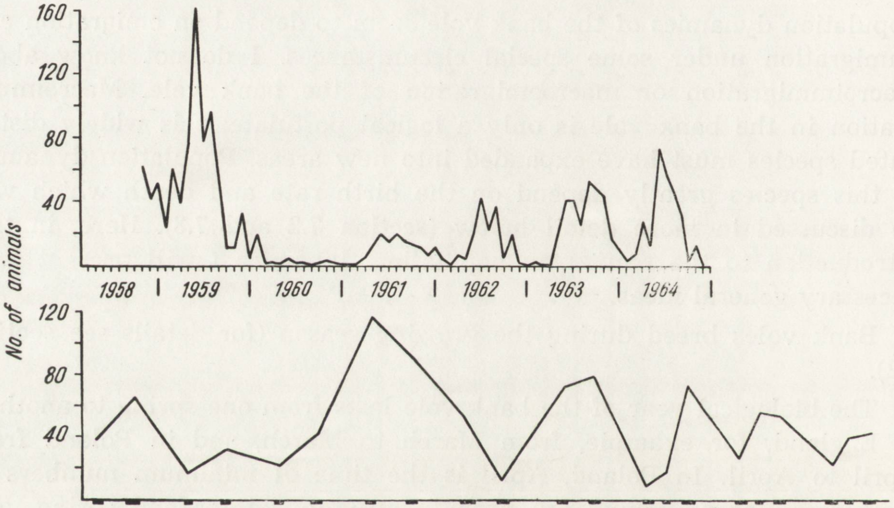

Fig. 7.2. Population dynamics of bank voles in the Białowieża National Park (1958—1973).
(after M. Pucek & Z. Pucek, unpublished data).

As far as seasonal fluctuations are concerned, usually the size of the basic stock, starting breeding in April, is much more stable than peak numbers. During the four-year study on Crab Apple island, the maximum basic stock was 1.2 times as high as the minimum basic stock, and the corresponding figure for the highest and lowest peak numbers was about three times (Petrusewicz *et al.*, 1971; Gliwicz, 1975). In the four-year study carried out in the Niepołomice forest, the ratios of highest/lowest basic stock were 3.2, 2.6, and 1.3, while the corresponding ratios for peak numbers varied from 5.0 to 22.0 (Bobek, 1973).

It should be added here that in absolute numbers (not as max/min ratio), maximum numbers often show larger fluctuations than minimum numbers. For instance, during the four-year study period on an island population inhabiting lake Bełdany, the lowest and highest minima ranged between 14.5 to 17.5 individuals per ha; thus the annual fluctuation was 3 individuals/ha. Maximum numbers, however, varied from 50 to 75 individuals per ha; thus the difference was 25 individuals/ha. This gave rise to a concept (Petrusewicz *et al.*, 1971) that in the population there are constant and variable parameters (Table 7.1). The constant parameters involve the size of the basic stock, production, and the number of born over a year. So far this concept has not been empirically confirmed.

Table 7.1.
Variable and stable parameters of population size on a 4-ha island (after Petrusewicz *et al.*, 1971).

Parameters	1966	1967	1968	1969	CV %
Peak numbers	304	201	399		27
Time of peak	July	Sept., Oct.	July		
Daily survival K_1	0.81	0.79	0.48		22
in percent of N K_2	0.32	0.56	0.83		37
Number born (v_r)	1048	1090	1011		3
Production (P) g live wt./4 ha/year	11429	11714	13061		6
Basic stock, April	56	68	70	62	6

Bank vole populations, like populations of other species, show an interesting property: closed populations are more dense than open ones; at the same time, their density increases with decreasing size of the isolated area occupied by the population (Petrusewicz, 1963, 1978; Petrusewicz & Uchmański, 1980).

The first attempt to explaining this phenomenon was made by Petrusewicz (1963, 1978). A detailed explanation was suggested by Petrusewicz & Uchmański (1980), and is summarized below. According to Krebs *et al.*, (1969), higher densities of confined populations are due to the lack of migration. This may be a logical explanation with some additional reasoning.

Both emigration and immigration should be considered here. In closed populations both processes are nonexistent. The confinement of a population can account for an increase in its density only if in corresponding open populations emigration outweights immigration. This is likely to be the case because migrating individuals are subject to heavier mortality than residents, as has been shown in studies carried out at the Institute of Ecology, PAS (see section 6.4). This implies that at any average site, emigration must be higher than immigration. In view of this fact, the density of a closed population, with no emigration and immigration, should increase not as an effect of the absence of emigration alone but as a result of the absence of an excess of emigration over immigration.

But the absence of emigration may be only one of the reasons for an increase in density. Density also increases when isolation is not complete. Islands, wooded areas scattered in croplands, and urban parks are all examples of partly isolated habitats. It can be assumed that the probability of encounters between individuals (interference) will be lower in a closed population than in an open one. In an isolated space only the individuals inhabiting this space can encounter. In an open space — assuming that this space can be covered by individual animals in a short time — the number of encounters with neighbours and with neighbours of the neighbours increases; hence, the interference is stronger, and the effects of crowding can intensify, with a consequent decrease in density. Differences in the number of contacts among individuals in closed as compared with open populations explain also what was not noticed by Krebs *et al.* (1969), who also explained why the densities of closed populations increase with declining space inhabited by these populations.

7.2. Reproduction

Gabriela BUJALSKA

7.2.1. Methods for Estimating Birth Rate

Birth rate as expressed by the number of individuals born per unit of time is, along with death rate and migration, a basic component of population dynamics. Birth rate depends on the number of pregnant females, litter size, and duration of pregnancy (Bujalska *et al.*, 1968).

Laboratory and field studies provide many data on stimulating or inhibiting effects of abiotic and biotic environmental factors on reproduction. These factors modify successive stages of the breeding cycle, starting from the attainment of sexual maturity, through the development of a normal oestrous cycle and fertilization, to parturition and rearing the young. Each stage is sensitive to the effects of different factors. An ecologist is chiefly interested in the range of variability and actual values of particular components of reproduction in the population.

The methods used in field studies, and particularly the *CMR* technique, allow the application of only simple *in vivo* procedures of breeding condition assessment. Puberty of females is determined by observation of the perforation ef the vaginal entrance. It usually is easily seen but sometimes a thin stick should be used to check the observation. Vaginal opening is almost always related to attainment of sexual maturity, though it happens that the first oestrus occurs later. Out of 42 cases of vaginal entrance opening occurred simultaneously in 33 cases; in one case it occurred after 8.5 days, and in seven remaining cases neither oestrous nor any other phase of the oestrous cycle was recorded over the observation period of 4.5 to 11.5 days (Bujalska, 1970). Therefore, the first oestrous should be considered as the unquestionable criterion of sexual maturity in females.

The phase of the oestrous cycle can be determined by analysis of vaginal smears. The method of taking vaginal smears is simple. Only a thin, cotton-tipped stick and a slide are needed. The material is stained and examined under a microscope. Bank vole cycles were monitored this way in the field by Larina & Golikova (1960), Bujalska & Ryszkowski (1966), Bujalska *et al.* (1968) and Bujalska (1970, 1973, 1975a, 1975b).

Distinguishing of pregnant females is possible by the analysis of vaginal smears (Bujalska & Ryszkowski, 1966; Bujalska, 1970) since absence of the oestrous cycle for longer suggests duration of pregnancy. Additionally vaginal smears of pregnant females may contain many erythrocytes (the exudation of blood from placenta), the mucus in smooth, unstructured, and frequented by leukocytes in 90% of pregnant females (Bujalska, 1970).

The presence of a copulation plug, and subsequent continuous increase in body weight 2—6 days before parturition are helpful (Bujalska, 1970). In *Clethrionomys rufocanus* 15-day pregnancy can be recognized visually (Kalela, 1957). When time extrapolation is possible, the most reliable sign of the past pregnancy is the presence of the young, or plucked fur around nipples.

The litter size can be determined *in vivo* only when parturition occurs in a trap, or in the nest if cannibalism can be excluded.

Also dead animals were examined, especially whan the "Standard Minimum", the method recommended by the IBP, is used (Grodziński *et al.*, 1966). In this case the analysis involves the state of gonads in males and females, the uterus (the presence of embryos, their size and number, the occurrence of placental scars indicating past pregnancy). This kind of data is more exact.

Sometimes lack of direct data requires use of indirect indices e. g., of reproduction rate and recruitment rate, determining realized reproduction. For example, the analysis of the population age structure can be used to estimate the recruitment rate (Gliwicz, 1975).

As it is easy to rear bank voles under laboratory conditions (Drożdż, 1963; Buchalczyk, 1970), some information difficult to obtain in the field, particularly physiological parameters, can be assessed in captivity. Here are mostly involved estimates requiring series of observations, thus related to the trappability of animals, such as the duration of gestation period in relation to the litter size and the female, age, or the duration of the oestrous cycle and its phases. Ecological parameters, such as the attainment of puberty, number of pregnancies per female over the breeding season, and other parameters modified by the state of the population, should be measured each time in the population under study.

To calculate the number of newborn animals in a bank vole population, the formula described by Bujalska *et al.* (1968) may be used. It is a modified version of the formula used by Edmondson (1960):

$$\nu_r = = \frac{\bar{N}_p T L}{t_p}$$

where ν_r is the number of newborn over time T, $\bar{N}_p$ is the average number of pregnant females, T is the study period in days, L is the litter size, and t_p, is the gestation period in days. The value of $\bar{N}_p$ allows the consideration of changes in the number of pregnant females, e. g. due to their mortality over the study period, but the calculated values of ν_r is overestimated as compared with the real number of born, particularly when the number of pregnant females, N_p, increases. This is the case because of the assumption that a pregnant female gives birth to $1/t_p$ offspring every day, while in fact she gives birth to the whole litter at once, after t_p days. Therefore, if a female dies after time equal to 1/2 t_p, one half of her litter size will be included into the number of born, while in fact zero individuals were bonr *. This error will be

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* As a result of the overestimation of ν_r also the death rate of young voles from their birth to first capture is overestimated.

reduced when time T approaches t_p and the mortality of pregnant females is low.

The application of this formula in the studies on productivity (Bujalska *et al.*, 1968; Petrusewicz *et al.*, 1968) and demography of *C. glareolus* population (Bujalska, 1975a, 1975b) enabled calculating of nestling mortality, which is otherwise difficult to determine. The application of this formula is discussed in detail by Petrusewicz & Macfadyen (1970) and Petrusewicz (1978).

7.2.2. Age at Sexual Maturity

An important factor determining reproduction is the age at which the current-year animals reach sexual maturity. Usually females are considered here as they are directly responsible for population reproduction.

The number of mature females determines the potential reproduction of the population (Bujalska, 1970), and the percentage of mature females, together with the percentage of pregnant females, is an index of reproduction rate (Kalela, 1957).

Female bank voles become sexually mature at an age of 1—1.5 months, and males at an age of about 2 months (Buchalczyk, 1970). Field observations suggest, however, that even females less than one-month-old can be sexually mature. For example, 45-day-old females gave birth (Bujalska *et al.*, 1968).

The first information on the variable age of voles at sexual maturity is given by Kalela (1957). He noticed that the proportion of mature males and females in the population varied from year to year over three successive study years. In 1954 and 1956, when the population was low, almost all voles reached puberty in the year of their birth, the rate of maturing being slower in the second half of the breeding season, when the population size increased. In 1955, when the population was high, some females and almost all males failed to reach maturity in the current year. Where the population size was twice as high as in other places that year, neither females nor males reached sexual maturity in the year of their birth. These facts exclude the effect of meteorological factors on the rate of maturing. The only logical explanation could be the effect of population density.

A similar interpretation concerning the effect of population density on the age at sexual maturity in the bank vole was suggested by Zejda (1961, 1964, 1967) and Jewell (1966).

Koshkina (1965) attempted to explain ecological mechanisms responsible for changes in the rate of maturing of current-year individuals at the beginning and at the end of the breeding season, as well as in different phases of the population cycle, on the basis of the studies conducted on a *C. rutilus* population in 1958—1964. This author relates the attainment of puberty to the actual population density and spatial requirements of mature individuals. Individual home ranges were larger at low- and smaller at high-population densities. Moreover, overlapping of home ranges increased with population density.

Therefore, the delay in reaching sexual maturity should be related to tendencies toward territoriality in mature voles. Territorial tendencies in mature females (in contrast to immature males and females) were also recorded by Naumov (1951) and Tanaka (1953) for *C. glareolus* and *C. rufocanus*. The relationship between the age at sexual maturity and the establishment of a territory implies that females can reach maturity at different ages and, critical for diagnostic purposes, at different body weights (Bujalska, 1970).

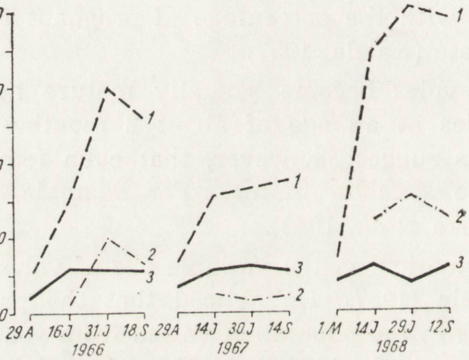

Fig. 7.3. Population size (1) and the number of immature (2) and mature females (3) of bank voles in different years.
Dates of censuses on the x-axis.

These facts and their interpretation are consistent with a high stabilization of the number of mature females in an island population of the bank vole (Bujalska, 1970). In 1966—1968, the number of mature females was almost constant and independent of the population size (Fig. 7.3). This means that the number of females reaching maturity over the breeding season equaled the number of mature females that died in this time. The hypothesis of territorialism in adult females has been verified by such indices as (1) spatial distribution (mature females were evenly spaced, while immature females had a clumped or random distribution), (2) overlapping of individual home ranges (home ranges of neighbouring mature females only partly overlapped, while those of immature females could overlap even three times), and (3) co-occurrence of females at particular trap sites: mature females were caught less frequently than randomly at the trap sites where more than one female occurred, while the trappability of immature females was independent of their number at a given trap site (Bujalska, 1970).

Then this hypothesis was experimentally tested when in June, 1969, about 50% of the females present in the population were removed. All of them were members of the first spring cohort (Bujalska, 1973). As the result, more females of the second and third cohorts reached maturity in July and September. In this way younger females "supplemented" the number of mature females to the level observed in earlier years (Fig. 7.4). Differences in the age structure between mature females in September of 1966—1968 and of the year of the experiment show that younger females, born in the second half of the breeding season, are able to attain maturity in the year of their birth. This process, however, can be delayed because of the lack of "free" space they need to establish their territories.

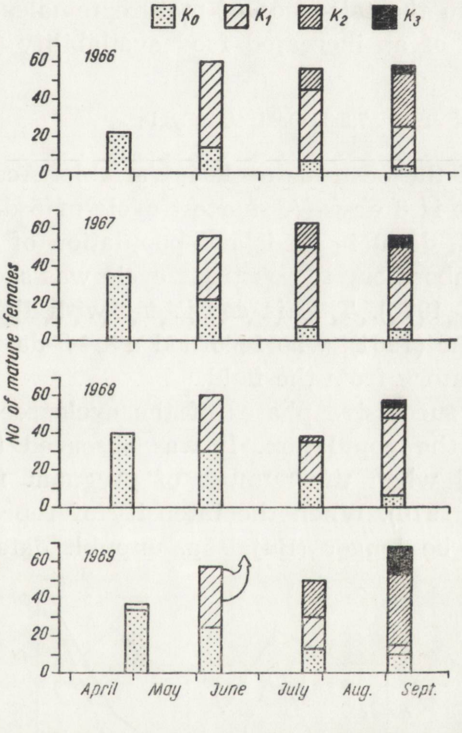

Fig. 7.4. Age structure of the mature female population. Arrow indicates number of voles removed.

It seems that tendencies toward territoriality in mature females are closely related to reproduction; after the breeding season both mature and immature females have random or clumped distribution (Bujalska, 1973). This suggests that the spacing of mature females, as expressed by the size of home ranges and the degree of their overlap, is related to the requirements of rearing young.

An experimental increase in food supply in the form of superabundant oast resulted in a decrease in the size of home ranges of all individuals, and this, in turn, was followed by an increase in the number of mature females (Bujalska, 1975a; Andrzejewski & Mazurkiewicz, 1976). No differences were recorded, however, in the type of spacing of the two female categories between the control and experimental years, though an increase in the tolerance of mature females could have been expected as a result of an increased food availability (Bujalska, 1975a).

7.2.3. Oestrous Cycle

Mean duration of the oestrous cycle is variable. According to Larina & Golikova (1960), it is 8 days. A shortest cycle of 5 days was observed by Bujalska (unpubl. data) in an island population of the bank vole in 1966—1968. In the laboratory the oestrous cycle was shorter and covered 4 days (Buchalczyk, 1970). This is consistent with the earlier data by Petrov & Ajrapetyanc (1961), who recorded a 4—5-day cycle in females brougth to the laboratory from the field.

The duration of successive phases of the cycle seems to be related to the situation in the population. It was observed that the oestrous cycle was prolonged when the number of pregnant females increased (Fig. 7.5) (Bujalska, 1970). When the intensity of reproduction declined dioestrus tended to be longer (Bujalska, unpubl. data), and when the

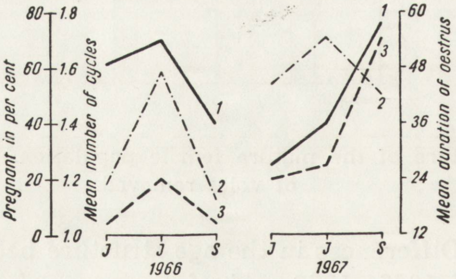

Fig. 7.5. Relation between percentage of pregnant females from cohort K_1 and variations in oestrous cycle.

1 — percentage of pregnant females, 2 — mean number of oestrous cycles per female during 14 days, 3 — mean duration of oestrous in hours. Dates of censuses on the x-axis.

population was overcrowded even all mature females stopped reproducing. In such cases symptoms of anoestrus (blocking the entrance to the vagina) occurred in females that reproduced 6 weeks earlier and resumed reproductions 6 weeks later, when the population declined (Bujalska, 1970).

According to unpublished data by Bujalska, in 1966—1968 proestrus lasted for 17.3 hours on the average, oestrus for 35.1 h, metoestrus 16.0 h, and dioestrus 56.3 h.

Post-partum oestrus can occur in the bank vole; at that time an effective copulation is possible as indicated by the occurrence of the vaginal plug immediately after parturition (Steven, 1957; Sviridenko, 1967). Post-patrum oestri and vaginal plugs were frequently observed in an island population of the bank vole. In 1966—1968, the post-partum oestrus occurred 39.1 hours, on average, after parturition (Bujalska, unpubl. data).

Few data exist concerning the effect of exocrine factors (pheromones) on the oestrous cycle in small mammals in the wild. Such an effect is known for *Oryctolagus cuniculus* (Mykytowicz, 1965) and for various species living under experimental conditions (see Vanderbergh, 1973). An indication of a similar phenomenon in the bank vole is the fact observed by Larina and Golikova (1960) that females in the phase of proestrus leave their home ranges when there were no males around.

7.2.4. Duration of the Gestation Period

The gestation period of the bank vole found by different authors in various habitats varied from 17 to 30 days. For example, Wrangel (1940) reports 17.5 days, Popov (1960) 17—18 days, Bujalska & Ryszkowski (1966) 22 ± 2 days, and Naumov (1948) 20—30 days. Under laboratory conditions pregnancy usually covers 18—25 days (Drożdż, 1963), and the time span between successive parturitions is 20—57 days (Buchalczyk, 1970).

The interval of 16—35 days between successive litters under laboratory conditions (Table 7.2) implies that copulation occurred immediately after parturition or weaning. Intervals of about 2 months could be caused by the resorption of embryos or by the cannibalism of entire litters. Intervals of 4—9 months occurred in autumn and winter (Buchalczyk, 1970 *.

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* There are no conclusive data on the delayed implantation, thus a seeming elongation of the gestation period. For *Mus musculus* and *Rattus norvegicus* this was described by Baevski (1963). According to Wrangel (1940), the gestation period of lactating females rearing the earlier litter is 21.5 days. Mazák (1962) reports similar values (21—22.5 days).

Table 7.2.

Frequency distribution of time intervals between successive litters of the bank vole as expressed in numbers of females (n) and their percentage proportions (after Buchalczyk, 1970).

Time interval	n	%
16—35 days	212	45.6
to 2 months	82	17.6
to 3 months	65	13.8
4—5 months	72	15.3
6—9 months	33	7.0
9 months	1	0.2
Total	465	100

7.2.5. Litter Size

According to Zejda (1966), litter size varies from 5.24 in May to 4.4 in September (Table 7.3). Sviridenko (1967) found a similar range, namely from 4 to 5.6 young per litter. According to this author, litters are smaller in the wild, and they increase in the laboratory under optimum

Table 7.3.

Seasonal changes in the litter size of the bank vole expressed in the number of embryos. Number of litters in parentheses (after Zejda, 1966).

Months	Number of embryos	
April	5.09±0.15	(55)
May	5.24±0.10	(147)
June	4.82±0.16	(67)
July	4.67±0.17	(42)
August	4.73±0.20	(30)
September	4.40±0.21	(20)

Table 7.4.

Geographic variability in litter size of bank voles. Number of litters in parentheses (after Zejda, 1966).

Location	Average litter size	
Great Britain	3.95±0.08	(158)
Brittany	3.84±0.16	(43)
Czechoslovakia	4.90±0.07	(388)
North Germany	4.98±0.18	(57)
Kola Peninsula USSR	5.27±0.13	(102)
Moscow, USSR	5.53±0.15	(72)
Komi ASRR	5.47±0.22	(43)
Tatar ASSR	6.10±?	(343)

conditions. Buchalczyk (1970) observed 1—10 young per litter in captivity (3.6 ± 1.46 on the average). 83.7% of the liters consisted of 2—5 young, and 3.3% were larger (7—10 young).

Zejda (1966) compared average litter sizes from different regions and he found that the litter size increased eastwards (Table 7.4). This may be related to climatic conditions.

The results obtained by Buchalczyk (1970) show that the litter size may be related to the age of females; females more than 15 months old delivered smaller litters than younger females.

Litter size can also be affected by resorption of embryos. For example, Coutts & Rowland (1969) observed a resorption of one or more embryos in 49—69% of pregnant females, and a resorption of more than 4 embryos in 5—6% of females.

7.2.6. Proportion of Breeding Females

The number of females taking part in reproduction of a population, e.g. the actual number of breeding females (Bujalska, 1970) varies considerably from season to season and from one year to another.

The proportion of pregnant females in the population examined by Sviridenko (1967) varied from 20—60% in different years. Bujalska & Ryszkowski (1966) have found that the proportion of pregnant females varied from 10 to 50% depending on the season, while Bujalska *et al.* (1968) found a 20—96% variation. Only in spring did the proportion of pregnant females approach 100% (Bujalska *et al.*, 1968; Bujalska, 1970).

Although there were differences in the number of pregnant females in an island population of bank voles, it has been found that the number of individual-days and, consequently, the number of voles born was stable in successive years (Bujalska, 1970, 1973). Removal of some individuals born in the year of the experiment (see section 7.2.2) resulted in an increase in the proportion of younger cohorts among mature females, and also accounted for the reproduction of females from the late-summer cohort (K_3). Females of this cohort did not reproduce in preceding years. This experiment confirms the earlier suggestions that recruitment of young cohorts to reproduction is of a compensatory character. As observations show, the percentage of pregnant females is always high for overwintered voles, while it waries grealty for the current-year cohorts (K_1 and K_2), always in an inverse proportion to the reproductive index of the overwintered females (Bujalska, 1970); Petrusewicz *et al.*, 1971). The percentage contribution of particular cohorts to reproduction in 1966—1968 as compared with that in 1969, when the removal experiment was carried out, is shown in Figure 7.4. Also Ryszkowski noticed that the number of breeding females in different habitats in 1967—1969 was more stable than the total population size.

There are no empirical data explaining why reproduction is stabilized, or indicating ecological mechanisms underlying this stability. An experimental increase in the available food supply was not followed by an increase in the proportion of pregnant females (the number of pregnant females was a little higher, but also the number of mature females rose (Bujalska, 1975b).

7.2.7. Duration of the Breeding Season

In central Europe the breeding season of the bank vole extends from early April to late September. It may be locally shortened or prolonged. The beginnig of the breeding season seems to be related to the time of snow melting and development of plant cover. For example, on Crab Apple island, in northwestern Poland, the onset of breeding was observed on April 1, March 25, March 30, and April 1, during 1966—1969, respectively (Bujalska, 1973).

The termination of breeding seems to be influenced by the population density. It lasts for a longer time at low population densities. For example, on Crab Apple island the breeding season of 1967, when the population was low, terminated with a delay of 10 days, that is, on October 10 (Bujalska, 1970). A similar relationship was observed by Zejda (1961) and Bergstedt (1965). Conversely, high population densities are coupled with a shortening of the breeding period (Zejda, 1961, 1964). The effect of climate, however, should not be neglected as the breeding season shortens northwards (Delany & Bishop, 1960).

Sometimes bank voles breed in winter. The reasons for this are not clearly understood. The results of Baker (1930) and Newson (1963) show that the winter breeding is not related to temperature. Zejda (1962) and Smyth (1966) suggest that food supply may be of some importance. This view has been supported by the results of a feeding experiment carried out in an island population of the bank vole. As a result of providing a superabundant oat supply the onset of breeding was accelerated by 6 weeks (Bujalska, 1975b), in effect, resulting in winter breeding (Andrzejewski, 1975). Also Watts (1970b) observed an earlier onset of breeding after enrichment of the habitat with food.

7.2.8. Recruitment of the Young

The realized reproduction, that is, the number of young becoming members of the trappable population depends not only on the birth rate, but also on the death rate during the nestling period, when the life and development of the young depend on maternal care. This period seems to be particularly critical for both lactating females and nestlings. Lactation is a costly process in terms of energy (Kaczmarski, 1966; see also section 8.1), therefore food deficiency severely affects lactating females and, consequently, their unweaned offspring.

Bujalska (1975a) found that the peak population of island bank voles was due to a decreased mortality of the voles of the spring generation, thus born shortly prior to the peak. Consequently, the average life span of this generation increased. The average length of life of the individuals of the autumn generation was much shorter, for example, in 1978, when the peak was high, the average life span of the spring and autumn generations (*K_3* and *K_4*) was 128 and 53 days, respectively. In years lacking a high population peaks, the average length of life of the two generations was similar and much lower than that of the spring generation born before the peak. For example, in 1967 the average life of the two generations was 72 days. A positive relationship between the mortality of females rearing offspring and the mortality of the young of particular generations shows that all these changes were determined by nestlings survival (Bujalska, 1975a).

Further investigations (Bujalska, 1975b) showed that nestling mortality was related to food supply. When the population was provided with additional food in the form of oats, mortality of young of both spring and autumn generations declined. This implies that the survival of nestlings has a regulatory aspect.

7.2.9. Regulation of Reproduction

It may be concluded from studies on the bank vole that the reproduction of this species, as expressed by the potential and actual number of breeding females, varies less than mortality and, in particular, nestling mortality. Stabilization of reproduction in the island bank vole population followed the pattern shown in Figure 7.6.

The results obtained by Koshkina (1965) indicate that this pattern can also be valid for *C. rutilus* and, particularly important, for open populations of *Clethrionomys*.

A logical consequence of this pattern is that the main cause of changes in the population size of the bank vole may lie in mortality especially in nestling mortality. Bujalska (1977) suggested that changes in the size of the island bank vole population could be brought about in the way outlined in Figure 7.7.

In view of these findings some comments are needed on the concept of density-dependent regulation of reproduction. A stable or nearly stable

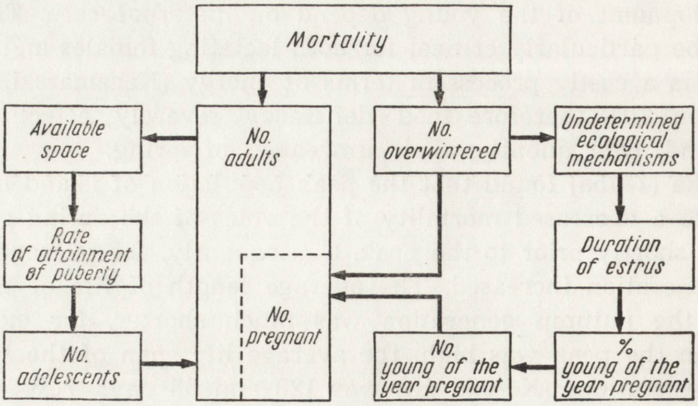

Fig. 7.6. Schematic representation of the processes stabilizing reproduction in an island population (after Bujalska, 1970).

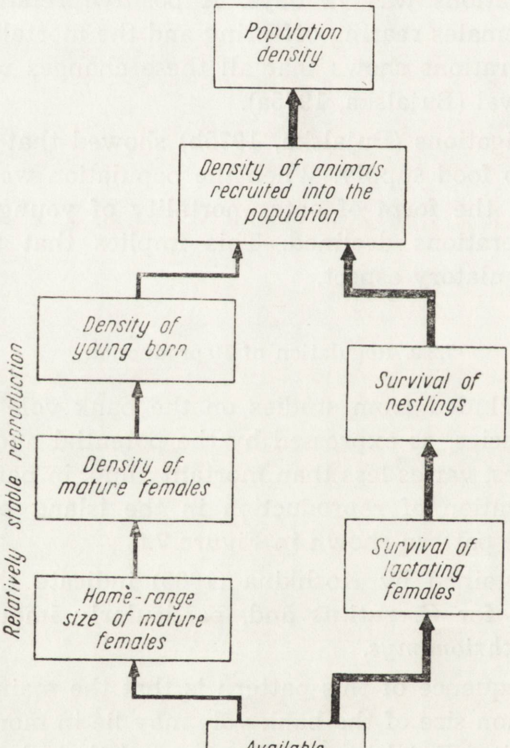

Fig. 7.7. A scheme of density regulation in a population of *Clethrionomys glareolus* (after Bujalska, 1977).

birth rate, compared with large changes in the population size, could be interpreted as being inversely proportional to the population density if, for instance, the proportion of mature or breeding females is analysed. In fact, birth rate is stabilized by spatial interactions between mature females, thus is independent of the population size.

The same concerns the survival (mortality) of the young. In the first half of the breeding season, population density depends on changes in mortality, and not conversely. Only in the second part of the breeding seasons mortality is likely to be density-dependent. But this issue requires further investigation.

7.3. Survival and Life Span

Joanna GLIWICZ

Death rate nad hirth rate are primary factors determining population dynamics. The literature analysing the role of these processes contains controversial views concerning their variability and relative importance to the ultimate character of population dynamics. The purpose of this paper is to characterize general patterns of mortality in the population of a typical rodent associated with forests of the temperate zone, and also to describe factors affecting this process as whole especially the lives of individual animals and the population. Against this background, the role of mortality as a factor regulating population numbers will be inidicated.

7.3.1. Mortality Patterns in Bank Vole Populations

Analysing mortality in populations of relatively short-lived mammals, it is easy to distinguish periods of different mortality in individual life and in phenological cycles of the population. Published data usually treat mortality in such distinct periods. Thus also in this paper four periods are distinguished.

Nesting Period or the Period of Dependent Life

It is generally assumed that young bank voles remain in their nests for about 21 days, and then they begin an independent life. A little later they begin to search a sufficiently large area and they attain a sufficient weight to be trapped. Only after this is it relatively easy to obtain direct information on their numbers and survival. All data concerning the earlier period are indirect estimates. For this reason the term "nesting period" covers here a considerably longer period than the actual nesting period does. For example, in the case of an island

Table 7.5

Survival of the bank vole as estimated by different authors.

Per cent survival in nesting period			Average
39—53% per 1 month	depending on the cohort	Ryszkowski & Truszkowski, 1970	
60% per 1 month	spring cohort		
68% „	summer cohort	Bobek, 1973	S = 47% per month or μ = 0.025 per day
31% „	autumn cohort		
37% per 6 weeks	only females	Bujalska, 1975a	
35% „	4-year mean for 4 cohorts	Gliwicz, 1975	
61—10% „	maximum differentiation, island population		
42% ca 2 months	newborn surviving till maturity	Radda, 1968	t = 42 days
Independent individuals — the Ist summer			
60% per 1 month	only females	Newson, 1963	
80—60% „		Smyth, 1968	S = 70% per month μ = 0.012 per day
66—80% „		Bobek, 1973	
65% per 6 weeks	average for island population	unpubl.	
59—72% „	only females	Bujalska, 1975a	
70% ca 1 month	old subadults reaching maturity	Radda, 1968	t = 75 day
Winter period			
85% per month		Chitty & Phipps, 1966	S = 85% per month
80—86% per month		Newson, 1963	
80% per month		Smyth, 1966	μ = 0.005 per day
83—85% per 6 weeks	only females	Bujalska, 1975a	
87—89% per month		Petrusewicz *et al.*, 1968	t = 180 days
Overwintered individuals in their second summer			
75% per 6 weeks	first half of winter		first half S = 80% per month μ = 0.007 per day
30% „	second half of winter	Gliwicz, 1975	
100—80% per month	first half of winter	Chitty & Phipps, 1966	
50—40% „	second half of winter		
89—75% per month	first half of winter		second half S = 40% per month μ = 0.031 per day
66% „	second half of winter	Newson, 1963	
60—50% per month		Smyth, 1968	
58—51% per 45 days	only females	Bujalska, 1975a	t = 90+90 days

population on Bełdany lake, the nesting period is considered to extend for 42 days (Table 7.5). Probably, however, non significant error is committed by pooling nesting mortality sensu stricto and the mortality shortly after weaning. The first weeks, and particularly first days of life of all mammals are characterized by low survival. It may be assumed that their mortality shortly after weaning is also high.

Data on survival in the wild population in this initial period are generally obtained by one of the two methods. One method uses indirect estimates of birth rate; the number of individuals born is estimated and this is then compared with the number of individuals trapped after some time. Obviously, the accuracy of this estimate of survival depends on the accuracy of the estimate of the number of newborn and on the time interval between parturition and the date of first capture, thus on the age of captured individuals. The other method uses data on the survival of individuals marked soon after their birth, the individuals surviving through the trappable age being counted. Usually the animals are marked in Howard's (1949) nest boxes that can easily be inspected. The accuracy of this method depends on whether a sufficiently large and representative group of young is marked, and whether or not the assumption is true that the animals living in artificial nests and marked in the first days of their lives survive as well as non-experimental individuals of the same age. This depends on incidences of cannibalism or abandonment by their mother, frequency of movement to another nest, etc. In the studies on the bank vole, this method was used by Ryszkowski and Truszkowski (1970).

Independent (Trappable) Individuals in the Year of their Birth

This is the most heterogenous group of all the groups considered. Members of this group differ by age (1.5—6 months on Crab Apple island), by reproductive condition (immature, maturing, and mature), and probably by some physiological or genetic properties as they were born in different periods of the breeding season. In the literature, however, most frequent were data on the survival of individual voles over the breeding season, and the great majority of them are mature animals older than three months. A few papers analysing particular periods or subgroups of individuals in this group are descriptive, with no quantitative data. Three papers will be discussed later, and here this heterogenous group will be considered as a whole to obtain the most general pattern of survivorship.

A difficult issue at this point is the length of the period for which this general mortality can be estimated. The time of individual life is superimposed on the phenological time, and individuals born early in the breeding period live under "summer" conditions for six months, this being the mean length of the growing season in Europe within the range of the bank vole distribution. Of these six months, they join the group of "independent" animals for 4.5 months, on the average (from 1.5 to 6 months). But animals born at the end of the growing season live zero months under summer conditions. It has been assumed that an average individual of this group lives equally long as an independent individual in its first growing season, that is, for about 2.5 months. This is the mean value (4.5+0):2 slightly modified on the assumption that slightly more individuals are born during the first half of the growing season.

Data on survival in this period and in all other periods are obtained by persistent recaptures of marked individuals (*CMR*) or by snap trapping (e. g. *SM*). In the first case, survival can be estimated from the number of individuals present at time t that surivived to time $t+1$. The accuracy of this estimate depends on the duration of period $(t+1)-t$ and on the turnover of individuals as a result of migration. When the second method is used, survival is estimated by comparing age structures of the captured part of the population at time instants t and $t+1$. In this case the estimate of population dynamics is based on the assumption that the area from which all the animals have been removed by trapping is then colonized by individuals with the same ecological characteristics.

Winter period. It has been assumed that winter extends for 6 months (November 1—April 1). The literature data concerning winter survival are extremely consistent. Particular emphasis is on the fact that the group of chronologically and physiologically differentiated individuals becomes homogeneous with respect to survival upon entering the winter period. It is frequently assumed that mortality is constant over the whole 6-months period. Distinguishing this period for the purpose of estimating survival is very simple and useful.

Overwintered animals (the second breeding season). Overwintered animals are a rather homogeneous group. All of them are mature and relatively advanced in age (7—12 months old). But a more detailed analysis shows some differentiation within this group, which will be discussed later on. This differentiation, however, does not seem to affect the general pattern of survival in this period of life. Mortality of this group tends to increase during the 6 months of the breeding season, and many data imply that clear differences in mortality occur at least at the beginning and at the end of the second breeding season of these animals. Therefore, this season has been divided into two three-month periods that differ in mortality of overwintered animals. The transition between these two periods is probably gradual. The number of individuals surviving beyond the end of the second growing season is so low that their further fates cannot be statistically described. It is only known that the oldest individuals living in wild populations were born in early spring of the preceding year and they died in late autumn of the following year at an age of 18 months (Sviridenko, 1966; Gliwicz *et al.*, 1968; Pucek *et al.*, 1968; Petrusewicz *et al.*, 1971). Single individuals survive in addition through a part of winter, thus 20—21 months (Zejda, 1961; Pucek *et al.*, 1968). Stein (1956) captured one individual (of 700=0.14%) which survived two winters. Bank voles surviving two winters are also known from an island population in northern Poland (Andrzejewski, personal communication). They were probably born at the end of the preceding breeding season, thus they were not more than 20—21 months old. These are sporadic cases, however.

Table 7.5. contains numerical data and statements indicating general trends. Since different authors used various indices of survival and various time units (per day, months, or six weeks), their were transformed for comparative purpose. Such indices have been celculated as the mean percentage survival $\frac{N_t}{N\ (t+1)} \cdot 100$ over one month, and the rate of the elimination of individual animals, μ, as calculated from the formula $N_{t+1} = N_t e^{\mu-1}$ for $t = 1$ day. These indices are used to characterize individual survival in each of the periods distinguished.

On the basis of these indices and taking into account the length of particular periods, a general survivorship curve has been obtained, which characterizes the rate of elimination from an average population living under "average" climatic and food conditions, in a year of average numbers (Fig. 7.8).

Generally, this curve is strongly concave. It shows that as many as 65% of the young bank voles disappear from the population before they can be recorded by trapping, that is, when they are less than 6 weeks old; additionally, 20% disappear in the growing season, and only 15%, which enter winter diapause, have a chance to survive some part of the following breeding season.

7.3.2. Factors Determining Survival in Different Periods

Nesting period. At this age mammals face difficult physiological changes, e. g. the development of thermoregulation, which in the bank vole is "completely developed" on day 19 after birth (Gębczyński, 1975), or the transition from milk to solid diet. It has also been found (Buchalczyk, 1970) that the mortality of these young significantly increases when their mother delivers another litter after the post-partum oestrus and before the young of the preceding litter become independent. A high mortality of the young during the nesting period is also related to such casual events as the death of a lactating female, flooding the nest, or the pressure of specialized nest predators such as vipers or weasels. As a result, generally entire litters die.

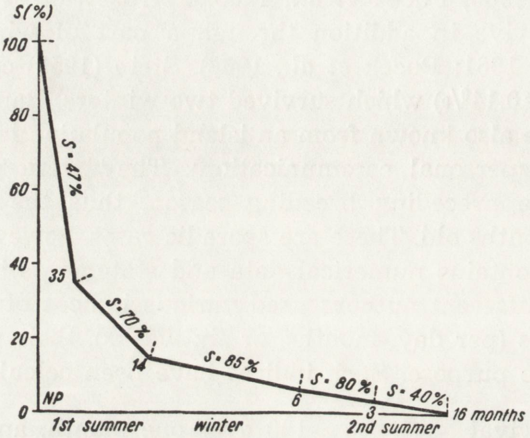

Fig. 7.8. Survival of the bank vole (mean values, according to different authors, see Table 7.5).
NP — nesting period = 42 days, *S* — survival in per cent per month.

In general nesting mortality of the bank vole is very high, reaching 60—70% during the first six weeks of life. A slight decrease in this mortality can significantly increase the level of population dynamics. Many authors show that the survival of the young in the first period of life depends on the time of birth and on the phase in the population cycle. Generally, young born in the first half of the breeding season survive the nesting period better than those born in the second half (Bujalska, 1975a; Gliwicz, 1975). Authors distinguishing three generations over the breeding season found that the voles born in mid-summer survive best (Zejda, 1961; Ryszkowski & Truszkowski, 1970; Bobek, 1973). Differences in survival related to the time of birth may result from changes in the habitat-food conditions over the breeding season, and also they may be due to the increasing population numbers towards autumn, causing stronger individual interactions and increased intraspecific competition. These factors always most severely affect the youngest individuals in the population.

Mortality of these individuals over the annual cycle also depends on the phase in the population cycle. An island population of voles experienced a two-year cycle over a four-year study period (after a year of high numbers there was a year of low numbers), the number of born being identical in the two years (see section 7.1, Bujalska, 1970). The young born in the first half of the year of high population numbers survived much better than those born in the year of low numbers (Table 7.6), and the opposite was true of the survival of inidividuals born in the second half of the year (Bujalska, 1975a; Gliwicz, 1975). Enhanced survival of the young of the spring generation in the years of high vole numbers may be related to better survival of their overwintered mothers (Bujalska, 1975a), especially since the age of overwintered animals is lower during high population numbers (Gliwicz, 1975). Differences in the survival of the youngest individuals, born in autumn, can be explained by changes in the pressure of older individuals on younger ones, which depends on the survival, and, consequently, on the number of individuals of the spring generation. As a result, in the years of low numbers, the survival of the young during the nesting period is considerably less variable than in the years of high numbers (Table 7.6).

Table 7.6

Survival of the youngest individuals (0—6 weeks old) in the bank vole population relative to the time of birth (after Gliwicz, 1975).
h — high population numbers, l — low population numbers.

Year	Spring generation *S* (%)	Autumn generation *S* (%)	Spring generation/ autumn generation
1966 (h)	53.7	10.3	5
1967 (l)	31.8	31.3	1
1968 (h)	61.3	25.0	2.5
1969 (l)	40.9	26.5	1.5

The first breeding season (trappable individuals). As already noted, the group of independent individuals in their first summer is very heterogeneous. With respect to their mortality, this heterogeneity is most pronounced for mature and immature individuals, even if the animals of the same age are considered. Immature individuals surivive much better than mature ones (Schwarz *et al.*, 1964; Bujalska, 1975a). Independent, trappable individuals which are not mature in the breeding season during which they were born usually belong to the autumn cohort. Schwarz *et al.* (1964) found an inverse relationship between the length of life and the intensity of growth, the rate of maturing, and the level of metabolism. In individuals of the spring generation, these processes proceed more rapidly than in individuals of the autumn generation, and are reflected in poorer survival of the former. According to Schwarz *et al.* (1964) the maximum length of life was 12 months for individuals of the spring generation and 14 months for those of the autumn generation. The period of increased mortality (related to reaching maturity) occurred in the third and tenth months for these two groups, respectively.

Also Chitty & Phipps (1966) and Kaikusalo (1972) suggested that the independent individuals of the autumn cohort have a longer maximum life span and survive better than do those of the spring cohort. Smirnov (1972) additionally noted that in *C. rufocanus* and *C. rutilus* the highest survival in this period of life is characteristic of the autumn generation in the years of increasing population numbers.

Thus, the survival of trappable individuals in the year of their birth strongly depends on the time they were born, on their physiological condition, and on the phase in the population cycle. Interestingly in studies quoted above voles born in autumn suffer much heavier losses during the nesting period than do similarly-aged individuals in spring. They survive better and live longer if they pass this critical period and reach independence. It is not an infalable rule, however, since long-term materials obtained from the intense study of an island bank vole population in Poland show that the voles of the autumn generation do not survive better in the year of their birth than the voles of the spring generation (Gliwicz, 1976).

Winter season. All estimates of mortality in bank vole populations show that winter is a period of the lowest mortality, usually not exceeding 20% of the number of voles per month (Newson, 1963; Schwarz *et al.*, 1964; Bergstedt, 1965; Chitty & Phipps, 1966; Ashby, 1967; Gliwicz *et al.*, 1968; Smyth, 1968; Petrusewicz *et al.*, 1969; Smirnov, 1972; Bujalska, 1975a). This mortality is constant over the winter and equally affects different physiological and age classes. Some authors (Tanton, 1969; Kaikusalo, 1972) have recorded a drastic, short-term decrease in survival at the end of February and early in March. At that time mostly the voles in particularly poor condition die (mostly of the spring generation), mortality returns to the earlier, low level. The mean length of life for the bank vole is about three months. Winter (no reproduction) lasts for about six months. It the winter mortality equalled to the summer mortality, all individuals would die by spring.

Notably, a mortality decrease was also observed in species greatly differing from voles in their habits (hares, wild boars, and roe deer). The reasons for a low winter mortality usually include a generally older age structure of the population, a higher tolerance among the population members due to cessation of breeding, as well as lower mobility and intensity of contacts, reduced intra- and interspecific competition, and the reduced impact of predators under snow cover (Schwarz *et al.*, 1964; Smirnov, 1972). According to the literature data, factors determining winter mortality are snow cover (particularly in northern and eastern

Europe) and food availability. The duration of snow cover influences both the mean value of winter mortality and differences in mortality for various periods of winter if snowfalls are followed by sudden thawings and snow-free periods (Ilyenko & Zubchaninova, 1963; Schwarz *et al.*, 1964). The years of abundant acorn and beech mast are characterized by a particularly low winter mortality in the bank vole (Bergstedt, 1965; Hansson, 1971b; Bobek, 1973).

The second breeding season — overwintered animals. In contrast to the total agreement on characteristics of winter mortality, views on the fates of overwintered animals are not consistent. There is a general opinion that in early spring (April and early May) vole mortality is not much higher than in winter, and then it gradully increases. In mid-summer or in autumn, the last overwintered animals die (Newson, 1963; Chitty & Phipps, 1966; Ashby, 1967; Smyth, 1968; Gliwicz, 1975). The already noted differences in views focus on the composition of the overwintered groups. Some suggest that overwintered animals derive from the generation born in autumn, thus maturing in spring (Schwarz *et al.*, 1964; Smirnov, 1972). But in other populations the composition of overwintered animals varied greatly from year to year and this variation significantly modified the mortality of this group (Hansson, 1967a; Zejda, 1967; Gliwicz, 1975). For example, Gliwicz (1975) found that during years of high population numbers more than 50% of the overwintered animals were of the last autumn generation. But during years of low population numbers, more than 80% of the overwintered animals were recruited from the last spring generation. When the age structure of the population was younger, the overwintered animals survived much better than when the age structure was older. The direct cause of the differential mortality of the overwintered animals was not their age, since in the years of higher survival both the spring and the autumn generations survived better. Some intrapopulation factors must account for differences in survival from year to year. Apparently the survival of overwintered animals can be an important component of the regulatory mechanism in the bank vole population.

To summarize this section, it should be stated that factors determining mortality level can differ in each period of an individuals life. During the nesting period, the generally high and variable mortality can result from physiological and abiotic factors (thermoregulation, flood, ground frost), and also from intrapopulation factors, e. g., population density. In the first breeding season, the survival od independent individuals is mostly determined by their physiological status (whether they are mature or immature), which, in turn, depends on many intrapopulation and external factors. In winter, survival is critically linked to environmental factors, and these factors do not fluctuate much, since winter mortality is very similar in various parts of the bank vole range. Conversely survival of overwintered animals can be heavily modified by intrapopulation factors. Because overwintered animals account for 100% of the population in early spring, changes in their mortality are of fundamental importance to population dynamics.

7.3.3. Other Factors Determining Survival

Annual changes in population mortality. When the data on the mortality are superimposed on general changes in the age structure of the population over the year, a pattern emerges of changes in mortality for an average population of the bank vole in the annual cycle. Though this is an average picture, it allows tracking in mortality against the background of population dynamics and changes in age structure (Fig. 7.9). In early spring (April) the survival of voles is very high as these are overwintered animals, which, as already noted, are characterized by a very high survival in the first half of the breeding season. Then their mortality increases and, at the same time, many young voles appear in the population, which are characterized by a low survival. Therefore, the poorest survival in an average population is in late spring and early summer. Afterwards (July-August), when most overwintered animals have already died and the population is composed of aging current-year individuals the surival increases. It should be remembered that the number of very young individuals, characterized by low survival, declines with the advance of the season, as the repro-

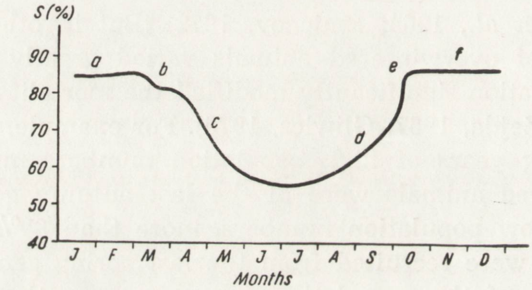

Fig. 7.9. Changes in survival for the whole population over the year. *a*, *f* — winter survival, *b* — early-spring decrease in the survival of overwintered animals, *c* — decrease in surival due to rejuventation of the population age structure, *d* — increase in survival due to growing up of population members, *e* — sudden increase in survival after the breeding season, *S* (%) — survival index in per cent per month.

duction declines nad the nesting mortality (of nontrappable individuals) increases. Consequently, the average mortality in the population should gradually decrease towards autumn, and then, as breeding declines, it should suddenly decrease to a minimum level that will be maintained, with small fluctuations, through winter.

Differentiation in mortality over the range of the species. The literature data on differences in the mortality of the bank vole in various parts of the range of this species are scarce. Generally, it seems that the maximum life span increases south-westwards. In southern Moravia, Czechoslovakia, Zejda recorded individuals that survived 21 months. Individuals living 18—20 months were recorded from Germany and southern Poland (Stein, 1956; Pucek *et al.*, 1968; Bobek, 1973). But the maximum recorded life span of bank voles from Scandinavia and Russia (central USSR) is 14—15 months (Ilyenko & Zubchaninova, 1963; Schwarz *et al.*, 1964; Bergstedt, 1965; Kaikusalo, 1972).

The permanency and depth of snow cover have the greatest effect on winter survival in northern and eastern areas of the range. In the populations inhabiting broad-leaved forests, autumn-winter mortality is clearly related to the abundance of food (mast years), this relationship being absent in other habitats (Bergstedt, 1965; Bobek, 1969; Hansson, 1971a).

Mortality from predation. To explain some poorly understood events occurring in the population, it is frequently hypothesized that the impact of predators on the population varies. However, papers on the real impact of predators (reptiles, birds and mammals) on rodent populations in general, and on forest rodents in particular, are notably few. Southern (1959) and Southern & Lowe (1968) analysed relationships between population dynamics of the tawny owl, *Strix aluco*, the bank vole, and long-tailed field mouse, *Apodemus sylvaticus*. They found that during the breeding season, these rodents account for 70% of the vertebrate prey in the diet of the owl and that the predation rate on the bank vole is proportional to the density of these rodents. Goszczyński (1972), who studied the communities of forest rodents (*C. glareolus, A. flavicollis, A. agrarius*), field rodents (*Microtus arvalis*) and the whole community of predations (birds and mammals), found that in the years of average numbers of forest rodents predators remove up to 69% of their population, thus potentially they can control the number of rodents. But in the years of high population number (usually occurring in the same year for the bank vole and the common vole), the reduction of rodents by predators drops to 13%, thus the increasing populations presumably escape from control by predators. In forests, one of the most important predators can be vipers (*Vipera berus* L.). It seems that among forest rodents they prefer the bank vole. The pressure of vipers in particularly high on the youngest animals on pregnant females, and on migrants (Pielowski, 1962; Pomianowska-Pilipiuk, 1974), thus in certain situations they can account for controlling numbers of the bank vole. Pearson (1966) has found that in open habitats (cropland, grassland, tundra), the 4-year population cycle observed in *Microtinae* rodents can be caused (directly and indirectly) by predators, while in forests such a regular cycle does not occur because of a much lower impact of predators on prey populations.

It should thus be stated that the effect of predators on population dynamics of the bank vole is still unknown. Even if it is not high in terms of numbers, it can be of great qualitative importance, particularly if the impact of predation increases during critical periods of the year for rodent populations, or if it affects selected age classes.

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 percentage 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_g) 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 (Petrusewicz *et al.*, 1971). Production due to growth of spring cohorts is much higher than that of autumn cohorts (68% versus 32%, Petrusewicz *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; Petrusewicz *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 (Petrusewicz, 1967; Petrusewicz & 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 Petrusewicz (1967) and Petrusewicz & 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 Petrusewicz (1978).

8.1.2. Parameters of Productivity

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

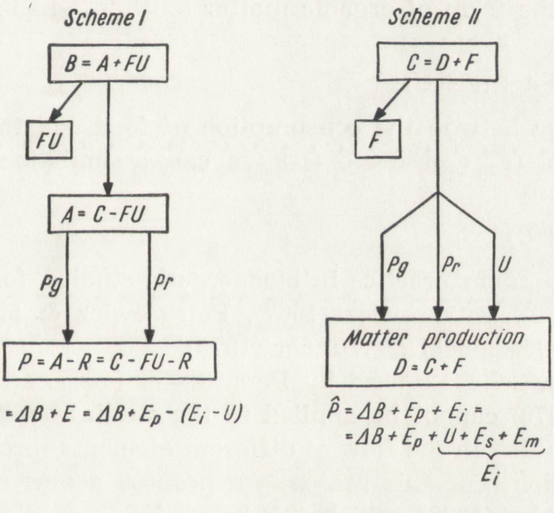

Fig. 8.1. Diagrams of matter and energy flow through a population; C — consumption, A — assimilation (energy input), FU — faeces and urine, P — production, R — respiration (maintenance costs), D — digested energy (assimilated), P — production and energy content of urine, P_g — production due to body 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., ΔB — 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 Petrusewicz, 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

$$MR = NU + C \tag{8.1}$$

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

$$C = D + F = A + (F + U) \tag{8.2}$$

A difference betwen 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).

$$A = C - (F + U) \tag{8.3}$$

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

Energy flow schemes used by Petrusewicz (1967) and Petrusewicz & 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 Petrusewicz (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 productivy parameters, depending on the ecological organization.

To estimate productivity we need many parameters, which can be classified into two large gropus: 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.

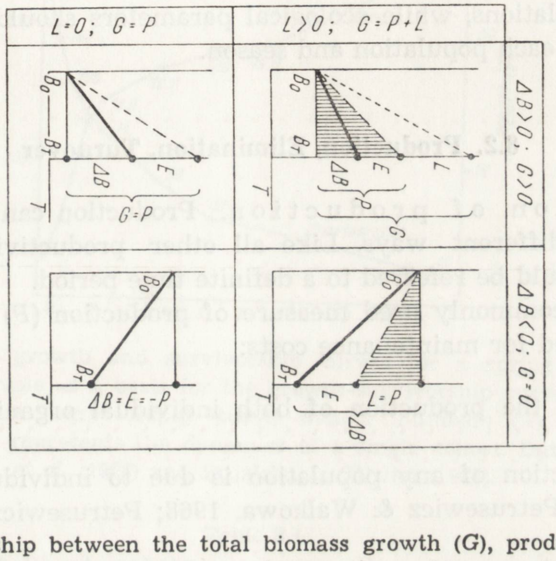

Fig. 8.2. Relationship between the total biomass growth (*G*), production (*P*), elimination (*E*), and weight loss (*L*), when $\Delta B \geqslant 0$, ΔB — biomass change, *T* — time.

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 axample, 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; Petrusewicz *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:

$$P = A - R \tag{8.4}$$

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; Petrusewicz & Macfadyen, 1970).

$$P = P_g - P_r \tag{8.5}$$

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

$$P_T = B_T - B_0 + E_T = \Delta B_T + E_T \tag{8.6}$$

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,

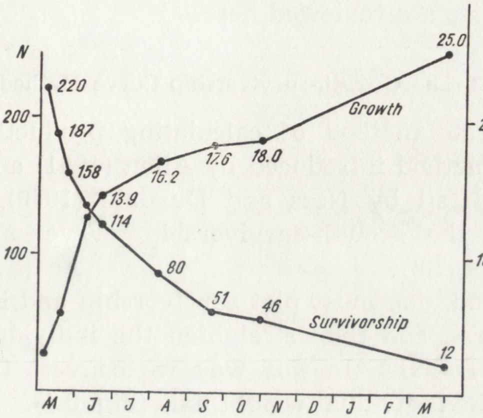

Fig. 8.3. Individual growth and survivorship curves for a spring cohort of the bank vole as a basis for the growth-survivorship curve.
The figures on the survivorship curve denote numbers (N) of individuals (γ) since this curve represents the dynamics of a single cohort. Data from Gliwicz *et al.* (1968) and Bujalska & Gliwicz (1968).

Table 8.1
Average daily metabolic rate (*ADMR* in ccm³ O_2/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 (ΔB) 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 Petrusewicz & Macfadyen (1970), and Petrusewicz & 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 (Petrusewicz & 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).

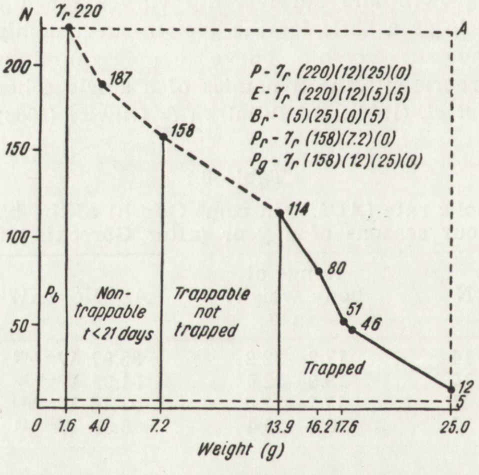

Fig. 8.4. A growth-survivorship curve calculated from data in Figure 8.3. The growth curve is straightened on the abscissa and the number of individuals is plotted against weight; the area below the growth-survivorship curve represents production (from Petrusewicz & Hansson, 1975).

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 Petrusewicz & Macfadyen (1970) and Petrusewicz *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 ν_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 righly 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 beginnig 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; Petrusewicz *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; Petrusewicz & 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

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

where $B_{(T)}$ is the average biomass for the time period T, and Θ_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 γ 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 (Petrusewicz *et al.*, 1971). In oak-hornbeam stand of the Niepołomice Forest, the mean production of a bank vole population varied between 600 nad 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 (Petrusewicz *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 (Petrusewicz & 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 of 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).

$$\Theta_B = P/\bar{B} \tag{8.8}$$

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 (Petrusewicz *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 (Θ_N) is about 4.7 (see section 5.1). The higher value of individual turnover (ν/N) as compared with biomass turnover ($P/\bar{B}$) is an effect of a high mortality of the youngest, not fully grown animals (ν 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 calorigenic 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 seassons. The resultant allometric functions of the form *ADMR* (ccm O_2/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^3 O_2).

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 homoiotherms 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 ef energy. The bioenergetics of this period in the bank vole was studied by Kaczmarski (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 (Kaczmarski, 1966), of which almost 50% goes for respiration, and about 8% for production of the young, including placentae and foetal membranes (Grodziński & Wunder, 1975). The increase in the energy requirements of reproducing females is shown in Figure 8.6.

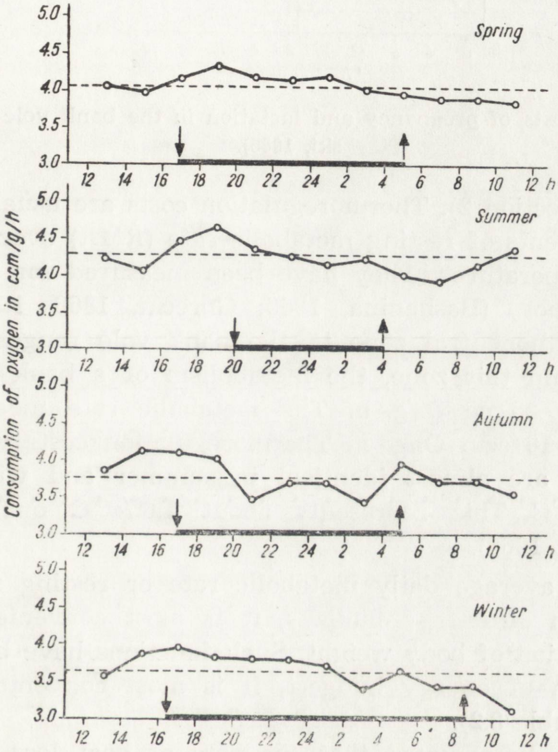

Fig. 8.5. Average daily metabolic rate (*ADMR*) of the bank vole in different seasons ((after Górecki, 1968).

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,

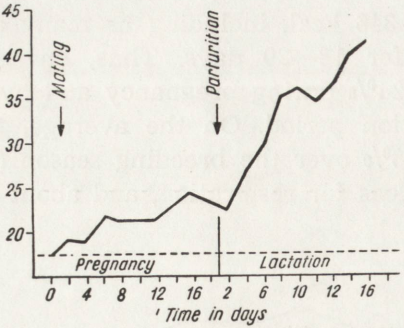

Fig. 8.6. Energy costs of pregnancy and lactation in the bank vole (after Kaczmarski, 1966).

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° and 32°C. Within this zone, the metabolism of a bank vole weighing 24 g is 2.33 ± 0.25 cc O_2/g h. The metabolic rate measured at 0°C reaches almost 10 ccm O_2/g h. Thermoregulation costs within a range of 0° to 25°C are almost identical in summer and winter, reaching 0.967 cal/g · h · °C. This represents about 5.6$^{0}/_{0}$/°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 budgest, 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 matebolic rate (*RMR*) and body weight at different ambient temperatures for the bank vole (after Górecki, 1966, 1968 and unpubl. data).

Ambient temperature	N	*RMR*, ccm O_2/g h = aW^b	Confidence interval of *b*
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 usualy measured in kcal/g · 24 h · °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° to 20°C, using equations from Table 8.2. Then *TC* has been calculated from the formula

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

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

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

where *W* is body weight in grams, and *TC* is thermal conductance in ccm O_2 · 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 ceacum 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 weigth. Then the energy content of food, feces and urine, as well as ash content are determined

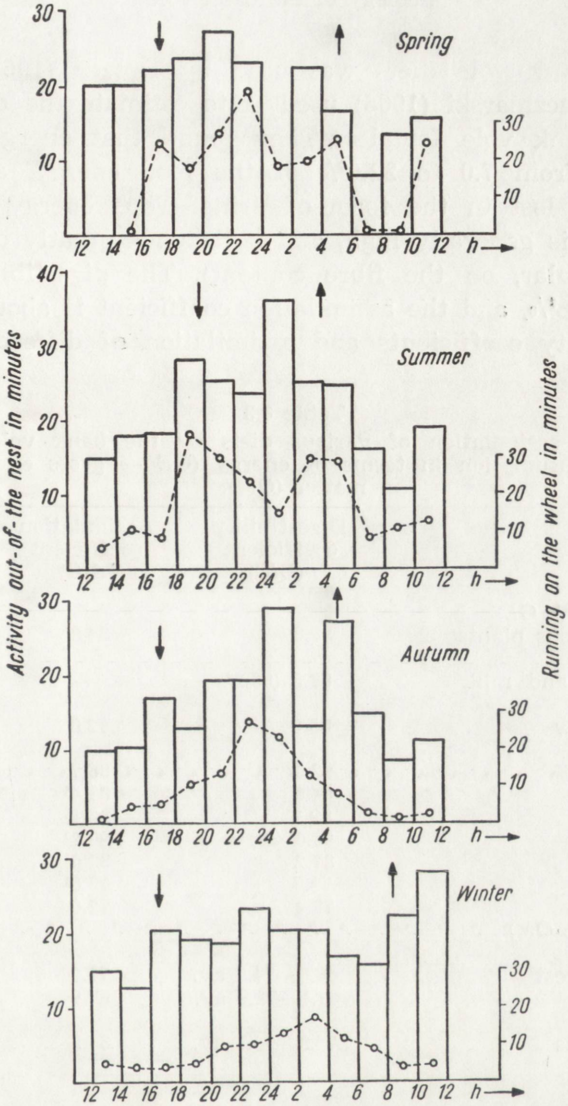

Fig. 8.7. Seasonal changes in the pattern of daily activity as measured in respiratory chambers for the bank vole (after Górecki, 1968).

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 Kaczmarski (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 comprising 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 (digestibilty 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

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 (% *GE*)			
Mixed (herbaceous plants and seeds)	87.8	84.8	Drożdż, 1968
Wheat, carrot and milk	88.5 (86.2[2]	—	Kaczmarski, 1966
Laboratory chow	85.0	82.8	Malinowska, 1978
Beechmast	92.9	88.7	Drożdż, 1968
Acorns	84.0	81.4[1]	Meese, 1971
Oats	89.1	86.1[1]	Drożdż, 1968
Oats	93.0	90.2[1]	Meese, 1971
Wheat	87.2	84.6[1]	Meese, 1971
Bluebell corns	79.7	75.6[1]	Meese, 1971
Greens	77.4	72.0	Drożdż, 1968
Tracer method (% *OM*)			
Natural diets[3]:			
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)

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

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 (fece 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 avaliable 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*, 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).

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

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 thermoregulation 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 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.

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)
ADMR (20°C) in the nest, including group effect (13%)	20 h × 3.65 ccm 0_2/g h = 0.0351	19.5 h × 4.29 ccm 0_2/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_2/g h = 0.135	4.5 h × 5.57 ccm 0_2/g h = 0.121
Cost of female reproduction	—	6.5% *ADMR* = 0.034
Corrected *DMR* values × average body weight	0.486 × 21.0 g	0.556 × 19.0 g
DEB in kcal/vole day	10.21	10.56

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 $D_2{}^{18}O$ 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*) 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 itselt 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" (Petrusewicz & 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

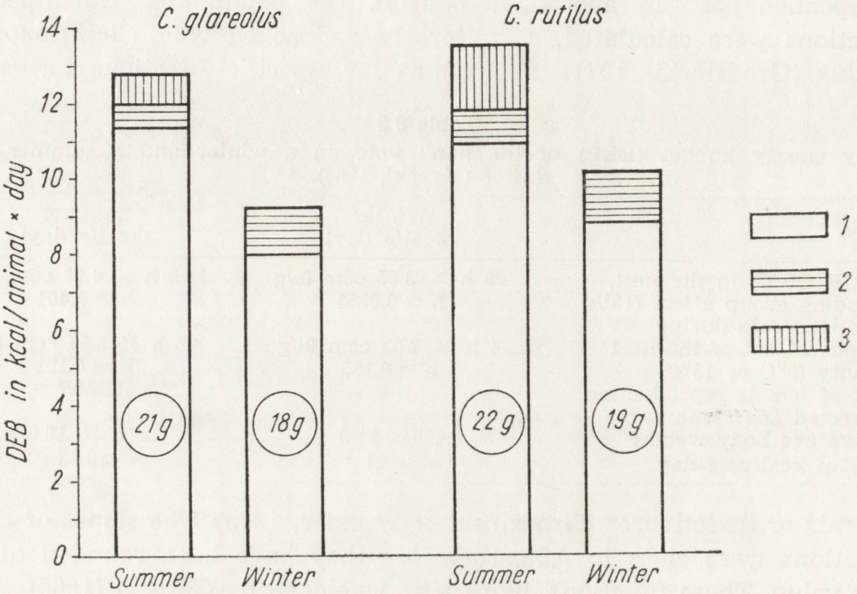

Fig. 8.8. Daily energy budgest (*DEB*) of the bank vole (*Clethrionomys glareolus*) and the tundra redbacked vole (*C. rutilus*) in summer and winter. These are budgets for adult voles of an average body weight (encircled figures); 1 — *ADMR*, 2 — thermoregulation costs in periods of activity beyond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

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 budgest, 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.

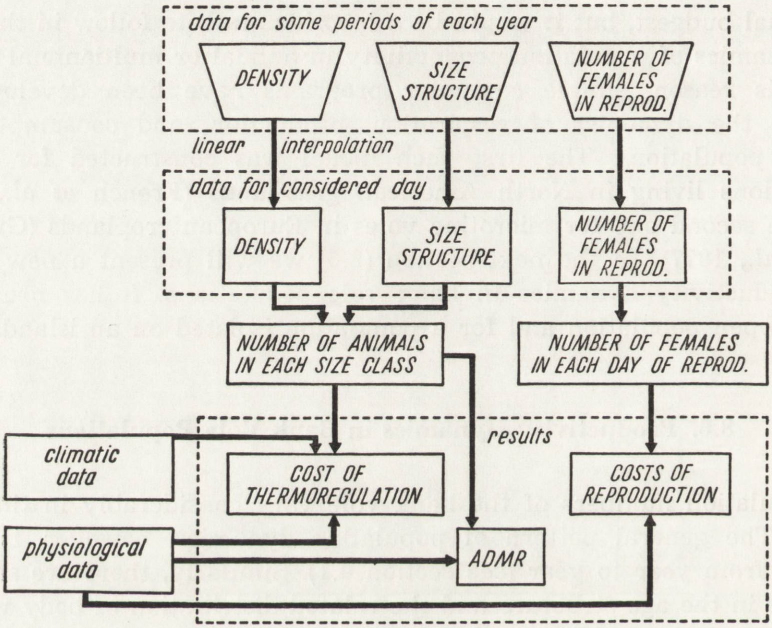

Fig. 8.9. Computation scheme of respiration at the population level.

Physiological data have been described in detail in section 8.3—8.5. Average daily metabolic rates (*ADMR*) 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 *ADMR* for consecutive days of the year was linearly interpolated from the *ADMR* calculated from the two nearest seasons. The costs of thermoregulation (*THERMO*) for animals of each body weight category were calculated from the equation:

$$THERMO = TC \cdot AP \cdot (t - 20) \tag{8.11}$$

where *TC* is thermal conductance (kcal/g · hr · °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, ahout 4 hours (Górecki, 1968). Thermal conductance is multiplied by the difference between 20°C and actual ambient temperature. The thermoneutral zone in the bank vole is close to 30°C, but the costs of thermoregulation between 20° and 30°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 af 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)

$$T_5 = -0.75 + 0.98\ T_{200} \tag{8.12}$$

where T_5 denotes temperature at a height of 5 cm, T_{200} is tempetarure 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°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 $n_{t,\,i}$ ($i=1$, ..., 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

$$n_{t+1,i} = n_{t,\,i-1}\ (1.0—0.02)\ (i = 2, \ldots, 36) \tag{8.13}$$

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

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

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 succesive 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 (Petrusewicz & Hansson, 1975), and for small mammals is described by the equation

$$P = 0.00643\ R^{1.116} \tag{8.15}$$

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)

$$P = 92.4\ \bar{N} \tag{8.16}$$

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^3 O_2 (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 Bełdany 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 Petrusewicz *et al.* (1971), and the number of pregnant females from Bujalska (1970). The description of body weigths 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 Petrusewicz *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 explantion of this, considering also other factors than lack of emigration, has been given by Petrusewicz (1967, 1978) and Petrusewicz & 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

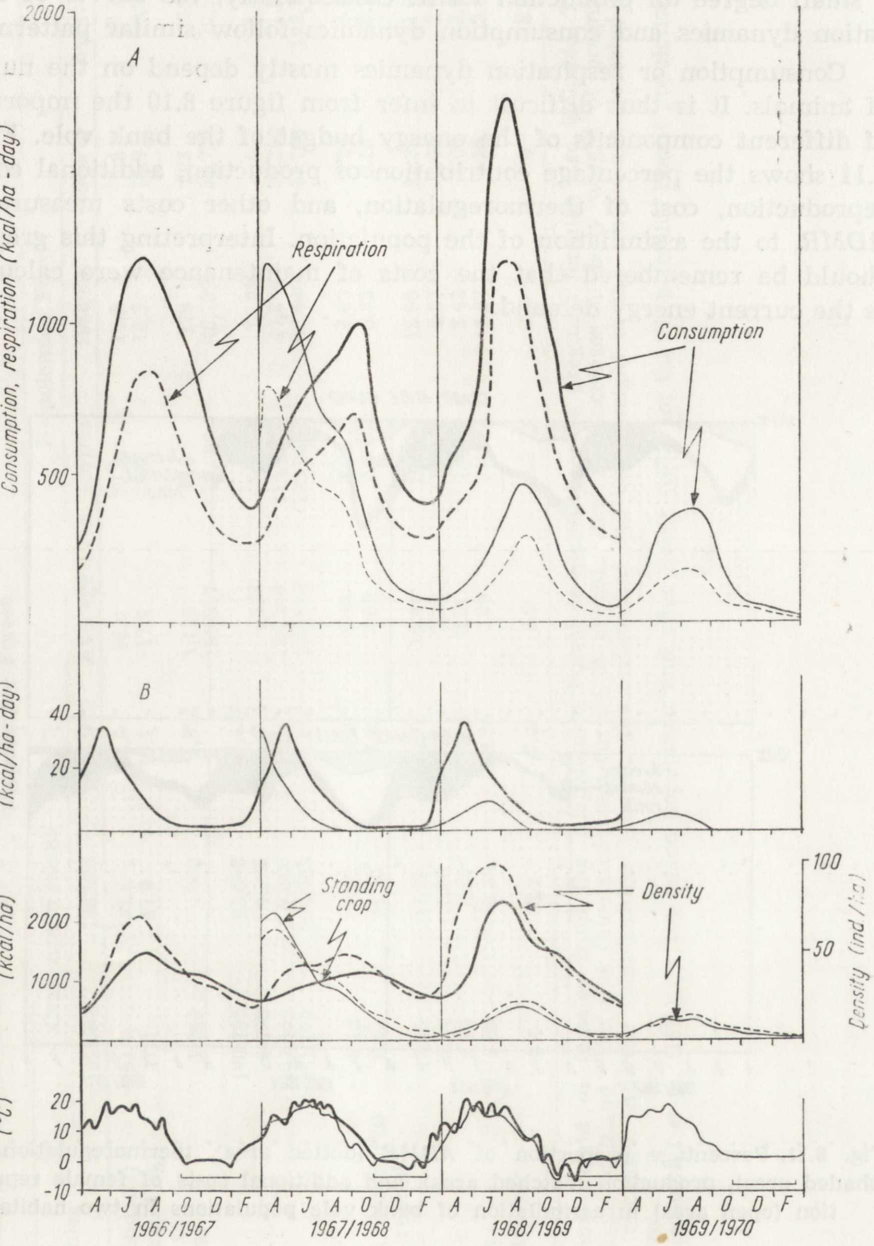

Fig. 8.10. Dynamics of consumption and respiration (A), production (B), numbers and standing crop (C) for bank vole populations on the Crab-Apple island (thick lines) and in the Niepołomice Forest (thin lines). Fig. 8.10 represents mean 10-day temperatures at the ground level (thick and thin lines are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

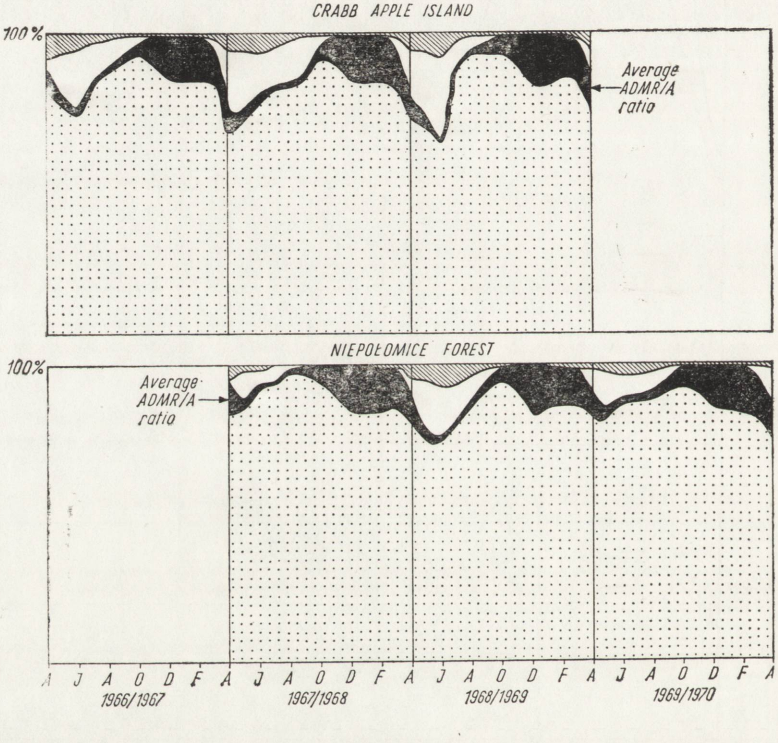

Fig. 8.11. Percentage proportion of *ADMR* (dotted area), thermoregulation costs (shaded area), production (hatched area), and additional costs of female reproduction (open area) in assimilation of bank vole populations in two habitats.

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)[1]	17.5	17.9	16.1	17.2	20.5	18.3	18.9	19.2
Standing crop of biomas (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 [2]	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 thermo-regulat./*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

[1] 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.

[2] After Petrusewicz *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 Petrusewicz & 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.

9. CONTRIBUTION OF BANK VOLES TO THE FUNCTIONING OF FOREST ECOSYSTEMS

Władysław GRODZIŃSKI & Kazimierz PETRUSEWICZ

We can estimate the role of the bank vole in the functioning of temperate zone forest ecosystems largely in terms of the contribution of this species to the total energy and matter flow. Bank voles as small homeothermic consumers have high costs of maintenance and a low net production (see section 8.3). In the trophic web of forest ecosystems they are chiefly primary consumers and only in part secondary consumers (see section 3.1).

Energy flow through *Clethrionomys* sp. populations has already been studied in a dozen or so forest ecosystems of Europe, North America, and Asia (Grodziński *et al.*, 1969/1970, 1977; Grodziński, 1971, Bobek, 1971, 1973; Hansson, 1971a, 1974c; Aulak, 1973; Kozłowski *et al.*, 1980; Jensen, 1981, Smal & Fairley, 1981; see also section 7.6). Many of these studies were initiated during the IBP period when the bank vole became a "laboratory mouse" (a model rodent) for ecologists. In all the papers quoted here both production and respiration were estimated for bank vole populations, and most of them also contain data on consumption (sometimes consumption was estimated directly from biomass, e. g. Ryszkowski, 1969/70), but only in some papers was the consumption of bank vole populations compared with the available food supply in their habitat (Table 9.1). Thus, these papers allow us to estimate what bank vole populations remove (consume) from the forest primary production, and also what they can offer themselves to their predators.

Table 9.1. compares the production of bank vole populations in 14 different deciduous, mixed, and coniferous forests, with also the consumption of northern redbacked voles (*Clethrionomys rutilus)* in a taiga forest. The annual consumption of these populations varied from 1 to 103 × 10^3 kcal/ha year. In open populations of the bank vole a higher consumption was found only in the years of their peak numbers. At that time it reached 192 × 10^3 kcal/ha year in a European deciduous forest and 380 × 10^3 in an Alaskan spruce forest (Table 9.1). In an isolated population on Crab-Apple island, the density of the bank vole

population was permanently high, thus the consumption was also high, and it reached 240—332 × 10^3 kcal/ha year (see section 8.6, Table 8.6).

In relation to the total primary production of these forests, bank vole consumption is negligible as it acconts for a hundredth part of one per cent. It should be remembered, however, that forest production is dominated by wood production. For this reason, it appears to be more reasonable to compare vole consumption with their food available in a forest. Grodziński (1968) defined the food available to small rodents as "food which is easy to find, is being chosen and being eaten by these animals". According to Drożdż (1966), the food available to bank voles in a beech wood comprises the majority of the herb layer vegetation, almost all tree-seeds, buds and twigs of trees, fungi, and some invertebrates. In the case of a beech wood in southern Poland, the food available to bank voles reached about 2 million kcal/ha year, nad accounted for only a small fraction of 4.5% of the total primary production of this forest, which was 44 million kcal/ha year (Drożdż, 1966).

Different authors give various estimates of the food available, ranging from about one to a dozen million kcal/ha year for various forest types. Available food considerably increased in the years with heavy crops of tree-seeds but then also the bank vole population increased (Bobek, 1971, 1973; Grodziński, 1971; see also section 8.6). The utilization of food resources by consumption in bank vole populations ranges from 0.1% to 14%, occasionally being higher, but usually on the order of few per cent. It is assumed that small homeothermic consumers destroy at least as much vegetation as they consume (Petrusewicz & Grodziński, 1973, 1975), therefore the material removed by bank vole populations would approach 25% of their available food.

Is this much or not, and what is the importance of vole consumption to the functioning of a forest? The consumption by bank vole populations presented in Table 9.1 usually predominates the total consumption by small rodents in these forests. It is more difficult to compare consumption by small rodents with energy utilization by other consumers. In pine- and deciduous forests of the Niepołomice Forest, the consumption by the bank vole and other small rodents was similar to that by other homeothermic consumers (birds, herbivore ungulates), but one order lower than by phytophagous insects (Górecki *et al.*, 1984).

Even a more important issue is the kind of materials consumed and removal by the bank vole in a forest. A high proportion of their diet consists of seeds and seedlings, and these materials are of great importance to every forest (Golley *et al.*, 1975b). In an Irish oak wood, for example, both voles and mice consumed merely 0.2% of the primary production, but as much as 7—51% of the seed and fruit materials

(Smal & Fairley, 1981). At the same time, bank voles store and sometimes carry over large distances tree seeds, enhancing in this way forest regrowth. Seedlings are browsed and destroyed by voles during the winter (Hansson, 1974c), and injures by voles can be higher than by fungi and/or insects (Golley *et al.*, 1975b). On the other hand, it should be remebered that insects are a permanent component of the bank vole diet (see section 3.1).

The role of the bank vole in nutrient cycling has been poorly studied. In two forest types of the Niepołomice Forest, the total pool of nutrients in vole and mouse excrements reached 640 and 815 g/ha year, while the concentration of nutrients in their bodies was 32 and 41 g/ha, respectively (Górecki & Szafranek, 1981). These nutrients consisted of nitrogen, phosphorus, potassium, and calcium. Small rodents recycled in those, two types of forest 600 and 763 g N, 25 and 33 g P, 29 and 37 g K, and 17 and 22g Ca per hectare over a year (Górecki & Szafranek, 1981). These are smaller amounts than those recycled by other consumers in those same forests, but nevertheless important because they are released in a form easily available to reducers. It seems that nutrients passing through the chain of grazing consumers are then rapidly decomposed (Batzli, 1978).

Bank vole production is an important source of food for many raptors and carnivore mammals. *Clethrionomys* species usually predominate number and biomass the small rodent communities of north-temperate forests. Seasonally their numbers are particularly high in subarctic taiga forests, where one to three redbacked vole species occur (*Clethrionomys glareolus, C. rutilus, C. rufocanus,* and *C. gapperi*), usually in cycling populations (Pruitt, 1968; Grodziński, 1971; Koshkina & Korotkov, 1975; Fuller, 1977; Wiger, 1979).

Mean annual standing crop of bank vole biomass varies from less than 100 g to 600 g/ha (see reviews by Grodziński & French, 1983). On Crab-Apple island, the standing crop of their biomass over three successive years was higher, reaching 660—945 g/ha (recalculated from section 8.6). An even higher standing crop of the bank vole biomass can occur in seasons of peak population density (Bobek, 1971, 1975), and its estimated value at this time can reach about 1.5—2 kg/ha of "vole meat".

Efficiency of net production in bank vole populations is very low, the turnover of these rodents is very high (section 8.2), and digestibility and assimilation are rather high (section 8.5), but at the same time their metobolic rate is extremely high (section 8.4). Recently, the efficiency of production was analysed in relation to respiration and assimilation (*P*/*R* and *P*/*A*) for 30 species of small mammals, including bank voles (Gro-

Table 9.1

Total consumption (C) in populations of the bank vole (*Clethrionomys glareolus* — rows 1—14) and the redbacked vole (*Clethrionomys rutilus* — row 15) as well as percentage of their food available (*F_A*) consumed yearly in various forest ecosystems.

Forest ecosystem	Population consumption (C)	Food available to voles (*F_A*)	*C*/*F_A* in per cent	References
	10³ kcal/ha-year			
1. Oak-horbeam forest *Tilio-Carpinetum* Niepołomice, Poland	102.7 (47.4—192.0)	2,920 (max. 8,200)	3.5	this study and Zemanek (1972)
2. Deciduous forests mainly *Tilio-Carpinetum)* Crab-Apple Island, Poland	277.5 (239.8—331.6)	—	—	this study
3. Oak-hornbeam forest (*Querco-Carpinetum*) Cracow, Ponald	57.0	2,050	2.8	recalculated from Grodziński (1961); Górecki & Gębczyńska (1962)
4. Sessile oak wood (*Quercus petracea*) Killarney, Ireland	6.7—9.4	28,560—50,570 [1] (670—1,620)	0.02 (10.0—5.8)	Smal & Fairley (1981), recalculated
5. Beech wood (*Fagetum carpaticum*) Ojców, Poland	40.8	1,950	2.1	Grodzieński *et al.* (1969/7 Drożdż (1968)
6. Beech wood (*Fagus sylvatica*) Rönde, Denmark	65.3 (39.6—105.0)	3,000	2.2 (1.3—3.5)	Jensen (1981), recalculated
7. Alder wood (*Circaeo-Alnetum*) Białowieża, Poland	137.6	—	2.2 (0.4—13.5)	Aulak (1973)
8. Mixed and deciduous forest, Kampinos near Warsaw, Poland	71.5	16,190	0.4	Ryszkowski (1969/70)

Table 9.1; concluded.

9. Oak-pine forest (*Pino-Quercetum*) Mazury Lakeland, Poland	58.0—89.4	13,040	0.4—0.7	Ryszkowski (1969/70)
10. Pine wood (*Vaccinio-Pinetum*) Mazury Lakeland, Poland	16.1—39.3	2,415—7,080	0.5—1.0	Ryszkowski (1969/70)
11. Pine wood (*Cladonio-Pinetum*) Mazury Lakeland, Poland	1.0	1,024	0.1	Ryszkowski (1969/70)
12. Yew wood (*Taxus baccata*) Killarney, Ireland	17.1—34.9	30,350—50,120[1] (2,870—3,550)	0.05—0.07 (0.6—1.0)	Smal & Fairley (1981), recalculated
13. Spruce plantation (*Picea abies*) Björnstorp, Sweden	29.3—34.6 32.5 (24.4—42.0)	14,700—19,200 16,500	0.2 0.2 (0.-5—0.25)	Hansson (1971a) Hansson (1974c), recalculated
14. Spruce forest (*Picea abies*) Björnstorp, Sweden	7.0 (4.5—9.6)	300	2.3	Hansson (1974c), recalculated
15. White spruce taiga (*Picea glauca*) Fairbanks, AL, USA	65.2 (10.9—380.1)	480 (470—790)	13.6 (2.3—48.0)	Grodziński (1971), recalculated

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[1] Total above-ground primary production (seeds and fruits available to small rodents, in parenthesis).

dziński & French, 1983). In bank vole populations the efficiency *P*/*R* is 2.70% and *P*/*A* is 2.62%. These are mean values for 18 populations and/or years (Grodziński & French, 1983). Analogous production efficiencies for the northern redbacked vole (*Clethrionomys rutilus*) averaged 2.07 and 2.03% (Grodziński, 1971), and for the large-toothed redbacked vole (*C. rufocanus*) 2.41 and 2.35% (Grodziński *et al.*, 1977). With respect to production efficiency, the bank vole are typical of omnivore rodents; their efficiencies are lower than those of herbivore rodents (*Microtus* sp., *Arvicola* sp.), and clearly higher than those of granivore rodents (*Sciuridae*) (Grodziński & French, 1983).

Mean annual net production for 18 open populations of bank voles was 699 g/ha year, but it varied widely from 76 g to nearly 2 kg/ha year (recalculated from Grodziński & French, 1983). Only the isolated island population had a higher production, reaching about 3 kg (2.826—3.223 kg/ha · year) (recalculated from Table 8.3). For the northern redbacked vole (*Clethrionomys rutilus*) and the large-toothed redbacked vole (*C. rufocanus*) there are only single data on biomass and production in their populations. In the Alaskan taiga, the computed biomass of the northern redbacked vole was 265 g/ha and production was 760 g/ha year (Grodziński, 1971). In a subalpine coniferous forest in central Japan, the estimated biomass of *C. rufocanus* was 55 and 95 g/ha, and their production was 170—300 g/ha · year (Grodziński *et al.*, 1977a). Thus bank vole populations provide the bulk of secondary production, which is available to specialized predators and intensely utilized by them (Ryszkowski & French, 1982).

It is much more difficult to estimate the paratrophic effects of the bank vole on forest ecosystems. Specific roles of consumers in different ecosystems, including small homeothermic consumers, has been analysed by some ecologists in the rodent last (e. g. Petrusewicz & Grodziński, 1973, 1975; Remmert, 1973; Chew, 1974; Abaturov, 1975; Lee & Inman, 1975; Batzli, 1978; Hayward & Phillipson, 1979; Górecki *et al.*, 1984). In addition to flowing energy and cycling nutrients, which are discussed here, small rodents can also influence soil structure, transportation of matter, decomposition rate, plant diversity, and spreading of some plants (authors previously quoted, and also Golley *et al.*, 1975). Some authors also believe that homeothermic consumers can act in ecosystems as "control bumpers", and influence vegetation diversity and stability (Turner, 1970; Lee & Inman, 1975).

The real role of the bank vole and other small rodents in a forest ecosystem could be analysed by a drastic extermination of these pretty animals from a forest area, and then maintaining this forest in isolation, free of small rodents (e.g. on a wooded island). Such an experiment, however, would be technically difficult and it should be continued for more than 100 years, this being the duration /of a complete forest succcession in our part of the temperate zone (Grodziński, 1959). Therefore, not waiting with this monograph for such an experiment, let us try to speculate how a forest free of bank voles and other small rodents could function. Such a forest is likely to grow at a slightly lower rate (slower matter cycling), its regrowth should be better, succession more rapid, and species diversity of the herb layer vegetation lower. But such a forest predators would not be so abundant, nad insects, especially on the forest floor, would be less well controlled.

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PAŃSTWOWE WYDAWNICTWO NAUKOWE ✱ WARSZAWA
Nakład 1320+100 egz. Obj. ark. wyd. 18,5. Maszynopis otrzymano 27.VII.1983 r. Podpisano do druku 16.XII.1983 r. Druk ukończono w grudniu 1983 r. Papier druk. sat. kl. III 80 g. Format B5. Białostockie Zakłady Graficzne. Zam. 1407/83. Cena zł 200.—