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*

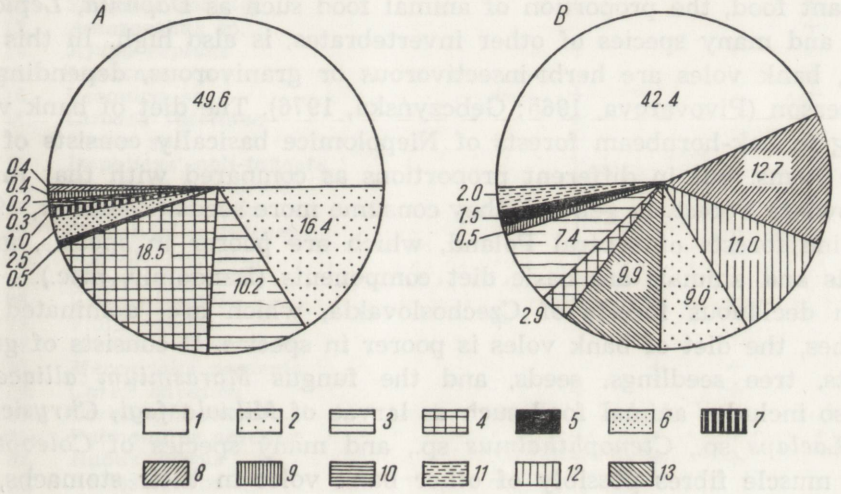

Fig. 3.2. Percentage composition of the diet of C. *glareolus* from the Białowieża Forest (A) and southern Moravia (B).
1 — green parts of herbaceous plants, 2 — animal food, 3 — seed, berries of herbaceous plants, 4 — seeds, fruit of trees, 5 — fungi, 6 — roots, 7 — mosses, 8 — leaves of trees and shrubs,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

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).

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

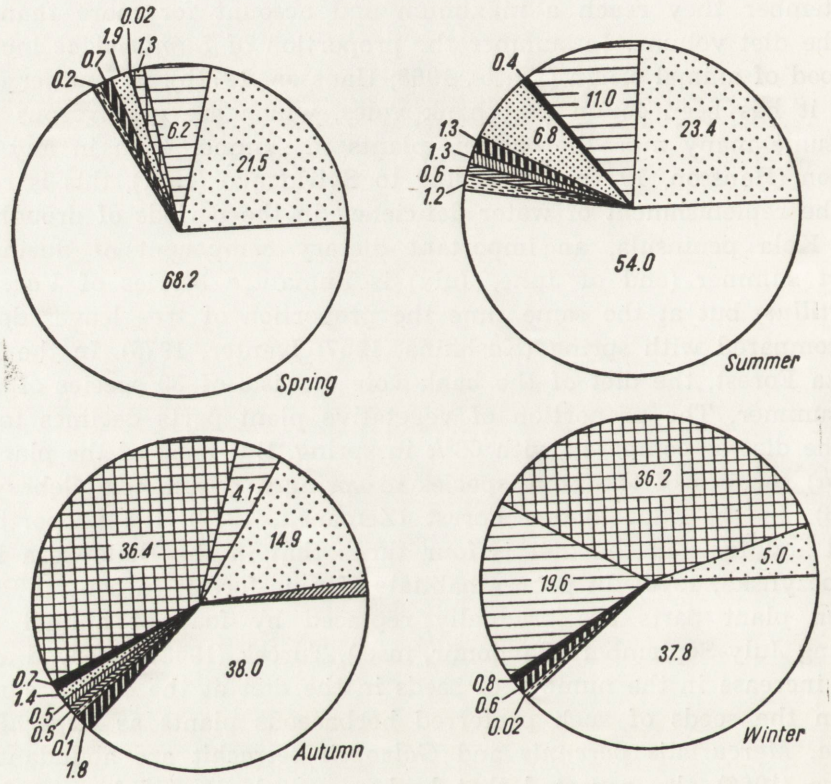

Fig. 3.3. Seasonal variability in the proportion of the diet components of *C. glareolus* from the Białowieża oak-hornbeam (symbols as in Fig. 3.2).

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

Jacek GOSZCZYŃSKI

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