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,

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.

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.

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 prefe-

rence 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 popula-

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).

tions. 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).

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.