3. HABITAT OF THE POPULATION

3.1. Habitat Preference

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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

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

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).

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 plan-

tation 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

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.

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.

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

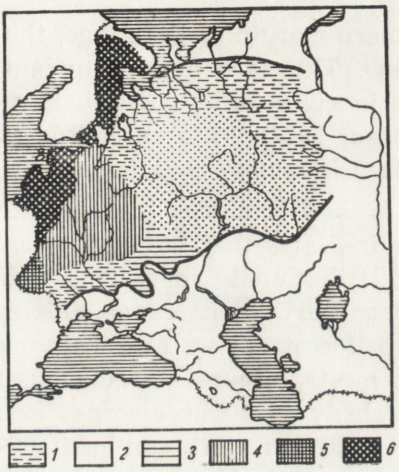

Fig. 3.1. Geographical variability in the maximum number of bank voles trapped in the European part of the USSR (number of animals per 100 trap-nights). After Golikova & Lapin, 1967.
1 — zero voles, 2 — 6 to 15, 3 — 16 to 25, 4 — 26 to 35, 5 — 35 to 55, 6 — more than 55.

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,

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