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Zonal and biotopic peculiarities of bank vole population abundance and its variability level

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The aim of the paper is to analyze geographical and temporal peculiarities of bank vole population abundance and its variability. Long-term studies have been carried out at 4 sites located in different parts of the geographical range. Data on the population dynamics are available from several sites in the same area with different vegetation composition. Variability in density depends both on the season and the location of the population within the species range. The amplitude of changes in the bank vole population increases when moving from the south (the zone of broad-leaved forests) to the north (the middle-taiga subzone). The bank vole populations living in primary forests are most stable. In secondary forests the values of the variability coefficient rise. Analogous changes to the seasonal dynamics are revealed in the successional series from the primary forests through all developmental stages of the communities to clearings of different age. The cyclicity index changes alongside with variability coefficients from the south to the north. Although the abundance variability of the southern populations from the secondary forests and that of the northern populations from the primary and the secondary forests seem to be similar, the mechanisms of its support are different.

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Density variability is closely connected with the habitat conditions (climate, soil, vegetation, etc.) and biological peculiarities of the studied population (nutrient availability, sex and age composition, breeding rate, the dynamics of population size, etc.). The interaction between external and internal factors results in a specific type of population size dynamics.

The problem of the causation of different levels of density variability in rodents has been tackled for a long time and has yielded a comparatively rich literature (Pitelka 1964, Chitty 1967, Christian 1971, Koshkina and Korotkov 1975, Lidicker 1978, Abaturov 1984, Bujalska 1985, Hansson and Henttonen 1985, Krebs 1985, Bondrup-Nelsen 1987, Lidicker 1987, Zhigalski 1992 and others). However, so far there is no clear understanding how these mechanisms are supported in nature.

Density variability has three components: temporal, biotopical, and geographical. Hansson and Henttonen (1985) have analyzed in detail the geographical component of density variability: they presented a list of 45 sites with long-term observations carried out in Fennoscandia from 55°45' to 68°N. They have shown rather convincingly that the variation coefficients rise towards the north with certain exceptions. For example, between 62° and 64°N the variation coefficients are between 96–120%, whereas according to the data obtained by Skaren (1972) for northern Fennoscandia (64°), the variation coefficient was 68%. There are habitats demonstrating opposite trends (increase in variability level) in southern Fennoscandia. However, the authors have not taken into account the possible connection between the variation coefficients and biotope conditions.

The aim of the paper is to analyze the geographical and biotopic peculiarities in density and density variability in

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Table 1. Numbers of bank voles and their variability (variation coefficient) (in parentheses).

Study area Habitat	Demographic characteristics, %				Mean numbers per breeding season, %	S*	Winter survival, %
Tula	April	June	Aug.	Oct.			
Oak-lime forests	11.1 (90.9)	15.0 (66.5)	24.3 (50.9)	20.3 (51.0)	17.7	0.37	46.9
Mary-El							
Spruce-lime forests	11.2 (87.8)	16.9 (10.3)	34.9 (55.1)	20.9 (63.7)	20.9	0.44	48.3
Birch forests	3.4 (120.7)	9.8 (116.0)	21.6 (66.6)	11.0 (115.7)	11.4	0.42	30.9
Regenerating 1957 Clearing	5.2 (89.4)	12.8 (96.7)	23.0 (68.4)	18.2 (74.7)	14.8	0.43	28.6
Regenerating 1968 Cutover	2.3 (153.6)	5.3 (159.5)	15.7 (86.8)	13.2 (90.3)	9.1	0.49	17.4
Udmurt:							
Lime-fir-spruce forests	6.3 (70.8)	12.8 (93.6)	21.0 (54.7)	13.7 (75.9)	13.5	0.42	47.5
Karelia	June	July	Aug.	Sep.			
Moss-spruce forests	2.0 (98.9)	2.8 (102.7)	3.8 (72.8)	9.2 (107.1)	4.4	0.8	31.5
Deciduous and mixed forests	1.3 (135.5)	1.8 (113.9)	4.1 (136.5)	7.7 (126.5)	3.7	0.84	22.7

*Cyclicity index according to Hansson and Henttonen (1985).

bank vole populations. Long-term studies at 4 sites located in different parts of the geographical range of the species (in the taiga zone and the zone of broad-leaved forests) provided the empirical data. Population dynamics in the Mary-El study plot at four sites with different vegetation composition has been evaluated earlier. Biotopic conditions, food and protective capacities on the one hand, and ecological requirements of the animals on the other hand determine the population structure and density in any subzone.

Material and methods

The work is based both on the observations and collections made by the author and on the long-term studies of A. D. Bernshtein, V. A. Korneev, E. V. Ivanter and T. V. Ivanter. These authors studied the population numbers and structure of the bank vole (*Clethrionomys glareolus* Schr.) at four geographically separated sites. The location of each study site has been chosen according to geographical and biotopic peculiarities of bank vole demography. The Tula study sites is situated in the zone of broad-leaved forests, within a region optimal for the bank vole (54°45'N, 37°W). A. D. Bernshtein followed bank vole numbers at this site for 15 yr (1966–1980) and had caught 13500 bank voles in 91 000 trap-nights. The Udmurtian, Mary-El, and Karelian study sites are situated in the taiga zone but in different subzones. Lime-fir-spruce forests dominate in the Udmurtian study site which is in the optimal range of the bank vole (Bashenina 1981). On the Udmurtian study site (57°20'N, 52°W) the investigations lasted for 13 yr (1973–1985). During that time 2500 bank voles have been caught in 20 000 trap-nights and examined.

At the Mary-El study site (56°30', 43°30'W) V. A. Korneev studied the population dynamics at four plots with different vegetation composition from 1972–1987: primary, mature, spruce-lime forests; secondary birch forests with broad-leaved species replacing them; and clearings (cut in 1957 and 1968). During that time, 3000 bank voles have been caught in 25 000 trap-nights and examined.

The Karelian study site in the subzone of middle-taiga forests is located at the periphery of the bank vole range (61°40'N, 33°30'W). E. V. Ivanter and T. V. Ivanter carried out the most long-term observations there (22 yr, 1966–1987). During that time there were 71 500 trap-nights and 1100 bank voles have been caught and examined. Observations were carried out in two plots. One plot is situated in full-grown, open, moss-spruce forest with a mixture of deciduous species. The other plot embraces mature deciduous and mixed stands including secondary forest types that appeared after felling, burning, clearings and other disturbances.

All vole populations were evaluated by the method of relative assessment using standard snap trap lines (Kucheruk 1952). Bits of bread soaked in sunflower oil served as baits. Voles were censused on the plots using lines of 50 snap-traps each, with the traps spaced 5 m apart. Census lines were set for 2 to 4 d, checked once per day four times annually (April, June, August, October) and, in certain years, monthly throughout the reproductive period.

I have calculated the mean numbers for each month as well as for a whole breeding season on the long-term basis, the coefficient of variation for each month, and the cyclicity index S according to Hansson and Henttonen (1985). These estimates have been obtained using standard statistical methods (Glass and Stanley 1976, Pollard 1977).

Results

In general, the plots were inhabited by the bank vole, the northern red-backed vole (*Clethrionomys rutilus* Pall.), wood mouse (*Apodemus sylvaticus* L.), striped field mouse (*Apodemus agrarius* Pall.), grey red-backed voles (*Clethrionomys rufocanus* Sun.), shrews and other small mammals. In summer, the bank vole is the dominant species in all the habitats studied. According to long-term observations, the fraction of this species in the population in different months of the snowfree period and at different permanent study plots varies between 55 and 85% (Zhigalski 1992). In felled and agriculturical areas, other species predominate in the course of succession. Conditions favour the grey red-backed vole in clearings and mice in secondary mixed and deciduous forests. Besides dominating at all permanent study plots, bank vole numbers varied less than the other species.

The seasonal dynamics of the bank vole was usually of the typical form for small mammals in the temperate zone (Bashenina 1981). Numbers are low in the beginning of the breeding season, rise gradually in summer, reach their maximum values by the end of summer, and decrease in autumn (Table 1). During the autumn-winter period the populations decrease, and in spring from 30 to 60% of the voles born in the preceding year are left. Two periods could be distinguished in the seasonal dynamics: growth (April–August) and decline (from the seasonal peak to the spring of the following year).

Geographical differences in the seasonal dynamics of the bank vole manifest themselves in different average density as well as in the amplitude of density fluctuation. Besides that, the breeding season both begins and ends later in the north (Ivanter 1975). Analogous changes in the seasonal dynamics take place in the succession series from primary forests through all developmental stages of the communities to clearings of different stands (Table 1).

An increase in vole populations in the southern parts of the area and in primary forests is in concordance with a decrease in the population increments during the reproduction period (from spring to the seasonal maximum). Negative correlations arise between the total population number and the value of its seasonal increment: the higher the vole numbers, the lower the increment. In the zone of broad-leaved forests at the Tula study site and primary subtaiga forests at the Mary-El and Udmurtian study sites, the seasonal increase of the population is 2.1–3.3-fold, while in the Karelian study plot and in secondary forests of the other territories the population increment is considerably higher and varies between 4.6 and 6.8. The population growth depends mostly on the spring numbers: the higher the abundance of voles in spring, the more numerous the population in summer and autumn (Zhigalski 1982). The picture is different when spring numbers are low. If the difference between spring and critical populations is larger, the population can raise its abundance during the reproduction season several times.

Low spring numbers of the bank vole in disturbed habitats and northern parts of the area may be caused by the lower carrying capacity of these environments (small number of refuges, severe weather conditions, impoverishment of food reserves, etc.), though high winter mortality of the animals may be of equal importance because of deterioration of living conditions and due to a great impact of predators in secondary forests and in the north. 47–48% of the animals born in the autumn of the preceding year overwinter in all southern populations living in primary forests. According to Tupikova and Konovalova (1971), in the southern taiga lime forests, average winter survival (from September to June) of the bank vole was 26%, varying for different ages from 17 to 90%. In the Karelian study site and in the southern secondary forests, winter survival of the voles is much lower and varies between 17 and 31%.

Bank vole populations are most stable in primary forests (coefficients of variation varying from 50 to 98%). In secondary forests their values rise up to 65–137% (Table 1). The variability in density of other vole species and shrews is much higher (from 110 to 250% for various zones).

Coefficients of variation of the bank vole populations changed in different months of the breeding season. In the beginning of the breeding season, the coefficients of variation in numbers in primary forests of different geographical zones were similar. In June, in the phase of maximum population growth, density variability of the bank vole had reached its maximum value (excluding the Tula study plot). The seasonal peak has been timed to August – September, and coincided with the period of population stabilization (Table 1).

Together with the seasonal component of the density variability, a geographical component is present. The amplitude of changes in the bank vole populations increases when moving from the south (zone of broad-leaved forests) to the north (midle-taiga subzone) (Table 1). The cyclicity indices calculated for the bank vole populations are given in Table 1.

Along with the decrease in variability southward, the density variation coefficients may change over wide limits at the same study sites but in different habitats. This was most pronounced at the Mary-El study site. In spring, variability in primary forests is almost half of that in clearings. In autumn, differences between intact and disturbed habitats, though becoming smaller, remain (Table 1).

Discussion

The amplitude of variability depends on several factors: seasonal dynamics (Ivanter 1975, Zhigalski 1992), geographical location (Kaikusalo 1982, Hansson and Henttonen 1985), habitat productivity (Tamarin 1978, Krebs 1979), and migration (Lidicker 1978, Boonstra and Krebs

1979, Abramsky and Tracy 1980). Most investigators distinguish, however, some basic groups of factors determining the variability level of bank vole populations: 1. Changes of climate and weather conditions. 2. Latitudinal differences in predator-vole interrelations. 3. The connection between rodents and plants (productivity and nutritive quality). 4. Intrapopulation factors (physiological stress, genetic and behavioural polymorphism).

However, it is impossible to distinguish one leading factor on the basis of available data. If voles followed only the rhythms of vegetation characterized by pronounced cyclicity, one could expect asynchronous fluctuations in sympatric species owing to specific food preferability of different vole species. However, all species numbers changed synchronously judging by the data obtained for the same geographical zones (Ivanter 1975, Koshkina and Korotkov 1975). In northern Fennoscandia the rise and lowering of the population level also occur synchronously for all species (Hansson and Henttonen 1985).

The relative role of intrapopulational (physiological stress, genetic and behavioural polymorphism) and external (climate, food, predator impact) factors in density fluctuations has been discussed. It may be assumed (Ivanter 1975, Koshkina and Korotkov 1975, Krebs 1979) that extrinsic factors are of greater importance in northern regions and intrinsic factors play a more significant part in southern regions (Ryszkowski et al. 1973, Ivankina 1987).

I have shown earlier that the effects produced by different factors acting upon small mammals are diverse in time. During the autumn-winter period and in the beginning of the breeding season, the external factors play a greater part, while during the reproduction cycle, intrapopulational factors would be of greater importance. To a greater extent intrapopulational factors determine the bank vole populations: they are responsible for up to 70% of the variance explaining the population processes, excluding the winter period and the early beginning of the breeding season, when the contributions of endo- and exogenic factors to number regulation become equal. Even in the unfavourable parts of the range, where the density of vole populations is comparatively low, intrapopulational factors determine the intensity of the population processes (Zhigalski 1992).

Since the level of the population variability depends on the combined effect of all the factors and the maximum value of each in different phases of the reproduction cycle varies, formal grounds for an evaluation of the efficiency of any individual factor (climate, weather, food, predation, anthropogenic impact, etc.) are absent.

Although density variations of the southern populations in secondary forests and northern populations in primary and secondary forests seem to be similar, the variability mechanisms manifest themselves in different ways. One cannot explain the high rates of the southern populations' increment before mid-summer and its subsequent slow drop in secondary forests by changes in the reproduction activity, as the fractions of breeding females are approximately the same both in primary and secondary biotopes. In the south, breeding stops early, and in August no more than 25% of young females continue to participate in reproduction. The observed differences in the rates of population growth and decline may probably be explained by the fact that in the secondary habitats the vole population increases not only at the expense of reproduction of the settled inhabitants but also due to migration (increased in early summer) of the young animals from the primary to the secondary habitats, where the population density is considerably lower. In northern populations, the reproduction season is longer: in August over 50% of young females still participate in breeding and even in September the fraction of breeding females is larger than in southern populations in spite of the fact that the weather conditions in autumn become worse for the northern populations. We may state that in the southern populations living in secondary forest the high population increments result from the immigration of young animals from primary to anthropogenic habitats, whereas in the northern populations the increments may be attributed to prolonged reproduction period and the general intensification of the reproduction of the young voles.

The numbers of forest voles of various species fluctuate considerably in different years, whereas the total number of animals which can find sufficient amount of food and conditions fit for the reproduction and maturation of the young is rather stable in spite of some differences between separate years. Specific conditions of each geographical zone (climate, weather, food, composition of forest-forming species, availability of refuges, etc.) determine the carrying capacity of the small mammals' habitat. It may influence the relative stability of total animal density. The ecological capacity of the biocenosis determines, in turn, the number of animals which can exist in a given territory. A decrease in numbers of one species may be concordant with population rises of the other species, thus maintaining and stabilizing the optimal relations between the total abundance of the animals and the ability of the habitat to provide their living conditions.

The lower limit of the population increment is the level, below which mortality exceeds reproduction. The upper limit of the population increment is determined by habitat capacity; displacing of the upper limit disturbs the equilibrium between the population numbers and the regeneration rate of the environmental resources (Freeland 1974, Zhigalski 1982, 1984, Abaturov 1984).

References

Abaturov, B. D. 1984. Mammals as a component of ecosystems – Nauka, Moscow. (In Russian).

Abramsky, Z. and Tracy, C. R. 1980. Relation between home range size and regulation of population size in *Microtus ochrogaster*. – Oikos 347–355.

Bashenina, N. V. 1981. Bank vole – Nauka, Moscow. (In Russian).
Bondrup-Nielsen, S. 1987. Demography of *Clethrionomys gapperi* in different habitats – Can. J. Zool. 65: 277–283.
Boonstra, R. and Krebs, J. 1979. Viability of large- and small-sized adults in fluctuating vole populations. Ecology 60: 567–573.
Bujalska, G. 1985. Fluctuation in an island bank vole population in the light of the study on its organization – Acta Theriol. 30: 3–49.
Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. – Proc. Ecol. Soc. Aust. 2: 51–78.
Christian, J. J. 1971. Population density and reproductive efficiency. – Biol. Reprod. 4: 248–294.
Freeland, W. 1974. Vole cycles: another hypothesis – Am. Nat. 108: 238–245.
Glass, D. and Stanley, D. 1976. Statistical methods in education and psychology. – Progress, Moscow. (In Russian).
Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. – Oecologia 67: 394–402.
Ivankina, E. V. 1987. Dynamics in numbers and the structure of the bank vole population in the Moscow suburbs. – Thesis abstract, Moscow. (In Russian).
Ivanter, E. V. 1975. Population ecology of small mammals of the taiga region of the USSR North-West. – Nauka, Leningrad. (In Russian).
Kaikusalo, A. 1982. Predatory mammals and vole populations in the fell regions of north-west Finland – Suomen Rsta. 29: 89–92.
Koshkina, T. V. and Korotkov, Y. S. 1975. Population regulation of the bank vole abundance in the area optimum. – Nauka, Moscow. (In Russian).
Krebs, C. J. 1979. Dispersal, spacing behaviour and genetics in relation to population fluctuations in the vole *Microtus townsendi*. – Fortschr. Zool. 25: 61–77.
– 1985. Ecology: the experimental analysis of distribution. – Harper & Row, New York.
Kucheruk, V. V. 1952. Quantitative censuring of the main rodent and shrew species. – Methods of censusing the numbers and geographic distribution of terrestrial vertebrates. 9–46. Nauka, Moscow. (In Russian).
Lidicker, W. Z. Jr. 1978. Regulation of numbers in small mammals populations – historical reflections and a synthesis. – In: Snyder, D. P. (ed.), Populations of small mammals under natural conditions. Pittsburgh, PA, pp. 122–132.
– 1987. Impacts of non-domesticated vertebrates on California grasslands. – In: Mooney, H. A. and Huenneke, L. F. (eds), California grasslands: structure and productivity. Junk, The Hague, pp. 273–278.
Pitelka, F. A. 1964. The nutrient-recovery hypothesis for arctic microtine cycles. – In: Grazing in terrestrial and marine environments. Oxford, pp. 55–56.
Pollard, J. H. 1977. A handbook of numerical and statistical technigues. – Cambridge Univ. Press, Cambridge.
Ryszkowski, L., Goszczynski, J. and Truszkowski, J. 1973. Trophic relationships of the common vole in cultivated fields. – Acta Theriol. 18: 125–165.
Skaren, U. A. P. 1972. Fluctuations in small mammal populations in mossy forests of Kuhmo, eastern Finland, during eleven years. – Ann. Zool. Fenn. 9: 147–151.
Tamarin, R. H. 1978. Dispersal, population regulation, and K-selection in field mice. – Am. Nat. 112: 545–555.
Tupikova, N. V. and Konovalova, E. A. 1971. Reproduction and mortality of the bank vole in the southern taiga of the Vyatka-Kama region. – Fauna and ecology of rodents 10: 145–171. Nauka, Moscow. (In Russian).
Zhigalski, O. A. 1982. Studies of density-dependent mechanisms of the bank vole abundance regulation. Simulation. – Zh. Obshch. Biol. 43: 121–128 (In Russian).
– 1984. A study on an imitation model of the effect of external and internal factors on the dynamics of population density. – Zh. Obshch. Biol. 65: 450–455 (In Russian).
– 1992. Factorial analysis of populations dynamics in rodents. – Pol. Ecol. Stud. 18: 1–141.