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The bank vole (Photograph by G. Bujalska)

Participants of the meeting at Pułtusk (Poland), April 15–18 1999. From left: L. Hansson, O.V. Osipova, J. Gliwicz, T. Saitoh, O. Locasciulli, G. Amori, G. Bujalska, R. Verhagen, A. Kozakiewicz, M. Kozakiewicz, H. Henttonen, N.Chr. Stenseth, A. Marchlewska-Koj, L. Oksanen, N.G. Yoccoz, L. Grüm

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Bank vole biology: Recent advances in the population biology of a model species				

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POPULATIONS OF THE BANK VOLE IN AN INDUSTRIAL ENVIRONMENT: DEMOGRAPHY AND POPULATION NUMBERS CONSEQUENCES

ABSTRACT: Industrial factors exert considerably influence on the level of bank vole abundance and dynamics in numbers of the bank vole by decreasing habitat quality and disturbing the balance of reproduction, mortality and migration. As a result of industrial degradation and fragmentation of habitats, accompanied by the reduction of their ecological capacity and area, the level of the bank vole abundance is considerably reduced. The dynamics in numbers of the bank vole in impact populations is characterized by a lower level and an increased amplitude of dynamics. At significant industrial loads, dynamics in numbers lose periodicity and are characterized by a longer phase of depression.

KEY-WORDS: bank vole, population, habitat quality, demography, numbers, industry

1. INTRODUCTION

An ever-growing human influence on the environment necessitates an examination of consequences of human activity for populations of the bank vole. In this report we discuss some empirical laws of the response of the bank vole's demography and population numbers on the industrial degradation of habitats. Industrial pollutants of metallurgy (heavy metals, acid gases etc.) combined with uncontrolled human activity were chosen as model agents of human impact on the bank vole. As most of the field studies on the effect of industrial factors on bank vole populations were made by the researchers of the Institute of Plant and Animal Ecology RAS (Ekaterinburg, Russia) in industrial regions of the Middle Urals, the present review is based mainly on these studies (Lukyanova 1990; Lukyanova *et al.* 1990, 1994a, b; Bezel, Mukhacheva 1995; Mukhacheva, Bezel 1995; Lukyanov, Lukyanova 1996; Mukhacheva 1996; Mukhacheva, Lukyanov 1997; Lukyanova, Lukyanov 1998a, b).

The level and the dynamics of population numbers are the basic parameters, which show, on the one hand, the ecological capacity of habitats, and on the other hand the degree of balance in reproduction, mortality and migration in populations (Odum 1971; Caughley 1977). In accordance with this idea we analyzed the influence of industrial factors on bank vole population numbers.

2. STUDY AREAS, METHODS AND MATERIAL

The basic research of the influence of industrial factors on the bank vole populations was carried out during June–September of 1987–1989 in two areas in the Middle Urals, affected by copper smelters in Revda and Kirovgrad (Sverdlovsk region, Russia). The territory of the Visim Nature Reserve (approximately 60° N and 57° E) at a distance of 20 and 60 km from these works was used as a control (background). The bank vole was studied on plots, located at different distances (1 to 17 km) from the sources of pollution in dark coniferous forests (mainly spruce, fir, birch and pine) with different degrees of disturbance.

The trap-line method with 50 snap traps spaced 10 m apart was used to catch bank voles. In each line, observations were made during 5–10 days. Seeds of the Siberian pine, a preferable natural fodder for the bank vole in the region, were used as bait. It is important to note that the quality of this bait does not depend on weather conditions. The traps were inspected every morning, and captures mapped. The data obtained during the first five days of trapping were used for estimation of indices of abundance and spatial distribution.

To estimate the abundance and spatial distribution of the bank vole the following indices were used (Lukyanova *et al.* 1994 b): the index of mean (total) abundance (I) – the number of individuals per 100 trap-nights in the whole study area; the index of ecological (partial) abundance (A) – the number of individuals per 100 trap-nights on microplots (10 × 10 m squares with a trap in centre) colonized by the bank vole; the index of occupation (C) – percentage of the total number of traps in a line in which the animals were trapped; and Whitford's (1949) aggregation index Ag=A/C.

Dispersal of bank voles was estimated using the removal method (Lukyanov 1988, 1997), specially adapted for the analysis of successive catches and based on the assumption that successive daily catches of residents decrease according to the exponential law, while catches of dispersers remain at the constant level. In conformity with this assumption, estimates of the initial numbers of residents N_0 in the trapping zone, the daily dispersers flow M through this territory, and the daily catchability of individuals p are computed on the basis of the following regression equation which connects daily catches C_t with accumulated ones K_t and the ordinal numbers of trapping days (t) (Lukyanov 1988):

$$C_t = p(N_0+M) - pK_{t-1} + p^2M\ (t - 1).$$

The dispersers proportion in all population was estimated from the following equation: $\nu=M/(N_0+M)$.

We measured the body weight and length, as well as weight of the heart, kidney, adrenal gland, liver, spleen, thymus, and genitals of the trapped animals. Functional-age groups showing age and reproduction status of individuals, were distinguished according to the degree of thymus development, body sizes, and the stage of the reproductive system. For each sex three functional-age groups were distinguished: overwintered individuals, breeding and non-breeding young of the year.

The concentration of heavy metals (Zn, Cu, Cd) in the bank vole organs was determined using an atomic absorbtion analyser ("Spectrum 4A–1").

On the whole, in the course of field studies 87 trap lines were arranged: 59 – in industrial zones, 28 – in control ones. The lines worked 36 000 trap-nights (20 500 – in industrial zones and 15 500 – in the control) and trapped 3455 bank voles (612 – in industrial zones and 2843 – in the control).

3. INDUSTRIAL HABITATS

In conformity with the studies, conducted in the Middle Urals nearby the sources of industrial pollution the quality of bank vole habitats was considerably lower, mainly, due to the reduction of food and shelters (Lukyanova 1990; Lukyanova *et al.*, 1990, 1994a, b; Mukhacheva, Lukyanov 1997; Lukyanova, Lukyanov 1998b). The decline of habitat capacity resulted from the industrial degradation of forest phytocenoses which was displayed in the change of their characteristics: reduced tree and undergrowth density; increased proportion of dead standing trees; impoverishment of the herbage composition and forest species replacement by meadow species and explerents (Vorobejchik *et al.* 1994). Habitats, as a rule, were considerably fragmented. Farther from the sources of pollution the environment quality was better, as the state of forest phytocenoses improved. The leading factor in degradation of the phy-

tocenoses there was the industrial pollution from copper-smelting works (Vorobejchik *et al.* 1994).

In zones of maximum pollution the concentration of heavy metals in food objects and internal organs of the bank vole was significantly higher in comparison with those in intact (control) zones (Lukyanova 1990; Lukyanova *et al.* 1994b; Mukhacheva, Bezel 1995; Mukhacheva 1996; Lukyanova, Lukyanov 1998a). Doubtless, the reduction of ecological capacity of an environment is one of main factors of an essential decrease of the bank vole abundance in industrial habitats (Lukyanova 1990; Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b).

4. DEMOGRAPHY

The demographic structure of the bank vole in impact and intact populations differed significantly (P<0.001) (Lukyanova 1990; Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b). In intact populations immature young of the year (70%, n=1775), prevailed while in the impact ones mature individuals prevailed (58%, n=505). This resulted from differences in character of mortality of individuals in the compared populations. The total sex ratio in intact populations was balanced (males – 52%, females – 48%, n=1775, P>0.1), while in impact ones it was biased (p<0.001) in favor of males (58%, n=505). Besides, tendencies in the change of sex ratio with age were various in the compared populations. In impact populations male proportion increased from among immature young of the year (50%, n=210) to among the mature (63%, n=162) and overwintered individuals (63%, n=133). Another tendency was observed in intact populations: the proportion of males among the immature young of the year made up 54% (n=1234), among the mature ones – 52% (n=243), among the overwintered individuals – 41% (n=298). Note, that in a natural environment sex ratio among the overwintered individuals was biased, as a rule, in favor of females, which can be explained by an increased mortality of more active males (Bashenina 1981; Bolshakov, Kubanzev 1984).

Reproduction intensity of the bank vole, estimated from fertility, was higher in impact populations than in intact ones (Lukyanova 1990; Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b). Estimates of both actual (average number of embryos per female), and potential fertility (average number of yellow bodies of pregnancy per female) were higher (P<0.01) in affected populations (5.91±0.166, n=53 and 6.51± 0.257, n=50, respectively), than in the control (5.37±0.122, n=102 and 5.76±0.132, n=95, respectively).

Both preimplantation (by 2.4%) and postimplantation (by 2.8%) embryonic mortality were higher in impact populations in comparison with the intact ones (Lukyanova *et al.* 1994b). The proportion of the young of the year in affected populations (73.7%, n=505) was significantly (P<0.001) lower, than in the control (83.2%, n=1775). In industrial zones there were on the average 2.8 young of the year per an overwintered individual, in the intact area, this estimate was almost twice higher (5.0). Hence, relative survival of the young of the year in affected populations was 44% lower, than in the control (Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b).

Estimates of mortality for the overwintered individuals were achieved by comparison of their abundance in beginning and at the end of the reproduction season with the assumption that the disappearance of individuals from the population as a result of their mortality approximates to exponential law (Caughley 1977). Mortality of overwintered individuals made up 56% per month in the industrial areas, and 50% per month in the control (Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b). However, difference in mortality among the young of the year from the impact and intact populations was considerably higher. This can be explained by specificity of life of the young of the year and of the overwinered individuals in industrial zones. Survival of the young of the year in conditions of a fragmented environment is basically determined by finding suitable microhabitats. Evidently, most young of the year die at the stage of dispersal. If suitable microhabitats are found, individuals are safe from the direct influence of industrial factors and the probability of their survival considerably increases. Thus mortality of the bank vole grows in industrial conditions. Mortality is especially high in the young of the year. This fact can explain the difference in the demographic structure of impact and intact populations.

In industrial areas maturation rate of year's young was higher than in the control

(Lukyanova *et al.* 1994b). Among mature animals the percentage of the breeding young of the year was much higher than in the control (54.9%, n=295 and 44.9%, n=541, respectively; P<0.01). In the affected populations there were 1.2 mature young of the year per an overwintered individual while in intact populations the figure was 0.8, i.e. maturation rate of the young of the year was approximately 1.5-times higher in industrial areas.

Thus, demographic processes, connected with reproduction, mortality and maturation are different in the impact and intact populations. Owing to negative influence of industrial factors the mortality of individuals in the affected populations was considerably higher, which caused intensification of reproduction process as a result of feedback. Reproduction in the impact populations increased, as the maturation rate of the young of the year increased and fertility of females was higher. As a result, this population response to the negative industrial pressure permits to somewhat compensate the additional deaths of animals. The demographic structure of the affected populations was firstly determined by complementary processes connected with a higher mortality of the young of the year on the one hand, and with their more intensive maturation on the other. Other processes, connected with differences in mortality of overwintered individuals, embryonic mortality and fertility do not significantly contribute to the demographic structure of the compared populations.

The proportion of the dispersers was higher in the impact populations (ν=47%, n=364) than in the control (ν=30%, n=2196), this evidenced of a higher intensity of the dispersal of the species in industrial conditions (Lukyanov, Lukyanova 1996). The proportion of the dispersers increased (P<0.05) as habitat quality deteriorated, maximum value being observed near the source of the emission and minimum in the intact background (Mukhacheva, Lukyanov 1997). With the help of this effect one can explain the bias of sex ratio in favor of males in the affected populations because among the dispersers males prevail, as a rule (Lukyanov, 1988, 1993; Lukyanov, Lukyanova 1997).

The data show that habitat suitability for the creation of stable colonies of the species decreased from the background and slightly disturbed habitats to significantly degraded ones. Near the sources of industrial emissions temporary seasonal habitats prevail, in which the bank vole can exist only during limited periods (spring–autumn). At a greater distance from the pollution source and as the environment quality improved, habitats became more and more similar to the donor ones, where stable existence of populations was possible. Colonization of more degraded temporary habitats resulted from emigration of individuals from the donor habitats (Bezel, Mukhacheva 1995; Mukhacheva, Lukyanov 1997).

5. ABUNDANCE, SPATIAL DISTRIBUTION AND THEIR DYNAMICS

The change of habitats and the demography of the bank vole under the influence of industrial loads results in the respective change of the basic parameters of abundance and spatial distribution.

The analysis of empirical data demonstrates significant (P<0.001) negative effect of industrial pollution on the abundance and spatial distribution of the bank vole populations (Lukyanova 1990; Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b). The impact populations were characterized by a low level of mean abundance (I) in comparison with the control (3.6±0.2 and 24.3±0.7 ind./100 trap-nights, respectively), primarily due to the lower index of spatial occupation (C) of industrial territories compared to the intact areas (3.3±0.7 and 57.1±1.4%, respectively). The capacity of suitable microplots on the affected and background territories play a considerably smaller role, which the index of ecological abundance (A) shows (27.0±1.5 and 42.6±1.2 ind./100 trap-nights, respectively). This can be explained by peculiarities of the destruction of habitats under the influence of industrial factors. Habitats are fragmented, and the number of fragments with suitable conditions is smaller; this is reflected in the pattern of the territory occupation. Individuals are preserved only in those fragments of the impact habitats where the ecological capacity permits maintainance of normal life. A more rapid decrease of the number of suitable microplotes *vs* their capacity causes an increased (P<0.001) spatial aggregation (Ag) in the affected populations (2.03±0.12 and 0.75± 0.02, respectively), i.e. in the industrial habitats the voles are concentrated on

a limited number of suitable microplots, where their abundance is high enough.

Values of the abundance and spatial structure of the bank vole populations changed on exponential law in dependence on the remoteness from the pollution source. Indices of the mean (I) and ecological abundance (A), occupation of territory (C) gradually increased ($P<0.001$–0.01) with remoteness from the industrial source reaching maximum on the background territory. For the aggregation index (Ag) the relationship was opposite ($P<0.001$) – the highest crowding of animals was observed on the territories adjacent to the pollution source; with remoteness from it the spatial aggregation became weaker, reaching minimum in the control (Lukyanova 1990; Lukyanova, Lukyanov 1998b).

To estimate the dynamics of the abundance and spatial structure dynamics the mean values of these indices in three phases of the numbers dynamics were used: during population depression, rise and peak. As a measure of relative amplitude of these indices the ratio between their maximum and minimum estimates was used (Lukyanova 1990; Lukyanova *et al.* 1994b; Lukyanova, Lukyanov 1998b).

The directions of dynamics in components related with the mean abundance (I), territory occupation (C) and spatial aggregation (Ag) were similar in the impact and intact populations: from the depression to the population peak the indices of the mean abundance (I) and territory occupation (C) increased, while spatial aggregation (Ag) decreased. A significant difference in the dynamics trends between the compared populations was displayed in the index of ecological abundance (A) in microplots occupied by the bank vole (Lukyanova, Lukyanov 1998b). On industrial territories the ecological abundance (A) of voles on suitable microplots did not depend on the phase of population dynamics and maintained at the constant level, while on the background territories this parameter grew from the population depression to the peak. Thus the numbers dynamics in the impact and intact populations was formed by different ways: in natural habitats the increase in numbers was a result of both spatial expansion and of the rise of ecological abundance, in an industrial environment it resulted mainly from space expansion and the abundance of suitable microplots was at a constant level. Note that in their quantitative characteristics the depression phase in intact populations was much similar with the peak phase in the affected populations.

The amplitude of indices of mean abundance, spatial occupation and aggregation in the impact populations was much higher (2–4 times) in comparison with the control (Lukyanova 1990; Lukyanova, Lukyanov 1998b). On the whole the amplitude was reduced in the following rank of parameters: mean abundance (I), territory occupation (C), spatial aggregation (Ag) and ecological abundance (A). The highest stability was typical of the parameter of ecological abundance, which can be explained by a regulatory effect of optimal microhabitats, where the local density of animals both from above and from below was limited which enabled the bank vole to support normal viability.

Thus, the effect of industrial factors considerably influenced on the dynamics of parameters of abundance and spatial structure of bank vole populations. The dynamics had characteristics typical of populations occupying the worst part of an area. This is explained by the destruction of initially favorable habitats under the influence of industrial factors, causing the decrease of both the number of suitable microhabitats and their ecological capacity. Therefore the influence of industrial pollution on the bank vole populations is somewhat identical to its displacement in the continuum "optimum–suboptimum" towards the litter. From this point of view the discussed data confirm the well-known statement that in the area ecological optimum population density is not only higher, but is also more stable, while in the worst conditions it changes in greater range (Ivanter 1975; Zhigalski 1989).

The most detailed long-term study of population dynamics of the bank vole in the gradient of industrial pollution was performed by Kataev *et al.* (1994) in the Kola Peninsula, Russia, in environs of copper-nickel smelter "Severonickel" in Monchegorsk. In conditions of northern Fennoscandia after twenty-years of functioning of the factory the bank vole numbers decreased, and their dynamics lost periodicity. Moreover, based on the data of these authors (Kataev *et al.* 1994), it is possible to conclude that in strongly affected areas the numbers dynamics of both the bank vole and two other *Clethrionomys* species (the red and the grey-sided voles) was characterized by a

longer depression phase which is typical of unstable, temporary colonies of small mammals in suboptimal habitats. This is confirmed both by the periodical absence on territory of voles and by a low abundance level during a year.

It is necessary to note that in extreme conditions of high latitudes *Clethrionomys* species (the bank and the red voles), suffer from industrial pollution most of all, as their food spectrum includes vegetation sensitive to pollution. Firstly the dynamics of these species lose periodicity and has a longer depression phase. While the numbers dynamics of species (the Norway lemming, the field and the root voles), feeding on vegetation tolerant to industrial pollution, does not change much (Kataev *et al.* 1994).

6. CONCLUSIONS

Industrial factors through the decrease of habitat quality and disturbing the balance of processes of reproduction, mortality and migration considerably influence on the level and the dynamics in the abundance of the bank vole. As a result of industrial degradation and fragmentation of habitats, accompanied by the reduction of their ecological capacity and reduction of the area, the abundance level of bank vole fell considerably. An inevitable consequence of environmental degradation was increased mortality of individuals in the impact populations, which to a certain degree was smoothed out by mechanisms of population compensation (intensification of reproduction and reparation dispersal). Owing to these effects the dynamics in numbers of the bank vole in the affected populations was characterized by a lower level and by an increased amplitude of the dynamics, i.e. acquired the main features characteristic for marginal populations. In critical situations, at significant industrial loads, the numbers dynamics of the bank vole lost periodicity and were characterized by a long-term phase of depression, evidences of deterioration of habitat quality and of its transition to suboptimal type.

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