

## The phenomenon of the shrinking size of bank vole (*Myodes glareolus*) in an anthropogenic environment (experience of 50 years of observations)

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Fifty years of continuous monitoring of the bank vole population (*Myodes glareolus* Schreber, 1780) revealed the phenomenon of shrinking body size of individuals, manifesting in significant reduction in their regular size and mass parameters. Field observations were carried out in the Kaniv Nature Reserve (Cherkasy region, Ukraine) during the first half of summer every year. In the forest biotopes of the reserve, this species is dominant in the group of rodents. The research period covered various stages of the existence of the protected ecosystem. Its small area, location in a densely populated region of Ukraine and interaction with neighboring territories which are involved in economic activities have always caused anthropogenic pressure on the protected area. Its nature and intensity determined the changes in the protection regime and the loss of reserve status in 1951–1968. Later, the territory of the reserve experienced increasing technogenic pressure accompanied by radioactive contamination. In this work, to compare their characteristics, four complete cycles of the density dynamics of the bank vole population (from depression to depression) were selected, the duration of which was 4–5 years. The first three cycles correspond to qualitatively different periods in the existence of the ecosystem and the population of the studied species, and the last one corresponds to the relatively current situation. Over the recent 30 years, the size and mass parameters of individuals of bank voles have decreased, – this phenomenon was called shrinking. The process was also observed to tend towards consistent increase in scale. Differentiated analysis shows that in different sex and functional groups of animals, the decrease in exterior parameters can reach 30.3%. Shrinking is especially notable in the group of adult females that are actively involved in reproduction (compared to the second cycle, considered as the control, the decrease in parameters among these is 33.2%). Juveniles of this sex lost 31.8% of their fatness. Besides, in the population of voles, the proportion of large-size individuals was significantly reduced. The group of animals that overwintered significantly reduced its representation, and its existing representatives had much smaller exterior parameters. The studies found that the shrinking process is stable over time, which does not allow it to be considered a random phenomenon or an artifact of research. This phenomenon has no correlation with the amount or availability of food. It occurs against the background of numerous changes in various aspects of population dynamics, which gives grounds to associate it with anthropogenic changes in the environment. Shrinking is believed to be realized through various mechanisms. Firstly, as a result of mortality, the largest individuals and reproducing females with the greatest energy needs disappear from the population, and secondly, the growth and weight gain of young animals is slower. As a result, decrease in the size and mass parameters of individuals reduces their specific energy needs and allows the population to bring their requirements in correspondence with the capability of the environment to support a certain number of resource consumers. An analogy was drawn with the Dehnel's phenomenon, described for shrews of the *Sorex* genus, whose body size and weight decrease is an element of preparation for experiencing adverse winter conditions. Based on similar concepts, the shrinking of its elements can be considered as a specific population strategy to maintain the ecological balance.

**Keywords:** size and mass parameters; shrinking; population dynamics; ecological balance.

### Introduction

The notion of ecological (energy) balance between biosystems and the environment can now be considered unalterable (Mezhzherin et al., 1991; Letnic & Dickman, 2010; Egerton, 2015). However, balance relations are very often declared rather simplistically, for instance, as the presence of relationships between structural or energy components, alteration in which has always negative and often completely destructive consequences (Gómez Fernández et al., 2016). Meanwhile, the presence of numerous external and internal interconnections of the biosystem determines the possibility of such transformations that have adaptive value (or will have it in the future). They allow even very unfavourable conditions to be overcome and provide further restoration of balance in cases of its alteration. The significance of it can hardly be overestimated because long-term existence in a disturbed balance is impossible for the biosystem and, in fact, only two scenarios are further realized – the biosystem either restores the balance or leaves the “arena of life”.

If we apply this scheme of reasoning to a population that exists in a specific environment (an ecosystem with all its components), it should be understood that the prerogative in the implementation of such adaptive

transformations is in the population. Hierarchical complementation of biosystems involves the adaptation of biosystems with lower level of organization to a system with higher level, that is, population to ecosystem (Yakimov et al., 2014; Rozenberg et al., 2016), and not vice versa. Undoubtedly, the population is also capable of changing the environment (this is known as the environment-transforming role of the population), but the scale of this phenomenon is smaller since the impact is carried out on a limited number of components involved in the interaction (Selås et al., 2013; Benincà et al., 2015). From these points of view, the species-specificity of the environment acts as a “guarantee” that under normal conditions no population causes the degradation of its own environment and or destroys the habitat of other species completely.

Constant monitoring of the state of environment for the population is a prerequisite for its existence (Shenbrot, 2014; Aalto & Lampinen, 2015; Ergon & Ergon, 2016). Maintaining the balance can be provided by various mechanisms, but their success is determined by the timely response to changes and correlating the needs of the population with the capabilities of the environment.

The anthropogenization of the habitat is directly related to the energy flows available to the population (Terry & Rowe, 2015; Pirota et al.,

2019). There is reason to believe that the amount of available energy in such situations most often decreases. In the worst case, this will lead to decrease in population functions that are implemented in specific conditions. A softer option involves redistributing energy between functions without reducing their number. This softer scenario cannot be considered as simply the initial phase of degradation processes under conditions of energy imbalance between the environment and the consumer (population). Unfortunately, our understanding of such processes is still imperfect. Among the many reasons for this, some are due to the practical complexity and laboriousness of research in this area. Moreover, they often require rather lengthy studies since the adaptive processes at the population level take place over significant periods of time (Rozenberg & Ryansky, 2005; Romero-Mujalli et al., 2021). This determines the relevance and high value of the results of long-term monitoring of the fate of specific populations in a constantly changing habitat.

The objective of this study was the analysis of the long-term trends in changes in the size and mass parameters of individuals of bank voles in relation to the state of the environment.

## Materials and methods

The study was carried out in accordance with modern requirements for the study of animals in the field. The provisions of the European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (Strasbourg, 03.18.1986) and the Law of Ukraine "On the Protection of Animals from Cruelty" (No. 3447-IV of 02.21.2006) have been satisfied.

Field observations were conducted at the Kaniv Nature Reserve (49°43'18" N, 31°28'48" E, Cherkasy region, Ukraine), where the condition of the rodent populations in a hornbeam grove has been continuously monitored since 1971. The dominant rodent in the group is bank vole (*Myodes glareolus* Schreber, 1780), the number of which is 75.3–80.2% of the total population of rodents in different years.

Half a century of research provided a unique opportunity to trace the long-term trends of changes in various aspects of the existence and functioning of the vole population. Such a long period of observations covered various stages of the existence of the protected ecosystem, due to both successive transformations and the specificity of the anthropogenic pressure. The small area, location in the densely populated region of Ukraine, interaction with neighboring territories, which are involved in economic activities, have always caused anthropogenic pressure on the protected area. Its nature and intensity determined the changes in the protection regime and loss of the reserve status in 1951–1968. Later, the territory of the reserve experienced increasing technogenic pressure, to which radioactive contamination was added (Orlov, 1998). The situation is exacerbated by the synergistic effect of chemical toxicants due to the location of the reserve in the zone of high soil toxicity (Grishchenko et al., 1993).

In this research, to compare their characteristics, four complete cycles of the density dynamics of the bank vole population (between adjacent phases of depression) were selected. The cycle of dynamics can last 4–6 years and be characterized by different levels of density, however, the use of averages makes it possible to correlate them. The first cycle (1971–1974) occurred in the so-called inertial period, which came after the 1968 re-establishment of the reserve status in the territory of educational and research forestry. Its specificity is associated with the gradual movement of the hornbeam grove to climax after a long period of felling and forest clearing, various forestry measures, and other forms of pressure. The first years of the reserve have not yet erased the consequences of economic activity and they inertially affected the population of rodents. The second cycle (1982–1986) corresponds to the minimum anthropogenic impact on the protected area. The third cycle (1996–2000) takes place in the period that began after the accident at the Chernobyl nuclear power plant in 1986, when a complex of reactions was recorded in rodent populations, indicating significant disruptions in the dynamics. The periodization of the state of the rodent environment and the corresponding effects on the population have been given in more detail in our previous studies (Mezhzherin & Myakushko, 1998; Myakushko, 1998, 2016, 2017; Mezhzherin et al., 2002). The last cycle (2008–2013) characterizes the current situation with the vole population. Trapping of animals was carried out using the tradi-

tional method of counting areas. In the hornbeam forest, the areas were located on slopes with different exposures and leveled plateaus, covering territories with varying degrees of undergrowth, herbaceous vegetation, and forest litter. Depending on the current number of rodents, to obtain the required sample, various numbers of counting areas were established. Within the framework of this study, the size and mass parameters of 2,622 individuals of bank voles were analyzed. In addition to the traditional exterior parameters (body weight (W), body length (L), foot length (Pl), tail length (Ca), the fatness index (W/L) was analyzed, which is an index and therefore more sensitive to displaying any impacts (Myakushko, 2005).

For a more differentiated analysis, we compared the parameters of individuals in separate size groups (SG). The criterion for this separation was reaching a certain body weight (Myakushko, 2005). Also, all individuals were divided into separate functional groups (FG). The specificity of this approach is that in the case of selection of such groups, the main criterion is the functional state associated with the specifics of growth, development, and integrity of the reproductive state. Typically, within a particular season, several adjacent generations are characterized by a similar functional load (Pacifci et al., 2013; Sobral & de Oliveira, 2014). The specificity of the functions (functional feature) of the group primarily means the participation of animals in reproduction, which inevitably affects most morphometric parameters. This approach is similar to detecting various functional and physiological groups (FPG) within the population. There are usually three FPGs: the first one (FPG-1) includes individuals that overwintered, the second one (FPG-2) includes individuals born in the current year which do not reproduce in the year of birth, and the third one (FPG-3) comprises individuals born in the current year which reproduce in the current year (Olenev, 1991, 2002). Unfortunately, the lack of accurate data on the age of the animals makes it impossible to use FPGs. Therefore, a simplified technique is used in this work – a division into three FG: FG 1 includes juvenile (immature) individuals, FG 2 includes individuals born in the current year which reproduce in the year of birth, FG 3 includes individuals that overwintered. The data were statistically analyzed using Statistica 8.0 software (Statsoft Inc., USA). The data are presented as mean values and their standard errors ( $\bar{x} \pm SE$ ). The differences between the values in different periods of the annual cycle were determined using ANOVA with Bonferroni correction. The differences between the compared parameters were statistically significant at  $P < 0.05$ . In paired comparison, to assess the significance of the differences between the percentages of the two statistical samples, Fisher's angular transformation criterion ( $\phi^*$ ) was used.

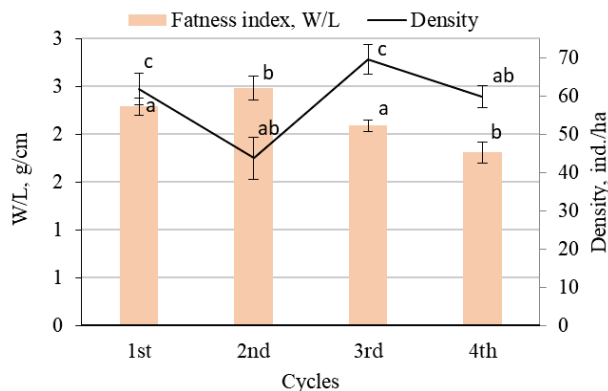
## Results

Figure 1 shows changes in the fatness of individuals during different cycles against the background of the average population density and at least two points in it draw attention. Firstly, the fatness index reaches its maximum in the second cycle, and since 1987 it has been gradually declining. This process has been intensifying – the fatness index of animals during the last cycle of density was 27.4% lower than the maximum. Secondly, this decrease was not associated with population density fluctuations. In total, over the past 30 years, there have been six complete cycles of dynamics lasting 4 to 6 years. Despite the different densities during the peak years, the fatness index of rodents has always decreased, and the process itself was characterized by increase in rates: 11.4–15.3% at the end of the twentieth century up to 22.3–27.4% nowadays.

A gradual decrease in the fatness index occurred simultaneously with the decrease in external parameters– body length, tail length, foot length, and body weight. In Table 1, these parameters are given separately for females and males. In both groups, a similar trend can be seen: after reaching the maximum values in the second cycle, they all decreased further. Analysis of differences in means and the ranges of the variability of characteristics in both sex groups revealed high significance of differences in all parameters. In other words, shrinking of individuals after the second cycle affected the fatness index and individual morphometric parameters. However, the scale of this phenomenon differs among males and females. In the latter group, shrinking was more notable, the parameters on average equaling 7.5–11.0% lower than those in males. It should also be noted that

there was an almost two-fold decrease in the variation coefficients, which indicates the stability of the shrinking effect.

To analyze these phenomena in more detail, all adult (mature) animals were divided by body weight into four size groups (SG): SG 1 included small individuals, SG 2 included animals with body weight below average, SG 3 included animals with body weight above average, SG 4 included large animals. This ranking by mass parameters was performed for the second cycle and subsequently taken as a basis for the comparison. Figure 2 shows their representation in the population in comparison with the size groups of the last period of time. It can be seen that in the population, the proportion of large individuals and individuals with body weight above the average decreased by 2.0–2.5 times. Most individuals in the population had small (below average) body weight, especially in the group of females, where the scale of shrinking was more significant.



**Fig. 1.** Changes in population density and the fatness index of individuals of bank voles during four cycles of dynamics (N = 2622); different letters for the fatness index and density denote values that differ significantly from each other for different cycles with the Bonferroni correction ( $P < 0.05$ )

It is quite clear that the implementation of certain vital functions is associated with the achievement of a certain physiological state and, most often, size and mass parameters. The FGs suggested above are somehow related to two main parameters: life expectancy (reaching a specific age) and the ability to reproduce. These groups had their own characteristic representation in the population and made specific contribution to reproduction and, accordingly, caused changes in population density. That is why

the scale of shrinking was expected to differ within individual FGs. To test this presumption, a comparison was made between their main size and mass parameters during the second and fourth cycles, when the maximum and minimum values were reached, respectively (Table 2).

The study revealed that shrinking occurs in all functional groups but to a different extent. The maximum percentage of decrease in parameters was recorded in the group of individuals that overwintered and were involved in reproduction (FG 3), as well as among juvenile animals (FG 1). In comparison with the second cycle, which was taken as the control, the fatness was 33.2% lower in overwintering females in the fourth cycle, and 31.8% in juvenile females. Rodents that continued to reproduce in the year following their birth were often characterized by the largest size. According to our data, the representatives of this group were largest during the second cycle of dynamics. However, subsequently, in the fourth cycle, they had the largest decrease in parameters. For all of the parameters, they began to be lower than individuals in FG 2, which has never happened before. To a lesser extent, however, a rather significant decrease was seen in the group of immature voles. One should also pay attention to the following nuance: mass (weight) parameters in all cases decreased more than dimensional (linear) ones.

For juvenile individuals of FG 1, a more detailed analysis was carried out, the results of which are shown in Figure 3. One can see two clearly separated clusters of parameters, one of which is shifted towards low values of length and body weight. It visualizes the phenomenon of shrinking among young individuals of the population during the last cycle. This gives grounds for the conclusion that the decrease in parameters occurred from the earliest stages of life. Unfortunately, the lack of accurate data on the age of animals precludes the possibility of establishing the mechanism and beginning of the shrinking processes, however, elementary logic suggests that there are two options or their combination – animals are already born with smaller size and mass parameters or grow and gain weight more slowly. A similar pattern was observed for the other two FGs, but the reason may be quite different – the loss of the largest individuals from the population as a result of their higher mortality rate.

Table 3 shows the decrease in the fatness index of individuals of different FGs during the last three cycles. After the second cycle, its value was constantly decreasing. It has different scales, which is quite natural, given the specific sizes of animals in specific groups. However, if we analyze the specific losses of the fatness index, they turn out to be the largest in the groups of young and old (previous year of birth) rodents. It is noteworthy that in all functional groups, loss of fatness was greater in females.

**Table 1**

The average value and variation of the main external parameters of rodents of different sex groups during the four cycles of population density dynamics

| Parameters | 1st cycle (n=645)         |                                |      | 2nd cycle (n=713)              |       |  | 3rd cycle (n=660)               |       |  | 4th cycle (n=597)              |       |  |
|------------|---------------------------|--------------------------------|------|--------------------------------|-------|--|---------------------------------|-------|--|--------------------------------|-------|--|
|            | $\bar{x} \pm SE$          | CV, %                          |      | $\bar{x} \pm SE$               | CV, % |  | $\bar{x} \pm SE$                | CV, % |  | $\bar{x} \pm SE$               | CV, % |  |
| Females    | Body length (L), mm       | 88.98 $\pm$ 1.31 <sup>a</sup>  | 32.7 | 90.11 $\pm$ 1.04 <sup>b</sup>  | 34.1  |  | 87.62 $\pm$ 1.54 <sup>ab</sup>  | 26.6  |  | 84.82 $\pm$ 1.12 <sup>a</sup>  | 18.2  |  |
|            | Tail length (Ca), mm      | 38.48 $\pm$ 0.66 <sup>a</sup>  | 15.7 | 38.71 $\pm$ 0.74 <sup>b</sup>  | 16.0  |  | 37.28 $\pm$ 0.87 <sup>ab</sup>  | 16.2  |  | 35.28 $\pm$ 1.13 <sup>a</sup>  | 12.9  |  |
|            | Foot length (Pl), mm      | 16.42 $\pm$ 0.21 <sup>a</sup>  | 11.4 | 16.73 $\pm$ 0.32 <sup>a</sup>  | 12.4  |  | 16.13 $\pm$ 0.05 <sup>b</sup>   | 8.3   |  | 16.02 $\pm$ 0.02 <sup>ab</sup> | 7.7   |  |
|            | Body weight (W), g        | 19.64 $\pm$ 1.11 <sup>a</sup>  | 52.1 | 23.48 $\pm$ 1.01 <sup>b</sup>  | 64.9  |  | 18.05 $\pm$ 0.91 <sup>ab</sup>  | 49.6  |  | 16.42 $\pm$ 0.41 <sup>a</sup>  | 38.4  |  |
|            | Fatness index (W/L), g/cm | 2.262 $\pm$ 0.081 <sup>a</sup> | 46.7 | 2.621 $\pm$ 0.133 <sup>b</sup> | 46.9  |  | 2.066 $\pm$ 0.074 <sup>ab</sup> | 43.1  |  | 1.912 $\pm$ 0.121 <sup>a</sup> | 22.1  |  |
| Males      | Body length (L), mm       | 87.91 $\pm$ 1.31 <sup>a</sup>  | 44.7 | 88.65 $\pm$ 1.40 <sup>b</sup>  | 52.0  |  | 85.98 $\pm$ 0.77 <sup>ab</sup>  | 42.3  |  | 83.68 $\pm$ 0.98 <sup>a</sup>  | 32.3  |  |
|            | Tail length (Ca), mm      | 36.05 $\pm$ 0.41 <sup>a</sup>  | 12.1 | 36.34 $\pm$ 0.22 <sup>a</sup>  | 16.4  |  | 35.23 $\pm$ 1.07 <sup>b</sup>   | 12.0  |  | 34.02 $\pm$ 0.52 <sup>ab</sup> | 10.5  |  |
|            | Foot length (Pl), mm      | 16.84 $\pm$ 0.5 <sup>a</sup>   | 13.4 | 16.52 $\pm$ 0.08 <sup>a</sup>  | 13.6  |  | 15.82 $\pm$ 0.71 <sup>b</sup>   | 8.8   |  | 15.77 $\pm$ 0.02 <sup>ab</sup> | 8.1   |  |
|            | Body weight (W), g        | 19.55 $\pm$ 0.23 <sup>a</sup>  | 66.2 | 19.65 $\pm$ 0.35 <sup>b</sup>  | 68.1  |  | 17.65 $\pm$ 0.11 <sup>ab</sup>  | 48.0  |  | 16.34 $\pm$ 1.09 <sup>a</sup>  | 23.8  |  |
|            | Fatness index (W/L), g/cm | 2.213 $\pm$ 0.047 <sup>a</sup> | 50.5 | 2.218 $\pm$ 0.044 <sup>b</sup> | 61.9  |  | 2.042 $\pm$ 0.063 <sup>ab</sup> | 40.9  |  | 1.941 $\pm$ 0.112 <sup>a</sup> | 26.4  |  |

Notes: different letters in the line indicate the values which significantly differed from each other for the cycles using the Bonferroni correction ( $P < 0.05$ ).

**Table 2**

Decrease in size and mass parameters of individuals of different functional groups (FG) during two cycles of population dynamics

| Parameters                | FG 1 (n=176)                      |                                   |                | FG 2 (n=929)                      |                                   |                | FG 3 (n=205)                      |                                   |                |
|---------------------------|-----------------------------------|-----------------------------------|----------------|-----------------------------------|-----------------------------------|----------------|-----------------------------------|-----------------------------------|----------------|
|                           | 2nd cycle<br>( $\bar{x} \pm SE$ ) | 4th cycle<br>( $\bar{x} \pm SE$ ) | decrease,<br>% | 2nd cycle<br>( $\bar{x} \pm SE$ ) | 4th cycle<br>( $\bar{x} \pm SE$ ) | decrease,<br>% | 2nd cycle<br>( $\bar{x} \pm SE$ ) | 4th cycle<br>( $\bar{x} \pm SE$ ) | decrease,<br>% |
| Body length (L), mm       | 76.92 $\pm$ 2.18 <sup>a</sup>     | 66.97 $\pm$ 3.18 <sup>b</sup>     | 13.0**         | 94.33 $\pm$ 2.19 <sup>a</sup>     | 86.47 $\pm$ 1.26 <sup>b</sup>     | 8.0*           | 96.13 $\pm$ 1.29 <sup>a</sup>     | 88.18 $\pm$ 2.14 <sup>b</sup>     | 8.2**          |
| Body weight (W), g        | 12.67 $\pm$ 0.23 <sup>a</sup>     | 10.34 $\pm$ 0.21 <sup>b</sup>     | 18.6***        | 24.13 $\pm$ 0.16 <sup>a</sup>     | 21.64 $\pm$ 0.33 <sup>b</sup>     | 9.8***         | 26.83 $\pm$ 0.68 <sup>a</sup>     | 20.24 $\pm$ 0.40 <sup>b</sup>     | 24.5***        |
| Fatness index (W/L), g/cm | 1.654 $\pm$ 0.144 <sup>a</sup>    | 1.381 $\pm$ 0.180 <sup>b</sup>    | 16.4***        | 2.534 $\pm$ 0.111 <sup>a</sup>    | 2.282 $\pm$ 0.154 <sup>b</sup>    | 8.8**          | 2.794 $\pm$ 0.081 <sup>a</sup>    | 2.111 $\pm$ 0.092 <sup>b</sup>    | 24.6***        |

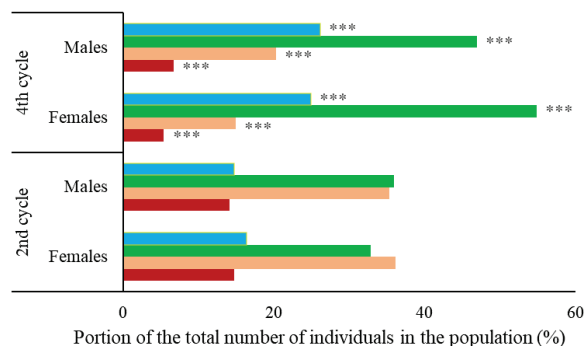
Notes: significance of the decrease by Fisher's angular transformation criterion ( $\phi^*$ ): \* –  $P < 0.05$ , \*\* –  $P < 0.01$ , \*\*\* –  $P < 0.001$  relative to 2nd cycle; different letters in the line indicate the values which significantly differed from 2nd to 4th cycles for each FG using the Bonferroni correction ( $P < 0.05$ ).

**Table 3**

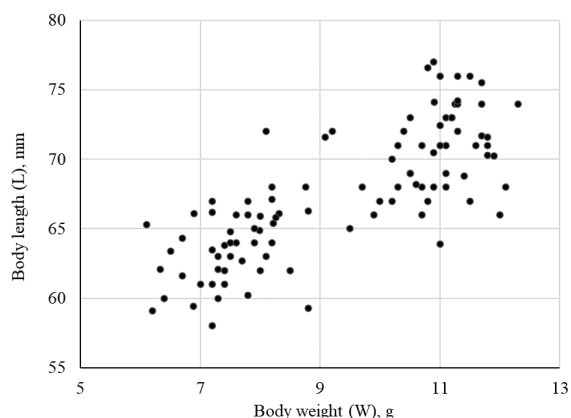
Changes in the fatness index (W/L, g/cm) of females and males of various functional groups during the last three cycles

| Cycles          | Functional group 1          |                             | Functional group 2          |                             | Functional group 3          |                             |
|-----------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
|                 | females (n = 184)           | males (n = 217)             | females (n = 837)           | males (n = 931)             | females (n = 211)           | males (n = 223)             |
| 2nd cycle       | 1.681 ± 0.112 <sup>a</sup>  | 1.533 ± 0.143 <sup>a</sup>  | 2.568 ± 0.128 <sup>a</sup>  | 2.343 ± 0.077 <sup>a</sup>  | 2.693 ± 0.201 <sup>a</sup>  | 2.517 ± 0.130 <sup>a</sup>  |
| 3rd cycle       | 1.398 ± 0.151 <sup>b</sup>  | 1.346 ± 0.089 <sup>b</sup>  | 2.341 ± 0.153 <sup>b</sup>  | 2.116 ± 0.196 <sup>b</sup>  | 2.398 ± 0.177 <sup>b</sup>  | 2.204 ± 0.145 <sup>b</sup>  |
| 4th cycle       | 1.146 ± 0.063 <sup>ab</sup> | 1.145 ± 0.137 <sup>ab</sup> | 1.997 ± 0.146 <sup>ab</sup> | 1.893 ± 0.154 <sup>ab</sup> | 1.799 ± 0.088 <sup>ab</sup> | 1.935 ± 0.137 <sup>ab</sup> |
| Fatness loss, % | 31.83 <sup>a</sup>          | 25.31 <sup>b</sup>          | 22.24 <sup>a</sup>          | 19.21 <sup>b</sup>          | 33.20 <sup>a</sup>          | 23.12 <sup>b</sup>          |

Notes: different letters in column for cycles and the line for fatness indicate the values which significantly differed from each other for the cycles using the Bonferroni correction ( $P < 0.05$ ).



**Fig. 2.** Representation of individuals of different size groups (SG) in the population (%): blue columns – size groups 1 (SG 1); green columns – SG 2; brown columns – SG 3; red columns – SG 4; significance of the decrease by Fisher's angular transformation criterion ( $\phi^*$ ): \*\*\* –  $P < 0.001$  relative to similar parameters of the 2nd cycle



**Fig. 3.** Size and mass parameters of individuals of Functional group 1 during the second (the cluster on the right) and fourth (the cluster on the left) cycles of density dynamics ( $N = 101$ )

## Discussion

For almost five decades of rodent research in the Kaniv Reserve, a complex of phenomena has been recorded, which ultimately led to changes in the dynamics of density and various types of population structure (Myakushko, 2018). It turned out that at the population level, the reactions of animals to current changes in the state of the environment were quite rapid and pronounced.

It should be mentioned that we noted the effect of shrinking in 2003 (Myakushko, 2005). It was proved that the external parameters of individuals of various species decreased by 12.3–18.1% and assumptions were made regarding the causes and consequences of this phenomenon. However, the research data available at that time did not allow for conclusions about the real scale of shrinking, as well as about the stability of the process over time. The results of the observations over the past 15 years have significantly added details to the picture, and differentiated analysis within individual sex and functional groups has provided grounds for understanding and generalizing the causes and mechanisms of animal shrinking under conditions of anthropogenic transformation of the environment.

The available data allow us to state that the tendency towards shrinking of individuals is not a temporary phenomenon. It not only has persisted for 30 years but also amplifies over time. This is evidenced by the minimum morphometric parameters of individuals achieved during the fourth cycle. Such an existing and quite pronounced trend can be traced even if we involve in the analysis not one cycle per decade, as has been done in this work, but absolutely all cycles. It is clear that shrinking occurs gradually, but in the case of comparison with the second cycle, the animals have already lost up to 1/4 of the size and mass parameters.

In the population ecology of rodents, there is a well-known phenomenon of interconnection between population density and animal size (Ozgul et al., 2010; Finn et al., 2018; Brouard et al., 2020). High population density can indeed lead to a decrease in the size of individuals against the background of limited resources, given the inertia of self-regulation mechanisms (usually, inhibition of the intensity of reproduction). However, such phenomena are short-term, as the population has many opportunities to restore the balance between the number of consumers and their resources relatively quickly (Wilson et al., 2018; Lidicker, 2020; Andreasen et al., 2021). In our situation, there is no connection with population density ( $r = 0.071$ ): the size of animals decreases regardless of density fluctuations. This happened in absolutely all phases of the dynamics.

It is logical to assume that the decrease in the size of animals is associated with insufficient food supply. Bank vole is a pronounced polyphage, which is capable of using a wide range of food and, if necessary, quickly switching from one component of the diet to another, which in principle causes its numerical dominance in many groups of rodents (Torre & Arrizabalaga, 2008). According to the available data, the food supply can have a limiting effect, therefore, the correspondence between the density and parameters of the food supply is a quite common occurrence (Prevedello et al., 2013; Bian et al., 2015; Soininen et al., 2018). According to our previous research, such a connection did exist until the end of the second period, then it disappeared, and all previous correlations were simply absent (Myakushko, 2001). Another feature should be taken into account: as a rule, the parameters of the food supply are associated with the number (density) of animals, and not with the dimensional parameters of individuals (Read et al., 2018). In other words, regulation is carried out at the expense of the number of consumers of resources, rather than their conditional “quality”. According to our data, such type of dependencies existed almost until the 1990s. Since then and until now, all the previous connections have disappeared, which gives no reason to associate the shrinking of individuals with fluctuations in the state of the food supply.

It is known that different sex and age groups of individuals provide different contributions to reproduction and, accordingly, to the current number (Fay et al., 2016; Xu, 2016; Ferrari et al., 2019). Perhaps this should be associated with different scales of shrinking in separate groups. It is reasonable to assume that the reason for the larger shrinking of females is the growth of their energy needs during the breeding season. Pregnancy, breastfeeding, and other effects associated with reproduction can increase the energy consumption of female rodents by more than 30.3% (Speakman, 2008; Rödel et al., 2016). It has been repeatedly shown that this fact increases their mortality rate (Efford et al., 2006; Rödel et al., 2015). On the other hand, maintaining higher biomass of the body requires a higher amount of energy. Therefore, it is natural that, first of all, as a result of mortality, either the largest or most fertile individuals disappear from the population (according to our distribution, these are FG 3 females, the relative number of which decreases by almost a third). It is the females that overwintered that suffer the most, and the losses

among this group cause a redistribution of the size and functional groups in the population. It should be emphasized that it is almost impossible to study changes in the mortality rate of various groups of individuals directly under natural conditions. The only source of data for analysis is the change in the characteristic connections between groups of living individuals, which are most often used in population demography (Krebs, 1996).

Based on the available data, the death of individuals with either simply large body sizes or increased energy needs as a result of the reproductive function can be considered a significant cause of shrinking. The causes and mechanisms of the shrinking of juvenile animals are more difficult to discuss. We may presume that the young are more likely to grow and gain weight more slowly (another assumption about the smaller size at birth, unfortunately, cannot be verified in the field).

Under any circumstances, the connection between the phenomenon of shrinking and the state of the environment is obvious. The complex of previously found population phenomena – reduction of reproductive efficiency, increase in mortality rate, stochastic dynamics, the violation of regular changes in the population structure – provide grounds for a negative assessment of these events (Myakushko, 2002). The considerable length of time during which the shrinking is observed suggests a kind of strategy that the population implements under such conditions. A decrease in the size and mass parameters of individuals reduces their specific energy needs and possibly optimizes their interaction with the environment. Decrease in size can be considered a very rational way to ensure survival in the suboptimal conditions of an anthropogenically changing environment. It is worth mentioning Dehnel's phenomenon, described for shrews of the *Sorex* genus: reduction in body size and weight as an element of preparation for experiencing adverse winter conditions (Dehnel, 1949). This phenomenon was later explained in terms of energy and was also recorded in other animals (Mezhzherin, 1964; Hope et al., 2010; Lázaro et al., 2018, 2021). Our data suggest that shrinking of individuals may be a more universal population strategy to maintain the ecological balance.

## Conclusions

Maintaining the ecological balance should be considered a priority for the survival of a population in the course of its interaction with the changing environment. The balance can be provided by various mechanisms, but their success is determined by a timely response to the state of the environment and bringing the needs of the population in accordance with its capabilities. Over the past 30 years, there has been a decrease in the size and mass parameters of individuals of bank voles, which is called the phenomenon of shrinking. It is found that with each cycle of population density dynamics, the scale of shrinking consistently increases. Differentiated analysis showed that the decrease in parameters is especially noticeable in the group of females. Besides, in the population of voles, the proportion of individuals with large sizes is significantly reduced.

The group of animals that overwinter significantly reduces its representation, and the group's existing representatives have smaller exterior parameters. The process of shrinking has a stable and pronounced tendency to progress, which does not allow it to be considered as a random phenomenon or an artifact of research. Shrinking occurs against the background of numerous violations of various aspects of population dynamics, which gives grounds to associate it with anthropogenic changes in the environment. It is suggested that the phenomenon of shrinking can be realized by various mechanisms. Firstly, as a result of mortality, the largest individuals and reproducing females with the largest energy needs disappear from the population, and secondly, the growth and weight gain of young animals is slower. As a result, decrease in the external parameters of individuals reduces their specific energy needs and allows them to better survive adverse conditions. From these positions, the shrinking of its elements can be considered as a specific population strategy to maintain the ecological balance.

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