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A VAIN ATTEMPT: WHY A CHANGE IN THE REPRODUCTIVE STRATEGY OF A RODENT POPULATION FAILED TO RESTORE ECOLOGICAL BALANCE

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Abstract

Based on long-term observations of a bank vole (*Myodes glareolus* Schreber, 1780) population, the preconditions, mechanisms, and consequences of changes in reproductive strategy to restore ecological balance are analysed. The studies were conducted in the Kaniv Nature Reserve during different periods of the ecosystem's existence affected by anthropogenic impact. The characteristics of two cycles of population density dynamics are compared. The first cycle covers the destabilisation stage of the dynamics, which precedes changes in reproductive strategy, whereas the second cycle demonstrates changes in breeding parameters. It was found that in order to compensate the high levels of mortality, reproductive processes intensify. This is achieved by the simultaneous launch of various mechanisms, from increasing individual fecundity to expanding the proportion of individuals involved in reproduction. The first scenario turned out to be unsuccessful and, without adequate ecological support in the form of sufficient feeding resources, caused even higher mortality rates. The size and number of litters dropped to minimum values, and reproduction parameters indicated only a slight success in realising the breeding potential. The most vulnerable was the group of large females, whose fecundity and, consequently, contribution to population growth are the highest. It was found that such processes changed not only the size and weight composition of the population (the proportion of large individuals decreased), but also the sex and age structure (the number of adult females decreased). The decline in the number of large breeding females only exacerbated the misbalance. Population collapse was avoided by expanding the number of females involved in reproduction (extensive reproduction). It is shown that restoration of ecological balance did not follow the change in reproductive strategy. This is supported by the following facts: preservation of signs of a destabilised population dynamics and absence of the previous interdependencies between demographic indices and parameters of feeding resources. As a result, after about a decade of intensive but ineffective reproduction, the population was 'forced' to switch to another strategy to restore ecological balance.

Cite as

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Невдала спроба: чому зміна репродуктивної стратегії популяції гризунів не забезпечила відновлення екологічного балансу

Станіслав Мякушко

Резюме. На матеріалах багаторічних спостережень за популяцією рудої нориці (*Myodes glareolus* Schreber, 1780) досліджені передумови, механізми і наслідки зміни репродуктивної стратегії з метою відновлення екологічного балансу. Дослідження проводили у Канівському природному заповіднику, а їх час охопив різні періоди існування екосистеми, обумовлені антропогенним впливом. Здійснене порівняння характеристик двох циклів динаміки щільності популяції. Перший із них припадає на етап дестабілізації динаміки, що передує змінам стратегії, а другий — демонструє власне зміни параметрів розмноження. Виявлено, що з метою компенсації високої смертності в популяції збільшується напруженість репродуктивних процесів. Це досягається одночасним запуском різних механізмів: від збільшення індивідуальної плодючості до розширення частки особин, які беруть участь у репродукції. Принаймні перший сценарій виявився невдалим, оскільки без відповідного енергетичного підтримання у вигляді достатніх кормових ресурсів, сам став причиною ще більшої смертності. Показники розміру і кількості виводків набули мінімальних значень, а величини індексів репродукції свідчили про незначну успішність реалізації потенціалу розмноження. Найуразливішою виявилася група крупних самок, чия плодючість і, відповідно, внесок у приріст чисельності, є найбільшими. Виявлено, що такі процеси змінили не лише розмірно-масовий склад популяції (зменшилася частка крупних особин), але й статево-віковий розподіл (зменшилася кількість дорослих самок). Зниження представленості крупного маточного поголів’я не тільки не сприяло вирішенню проблем, але й посилило їх. Запобігти обвалу чисельності вдалося завдяки розширенню кількості самок, що беруть участь у відтворені (екстенсивний варіант відтворення). Показано, що зміна репродуктивної стратегії не супроводжувалася відновленням екологічного балансу. На користь цього свідчать наступні факти: збереження ознак дестабілізації динаміки, відсутність колишніх взаємозалежностей між демографічними параметрами та узгодженості з показниками кормових ресурсів. В результаті, після приблизно десятиріччя реалізації напруженого, але малоефективного розмноження, популяція була «вимушена» перейти до іншого варіанту відновлення балансу.

Ключові слова: *Myodes glareolus*, розмноження, динаміка популяції, екологічний баланс.

Introduction

Our understanding of biological systems at population level has been changing gradually at least for the past two decades [Egerton 2015; Matthiopoulos *et al.* 2019; Andreassen *et al.* 2021; Lobkov 2016]. In the centre of the paradigm that dominated in the not so distant past were such issues as population limits, fluctuating processes and their patterns, and reactions to the impact of external factors, including those of anthropogenic nature [Stenseth & Ugland 1985; Krebs 1996; Gockel & Ruf 2001]. In most cases, however, the population itself was considered a passive system that only ‘mechanically’ adjusts its parameters in response to environmental conditions and thus supporting ecological balance and its own survival. Undoubtedly, many of such ideas are true and, in their time, significantly enriched our ideas about the essence of natural processes. Although now they should be regarded as simplified versions of the real picture. The population is rather a more plastic system and notably so, and its capabilities to ensure its own existence are wider than we thought earlier.

Instead of giving a straightforward response to changes in the environment, the population faces an array of possible options of how to react, which, in turn, may include alternative mechanisms of implementation. In other words, there is always an option to choose the further trajectory of development under the new conditions. The constant evaluation of consequences allows for multiple changes in the strategy in case the results are unsatisfactory. In this, a natural logic can be traced. For example, scenarios that had already been tested by the population (species) in the course of its evolutionary history under similar environmental conditions are implemented first.

This works in most cases and the population's 'experience' helps to address the current problems—to restore balance when it is temporarily violated or even to prevent disbalance. However, it practically does not concern cases when the population faces powerful and non-specific anthropogenic impact. The engagement of available response reactions not always accompanied with success. This is exactly where the plasticity, susceptibility, and reactivity of biological systems at this level of organisation manifest: the population replaces its unsuccessful strategy, continues to seek and implement a different approach. Apparently, this is exactly the situation we encountered in our reseach.

The aim of this study was to identify the mechanisms and consequences of changing the reproductive strategy of a bank vole population to restore ecological balance, as well as the possible reasons of its failure and subsequent replacement with an alternative response reaction.

Materials and Methods

Since the 1970s, complex monitoring of forest-dwelling rodents has been carried out in the Kaniv Nature Reserve (Cherkasy Oblast, Ukraine). The studies were initiated by a research group led by V. O. Mezhzherin, who laid down the basic principles and approaches of investigation of small-mammal populations. For the entire period of monitoring, field data were collected in the same timespan (first half of summer) using the same methods, which allows comparing the data between any selected periods. An addition to the results of 30 years of personal observations, data collected by a large group of researchers and students of the Taras Shevchenko National University of Kyiv are also analysed.

In a series of our previous works, the presence of different periods in the existence of the protected ecosystem due to changes in the environment's attributes was substantiated [Myakushko 2002; 2024]. These changes are related to both transformations of the biota due to ecological successions and specific forms of anthropogenic impact. Having a small area, being located in a densely populated region, and interacting with adjoining agricultural lands are factors that have always contributed to some level as anthopogenic pressure on the protected ecosystem. Changes in conservation regime and the cancellation of the reserve status in 1951–1968 followed by utilisation of biotic resources of the territory should be noted as priority influencing factors. After conservation regime in the Reserve was restored, these factors disappeared, although the consequences have changed the trajectory of ecosystem development to a climax state after a long period of logging and forest clearing, various forestry-related activities, and other forms of anthropogenic load. In the first years of restored protected status, the consequences of human disturbance could not have been tackled, which had an inertial effect of rodent populations. The start of monitoring studies in 1971 coincides with this very period. Later, the area suffered from increasing technogenic pressure exacerbated by radioactive contamination following the Chornobyl disaster. The situation was worsened by the synergistic impact of toxic chemicals related to the Reserve's location in the zone of highly toxic soils [Orlov 1998]. Monitoring and analysis of long-term fluctuations of other factors (weather and climate, number of predators, trophic resources, etc.) do not allow considering that changes in population parameters in the studied period are particularly related to their impact.

Such distinct periods in the existence of the protected ecosystem certainly affected the state of local populations, substantiating the identification of various stages in the response of rodent populations to environmental changes. It was revealed that the response reactions of different rodent species were quite similar [Myakushko 2022, 2024]. The present research focuses on the stage defined by a change in the reproductive strategy of the bank vole (*Myodes glareolus* Schreber, 1780) population. This species predominates in local rodent communities, having an abundance exceeding that of two other common species combined: the European pine vole (*Microtus subterraneus* de Selys-Longchamps, 1836) and the yellow-necked wood mouse (*Sylvaemus flavicollis* Melchior, 1834) (*Terricola subterraneus* and *Sylvaemus tauricus* according to Zagorodniuk & Emelyanov [2012] and Zagorodniuk & Kharchuk [2020]).

Bank voles were trapped according to the traditional method of survey plots, which were located in a hornbeam forest within the Reserve's territory, on slopes of various exposure and on flat plateaus, in areas of differently developed understorey, grass cover, and forest floor.

Depending on the current abundance of rodents, a different number of survey plots were used in order to obtain a required sample. In total, body weight, body dimensions, and reproductive parameters of 1523 bank vole specimens were analysed, of which 722 were females and subjected to a more detailed study of their participation in reproduction. Data of two cycles of population dynamics were used; each cycle consisted the same number of years and lasted from depression to depression (the first cycle in 1996–2000 and the second cycle in 2007–2011).

In addition to the traditional external parameters (body weight, W, and body length, L), the body mass index (W/L) was also calculated, which is sensitive to any kind of impact [Myakushko 2005]. For a more differentiated analysis, individual body parameters were compared in different size groups. All adult specimens were divided into four groups according to their body mass index, and the percentage size composition of the population during the first cycle was chosen as control for comparison. The age structure was analysed only at first approximation and two groups were identified—juvenile and adult (mature) individuals. It partly also corresponds to the functional role of individuals in the population. This approach is specific in that the main criterium in age determination is the functional state of the individual, which is related to patterns of growth, development, and reproductive status. The lack of more accurate data on the age of animals excludes a more differentiated analysis. Thus, in this study, we use a simplified approach by identifying three groups: juveniles (immature individuals); adults that reproduce/have reproduced; and adults that are mature but do not reproduce.

The analysis of traditional demographic parameters (number of pregnant females, number of females that gave birth, litter number per reproducing female, and litter size) was amended with several complex (calculated) parameters. In addition to individual fecundity (litter size), population fecundity was also considered as litter number multiplied by litter size. It is also appropriate to include the number of breeding females in this complex indicator, and thus obtain an idea about the intensity of reproduction processes at a given time. Fecundity used in this study is the product of these three parameters. The reproduction coefficient or index (IR) reflects the level at which reproductive potential is realised, and the specifics of its application have alredy been tested in our previous studies [Myakushko 2023]. Statistical analysis of the data was carried out according to generally accepted methods.

Results

When comparing population parameters between the two cycles of population dynamics, their changes can be seen as directly or indirectly related to breeding and reproductive strategy. The average population density during the second cycle was 21% higher than during the first cycle. Despite reaching a higher density level, almost all of the analysed demographic parameters demonstrate lower values. At first glance, the situation appears to be paradoxical, when it is impossible to explain the mechanism that enables population growth.

In the sex compositon of the population, according to the trapping results, males always have a slightly higher ratio (Fig. 1). However, their prevalence in years of the first cycle is insignificant (52.1%) and practically within the limits of statistical error. A completely different situation can be observed during the second cycle, when the proportion of females decreased to 41.6%. The changes in the age structure of females are also notable: the share of adult individuals decreases substantially, whereas the proportions of juveniles practically remains on the previous level. Differences are detectable also when analysing the age-sex structure of the population at different phases of the cycles. During the first cycle, the phases of depressions and peaks have similar parameters (25.2% and 24.9% of mature females, respectively), whereas these parameters during the second cycle are lower, especially in the depression phase (15.3% and 21.4%, respectively).

The success of the reproductive strategy depends directly on the state of breeding females, particularly their weight, body dimensions, and body mass index. To analyse this aspect, all adult females of the bank vole were separated into groups based on their body mass index, and the distribution of females during the first cycle was used as a special ‘control’. When compared, a more than two-fold decrease in the ratio of large females was revealed during the second cycle (Fig. 2).

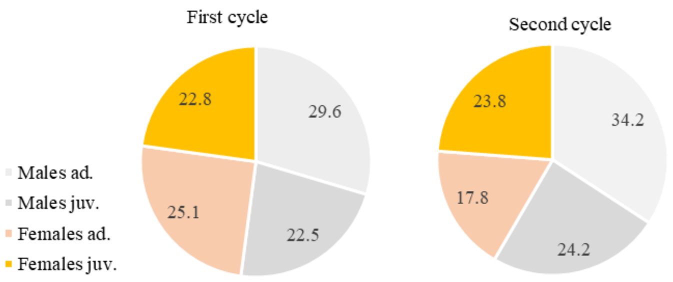

Fig. 1. The proportion of different sex and age groups in the bank vole population during the two cycles of population density dynamics (%).

Рис. 1. Представленість статевих і вікових груп в популяції рудої нориці упродовж двох циклів динаміки щільності (%).

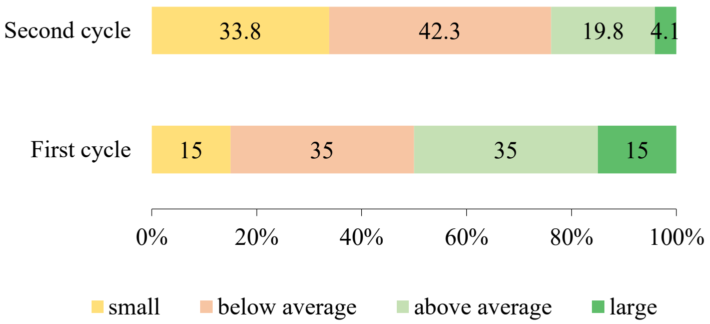

Fig. 2. Different groups of adult females (by body mass index) during the first and second cycles (first cycle as control).

Рис. 2. Різні групи серед дорослих самок (за вгодованістю) упродовж 1-го і 2-го циклів (1-й цикл — контроль).

Further analysis revealed that the groups of females conditionally named as 'small' and 'large' (below or above average body mass index, respectively) are characterised by different fecundity parameters, although each cycle has its own specifics (Table 1). In years of the first cycle, large females always had larger litter sizes and, in average, had a higher number of litters in the study period. At the same time, these parameters always reached maximum values in the depression phase and minimum values in the peak phase (intermediate values were recorded in other years).

Changes in population fecundity and reproduction index demonstrated similar patterns. During the second cycle, the situation changed entirely. All parameters of individual and population fecundity decreased substantially, the previously recorded specifics of particular phases disappeared, and significant differences between reproductive parameters of large and small females were not detected. The success of reproduction (IR) decreased by 23–30%, and this was the most obvious among large individuals.

Table 1. Reproductive parameters of small and large females of the bank vole during cycles and separate phases of population density dynamics

Таблиця 1. Показники розмноження дрібних і крупних самок рудої нориці упродовж циклів і окремих фаз динаміки щільності популяції

Cycle	Phase	Litter size		Litter number		Fecundity		IR	
		S	L	S	L	S	L	S	L
1	Peak	4.79	5.02	1.22	1.44	3.24	4.13	0.73	0.77
	Depression	5.63	5.87	1.41	1.68	4.55	5.69	0.85	0.89
	Total	5.41	5.70	1.33	1.49	4.27	4.97	0.85	0.82
2	Peak	4.66	4.53	1.10	1.00	3.33	3.64	0.62	0.60
	Depression	4.73	4.79	1.09	1.11	4.67	4.12	0.66	0.52
	Total	4.58	4.65	1.13	1.06	4.44	4.31	0.65	0.55

Note: S—small individuals, L—large individuals, IR—index (coefficient) of reproduction.

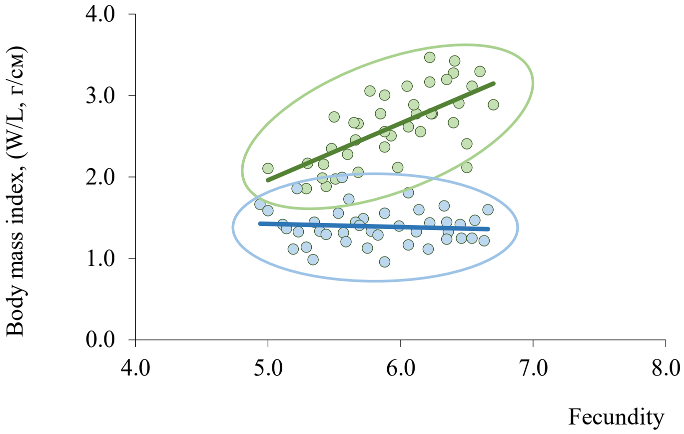

Fig. 3. Dependence between fecundity and body mass index of female bank voles during the first (top cloud) and second (bottom cloud) cycles of population density dynamics.

Рис. 3. Залежність плодючості самок рудої нориці від їх вгодованості упродовж 1-го (плеяда зверху) і 2-го (знизу) циклів динаміки щільності.

Table 2. Parameters of the involvement of females in reproduction during cycles and separate phases of population density dynamics

Таблиця 2. Показники залучення самок до розмноження упродовж циклів і окремих фаз динаміки щільності популяції

Cycle	Phase	Proportion of breeding females (%)	Proportion of pregnant individuals among breeding females (%)	Proportion of non-breeding mature females (%)
1	Peak	49.3	61.0	4.2
	Depression	58.9	62.4	1.1
	Total	54.1	61.1	2.5
2	Peak	64.8	73.4	7.2
	Depression	68.2	73.4	7.1
	Total	66.5	70.2	6.9

The relation between body mass index and fecundity of adult females is shown in Fig. 3. During the first cycle (top cloud), there was a direct correlation—increase in body mass index was accompanied with increase in individual fecundity. That is, larger females delivered a larger number of offspring. This pattern was absent during the second cycle: practically there was no difference between the fecundity of large and small females in this period, although it was notably lower than during the first cycle.

However, not all of the obtained data indicate that reproduction of the population slowed down during the second cycle. The proportion of breeding females, on the contrary, increased (Table 2). Similarly increased the ratio of pregnant individuals among them. These facts clearly indicate the intensity of reproductive processes in the population, which is now unrelated to the phase of the cycle (i.e. current population density). At first glance, it might seem odd that the number of individuals that are mature but do not participate in reproduction increases in the population. A potential explanation for this, however, is proposed further.

Discussion

The reasons for the bank vole population to change its reproductive strategy were the events that had taken place a decade earlier. In the course of long-term monitoring of the population, it was revealed that the period between 1987 and ca. 1995 was characterised by an unusual destabilisation of population dynamics (noteworthy that a similar situation was discovered in populations of two other species). In addition to the increase in density average for the cycles, disruption of the rhythm of alternation of population phases also occurred. It was accompanied with a wider range of density fluctuations, mainly due to achieving higher values during peak phases. The amplitude and range of density fluctuations increased 3.0–3.5 times compared to the previous period.

The obtained results indicate that the type of population density dynamics changed during this time—it became less stable, gained stochastic features, and almost all previous patters of this process disappeared [Myakushko 1998, 2024]. The fact itself that population density (abundance) increased does not allow for an either optimistic or pessimistic evaluation of the situation, although the destabilisation of the dynamics directly indicates the negative consequences for the population due to violation of ecological balance. The destabilisation itself can be considered as a side effect of the population's search for adequate ways to tackle the misbalance.

The years of the first cycle of population density dynamics coincide with the destablisiation stage. The analysis of demographic parameters of this period revealed increased breeding compared to the previous years. However, previous relationships were retained: the population's reproduction depended on current density that was changing during various phases following a pattern. This pattern was the enhancement of reporoductive processes during phases of density depression and decrease during peak years. To achieve this, the population could have employed alternative regulatory mechanisms of reproduction. For example, the increase in reproduction in the phase of depression can be achieved by increasing individual fecundity, litter number per breeding season, or the number of females taking part in reproduction [Krebs 2013]. Such phenomena were observed repeatedly in populations of many small-mammal species by other researchers [Smith *et al.* 2006; Lidicker 2020] and us as well in the first 15 years of monitoring studies [Myakushko 1998, 2002].

If the changes in the intensity of reproduction are clearly correlated with population density dynamics, it is unlikely that they are the reseason of destabilisation of density fluctuations. Therefore, we can assume that destabilisation was caused not by the changes in breeding intensity, but by subsequent events related to the survival of the animals. The analysis of the state of feeding resources allowed getting closer to a possible unravelling of this complex of issues, which was carried out simoultaneously with population monitoring. These issues were discussed in more detail in our previous works [Myakushko 2022], although it is appropriate to describe them briefly here for a better understanding of the entire sequence of events.

There was a loss of congruence during the stage of destabilisation between population density and the parameters that characterise feeding resources. Earlier, these factors (i.e. the density of individuals and the qualitative and quantitative properties of the food base) had been clearly correlated. The loss of this correlation was interpreted as a violation of ecological (energy) balance between resources and their consumers [Mezhzherin *et al.* 1991]. A situation emerged in which population fluctuations (including those in the intensity of reproduction) can either coincide with changes in the food base or be desynchronised. In the first case, fairly intense reproduction will take place on the background of ample resourses being provided and will be accompanied with reaching a high level of population abundance. In the other case, the process will be accompanied with low survival rates and a catastrophic collapse of abundance. More or less the latter situation occurred during the destabilisation stage, which coincides with the first cycle of density dynamics.

Intensive reproduction, the production of biomass with further loss of its substantial portion can hardly be considered an effective strategy. Since long-term existence of biological systems under conditions of violated ecological balance is impossible, the population aims to restore balance, which can be impleneted via various scenarios and mechanisms. According to currently widespread views, the easiest way a population can react is regulation of reproduction in order to achieve abundance levels that comply with changing carrying capacities [Caswell *et al.* 2018; Shuster *et al.* 2023; Bhairavi *et al.* 2024; Polischuk 2024]. A 'soft spot' in this scheme is the inertia of reproduction processes that need a certain amount of time to be realised. On the other hand, a radical though much quicker way of regulation is changing mortality ratios. This option, however, results in irreversible biomass losses, which is energetically impractical. Therefore, it can be expected that the latter scheme would be implemented only as a last resort.

What we witness during the second cycle of population dynamics is the population's attempt to restore balance by changing reproductive strategy. The increase in density in the second cycle indicates a more active breeding, although it is achieved at a high cost. There are reasons to suggest that this process ends with high mortality rates, mainly among large and fertile females.

It is the likely reason for no increase in many reproductive parameters. This hypothesis, however, is the logical explanation of many of the observed processes.

A certain predominance of males among the trapped animals is no surprise, since males are characterised by greater mobility and are more likely to fall into traps. A substantial shift in the sex ratio in favour of males in the second cycle can be explained by a decrease in the proportion of females, especially in the adult group. Such individuals, in addition to having a larger body mass, take an active part in reproduction, which determines their greater energy needs. In the absence of opportunities to satisfy them, their mortality increases. This is consistent with data on changes in the body mass index of mature females: the proportion of females having above average body mass index is almost halved, and large individuals are almost absent in the population.

The notably lower fecundity values during the second cycle, in our opinion, are related not so much to a less intensive reproduction, but rather to the fact that the most fertile individuals simply fall out of the population due to their death. Based on the available data, it is impossible to determine at what stage of the life cycle (pregnancy, lactation, or post-reproductive revocery) this mass mortality occurs. There is no doubt, however, that all this is connected with reproduction that notably increases the total energy expenses of the organism [Krebs 2013]. Large, adult females characterised by maximum resource demands randomly disappear from the population. Reproductive success decreases to 20–25%, reaching a minimum particularly among large individuals.

Arises the question of how exactly abundance increases when reproductive parameters decrease substantially. This is explained by the icreased number of females that are involved in reproduction, as well as by the increased number of pregnant individuals among them. Even the two- to three-fold increase in the number of non-breeding individuals can be explained following this line of argumentaion. Most likely, this group in the population expands not because of the direct increase in the number of barren females, but as a result of higher mortality among breeding females. Although it cannot be excluded that barren females also survive in greater numbers.

The above suggestions are also indirectly supported by the different relationship between the values of fecundity and body mass index. There was a positive correlation between these two characters (i.e. the largest individuals are the most fertile), whereas there is no correlation during the second cycle. In other words, fecundity does not depend on the body mass index of breeding females. However, as in the former cases, this phenomenon is secondary and related to the increased mortality among large females.

To sum up, the main directions and mechanism of changes in reproductive strategy should be characterised. The almost decade-long destabilisation of population density dynamics led to changes in basic reproduction parameters. The unstable and stochastic character of the population dynamics led to the loss of connection to the state of trophic resources, which resulted in either excessive density levels (overpopulation) or catastrophic decrease in abundance. The violation of the balanced interdependencies between population dynamics and environmental conditions was accompanied with a decrease in survival rates and an increase in mortality.

The latter has triggered reactions that can be considered typical for populations under such conditions, since they were observed in various small-mammal species [Sibly & Brown 2009]. In order to compensate the negative consequences of high mortality, the population increases the intensity of reproductive processes via various mechanisms, from higher individual fecundity to increasing the number of breeding individuals. The first scenario was ineffective, because without respective energetic support in the form of sufficient feeding resources the reaction itself led to an even higher mortality rates. The most vulnerable turned out to be the group of large females, whose fecundity and, respectively, contribution to population growth are the highest. The decreased proportion of large breeding females only exacerbated the problems instead of solving them. Population collapse was likely avoided by an increase in the number of breeding females. During the second cycle, at the time of the study, a record number of females were taking part in reproduction, the highest for the entire period of monitoring. This form of reaction can be considered extensive; the intensive variant of reproduction (increased fecundity) did not justify itself. The mechanism of this effect remains unknown; it may be related to changes in the rate of maturation of individuals or more successful survival during winter. For example, low population density allows existing individuals to occupy optimal habitats and better survive adverse winter conditions. These effects are known for rodents and were described in many studies [Hodgson *et al.* 2011; Savazza *et al.* 2023].

The remaining question to answer is why the change in reproductive strategy was unsuccessful in restoring ecological balance. There are several reasons. First, population density dynamics did not stabilise and the regular relationships between the parameters did not recover. Second, interdependencies between population parameters and those of the food base were absent during the entire time. This, in turn, introduced the element of randomness into the dynamics, due to which the overlap between the peak phase and the year of sufficient food base was accompanied with normal survival rates and high abundances in contrast to the catastrophic decline when these parameters did not coincide. The third reason, in our opinion, is the most important. It is the fact that beginning from ca. 2005, the population 'refused' to restore ecological balance via changing its reproductive strategy and implemented a totally different approach, which is smaller body size of the individuals [Myakushko 2021*a–b*].

Conclusions

1. After a decade-long period of destabilisation in its dynamics, a change in the reproductive strategy of a bank vole population was observed. The reason for this change was the violation of balanced relationships between population parameters and those of the food base of these rodents, which led to increased mortality rates in cases when energy needs of the population could not be met.

2. In order to compensate the high mortality in the population, the intensity of reproductive processes increased. Via increasing the proportion of breeding females (extensive form of reaction), the population could somewhat raise its density, although population dynamics in general remained unstable.

3. The intensive form of the population's reaction, which was increasing individual fecundity, turned out to be ineffective. The size and number of litters at this time became notably smaller, while higher indices of reproduction indicate that there was little success in realisation of the population's reproductive potential.

4. Intensive reproduction was accompanied with higher mortality rates among breeding females. The most affected was the group of large females that had the highest fecundity. The latter changed not only the size and weight composition of the population (the proportion of large individuals decreased), but also the age-sex ratio (the number of adult females decreased).

5. A hypothesis is proposed and substantiated, according to which the change of reproductive strategy did not restore ecological balance. This is supported by the following facts: population dynamics retained signs of destabilisation and lack of formerly present interdependencies between demographic parameters and parameters of feeding resources. All this led to the fact that after 8–10 years of having implemented an intensive but ineffective reproductive strategy, the population was 'forced' to shift to another mechanism to restore ecological balance.

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References

Andreassen, H. P., J. Sundell, F. Ecke, S. Halle, M. Haapakoski, [*et al.*]. 2021. Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia*, **195**: 601–622. CrossRef

Bhairavi, K. S., R. Borah, B. Bhattacharyya, S. Borkataki. 2024. Feeding and reproductive ecology of rodents: a review. *Research Biotica*, **6**: 1–6. CrossRef

Caswell, H., C. de Vries, N. Hartemink, G. Rothand, S. F. van Daalen. 2018. Age × stage-classified demographic analysis: a comprehensive approach. *Ecological Monographs*, **88**: 560–584. CrossRef

Egerton, F. N. 2015. History of ecological sciences. Animal population ecology. *The Bulletin of the Ecological Society of America*, **96**: 560–626. CrossRef

Ferrari, M., A. K. Lindholm, A. Ozgul, M. K. Oli, B. König. 2022. Cooperation by necessity: condition- and density-dependent reproductive tactics of female house mice. *Communications Biology*, **5**: 348. CrossRef

Gockel, J., T. Ruf. 2001. Alternative seasonal reproductive strategies in wild rodent populations. *Journal of Mammalogy*, **82**: 1034–1046. CrossRef

Hodgson, J. A., A. Moilanen, B. A. Wintle, C. D. Thomas. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, **48**: 148–152. CrossRef

Krebs, C. 1996. Population cycles revisited. *Journal of Mammalogy*, **77**: 8–24. CrossRef

Krebs, C. J. 2013. *Population fluctuations in rodents.* University of Chicago Press, 1–306. CrossRef

Lidicker, W. Z., Jr. 2020. Reproductive adaptations to high densities in social mammals. *Therya*, **11**: 440–446. CrossRef

Lobkov, V. A. 2016. *Intrapopulation Regulation in Mammals*. I. I. Mechnikov University of Odessa, 1–237. [Russian]

Matthiopoulos, J., C. Field, R. MacLeod. 2019. Predicting population change from models based on habitat availability and utilization. *Proceedings of the Royal Society. B: Biological Sciences*, **286**, 20182911. CrossRef

Mezhzherin, V. A., I. G. Emelyanov, O. A. Mihalevich. 1991. *Comprehensive Approaches in Studying of Populations of Small Mammals*. Naukova dumka, Kyiv, 1–204. [Russian]

Myakushko, S. A. 1998. Changes in the dynamics of populations and communities of rodents as a result of anthropogenic impact on the protected ecosystem. *Vestnik zoologii*, **32** (4): 76–85. [Russian]

Myakushko, S. A. 2002. Long-term dynamics of populations of rodents as a criterion of the environment. *Visnyk L'vivs'koho universytetu. Seriya biolohichna*, **30**: 30–34. [Ukrainian]

Myakushko, S. A. 2005. Changes in body weight and body size of rodents under various forms of anthropogenic load. *Zapovidna sprava v Ukrayini*, **11**: 34–40. [Ukrainian]

Myakushko, S. A. 2021a.The phenomenon of the shrinking size of bank vole (Myodes glareolus) in an anthropogenic environment (experience of 50 years of observations). *Biosystems Diversity*, 29 (3): 211–216. CrossRef

Myakushko, S. 2021b. Shrinkage of body size in rodents as a strategy of populations under anthropogenic conditions (results of 50 years of study of rodent populations). *Theriologia Ukrainica*, **22**: 133–143. [Ukrainian] CrossRef

Myakushko, S. 2022. Peculiarities of trophic relations of rodent populations in case of change of survival strategy. *Ecological Sciences*, **40**: 55–61. [Ukrainian] CrossRef

Myakushko, S. 2023. Adaptive responses of the pine vole (Microtus subterraneus) population to anthropogenic environmental changes. *Ecological Sciences*, **46**: 125–131. [Ukrainian] CrossRef

Myakushko, S. 2024. Stages in the response of rodent's populations to anthropogenic environmental changes. *Ecological Sciences*, **52**: 66–71. [Ukrainian] CrossRef

Orlov, O. O. 1998. Goals, objectives and methods of radioecological research in natural reserves of Ukraine, which are contaminated by the Chernobyl accident. *Zapovidna sprava v Ukrayini*, 4: 65–68. [Ukrainian]

Polischuk, I. 2024. Demographic structure and long-term population dynamics of Muroidea in the Askania-Nova Biosphere Reserve. *Theriologia Ukrainica*, **27**: 119–137. [Ukrainian] CrossRef

Radchuk, V., R. A. Ims, H. P. Andreassen. 2016. From individuals to population cycles: the role of extrinsic and intrinsic factors in rodent populations. *Ecology*, **97**: 720–732. CrossRef

Savazza, S., P. Bartolommei, S. Gasperini, A. Bonacchi, E. Manzo, R. Cozzolino. 2023. Should I stay or should I go? Seasonal fluctuations of wood mouse populations in fields surrounded by woodlands. *Animals*, **13**: 2017. CrossRef

Shuster, S. M., B. Pyzyna, C. Ray, L. P. Mayer. 2023. The demographic consequences of fertility reduction in rats and voles. *Journal of Pest Science*, **96**: 1313–1329. CrossRef

Sibly, R. M., J. H. Brown. 2009. Mammal reproductive strategies driven by offspring mortality-size relationships. American Naturalist, 173: 185–199. CrossRef

Smith, M. J, A. White, X. Lambin, J. A. Sherratt, M. Begon. 2006. Delayed density-dependent season length alone can lead to rodent population cycles. *American Naturalist*, **167**: 695–704. CrossRef

Stenseth, N. Chr., K. I. Ugland. 1985. On the evolution of demographic strategies in populations with equilibrium and cyclic densities. *Mathematical Biosciences*, **74**: 89–109. CrossRef

Zagorodniuk, I. V., I. G. Emelyanov. 2012. Taxonomy and nomenclature of mammals of Ukraine. *Proceedings of the National Museum of Natural History*, **10**: 5–30. [Ukrainian]

Zagorodniuk, I., S. Kharchuk. 2020. List of mammals of Ukraine 2020: additions and clarifications. *Theriologia Ukrainica*, **20**: 10–28. [Ukrainian] CrossRef