## = GENERAL BIOLOGY =

# Winter Reproduction of Cyclomorphic Mammals: From a Case to the Phenomenon

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**Abstract**—In 2010 (a year of drought), the true winter breeding (TWB) of the pygmy wood mouse (*S. uralensis*) was first recorded in the Southern Urals and confirmed by the morphological parameters and age markers. The young born in winter fulfilled successfully their reproductive potential under favorable climatic conditions. The true winter breeding and the age cross of animals during the year of drought promoted the maximum population growth and enhanced population genetic heterogeneity. In subsequent years, TWB of *S. uralensis* became common, which is regarded as a climatic pattern. Extreme drought rearranged the rodent community and caused TWB of *S. uralensis*, which resulted in a higher abundance of the species.

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The rates of reproduction and mortality are the main parameters that determine population density depending on its interaction with the environment. The initial (spring) population abundance determines, as a rule, the dynamics of the cyclomorphic mammal population (CM rodents) of a certain year. The TWB biological meaning is to fulfill the potential of survival and subsequent development of the additionally born young that, together with overwintering individuals, start a new population cycle at a higher initial abundance. The TWB of rodents is one of the most interesting and poorly studied ecological phenomena. Cases have been described of the snow-covered breeding of the steppe lemming, gray and red-backed mouse, as well as of the field and house mouse inhabiting different regions [1]. Quite often the late prolonged breeding in autumn and early spring breeding are considered as TWB. This breeding type is common of regions with mild winters (Ukraine). Winter breeding is often caused by the anthropogenic factors, such as feed availability (winter crops, hay ricks, etc.) and is attributed to the artificially provoked winter breeding [2]. The cases of the year-round breeding in countries of Central Europe are of special interest [3].

True winter breeding is an unseasonable rodent development and breeding under winter conditions under a high snow cover and negative temperatures, which occurs in natural biotopes in the absence of available anthropogenic feed. Lemming breeding in the Subarctic is an example of this phenomenon [4, 5].

For the Urals, with its continental climate, severe win-

The frequency of TWB cases in different species was usually correlated with their proportion in a biotic community. The most indicative in this respect are the background species. For the Ural region, these are the bank vole (Myodes glareolus Schreber, 1780) and pygmy wood mouse (Sylvaemus uralensis Pallas, 1811). The effect of food supply and climatic conditions of overwintering are also dependent on the species features. During the 46-year period of our study in the forest zone of the Southern Urals (II'men Nature Reserve, Chelyabinsk oblast), the only TWB phenomenon has been observed in M. glareolus (1986) [6]. In the February sample, we have found adult breeding animals and the newly born young. The factor that provoked vole maturation was an uncommonly rich yield of bird cherry seeds. We have found a kind of little tables with gnawed bird-cherry nuts. Feeding nuts to the voles under vivarium conditions led to a damage pattern similar to that on the feeding tables. No breeding was observed in other rodent species. In the Urals, survival of the vole winter-born young was extremely low; they did not reach puberty as a rule [2].

ters, snow cover, and at ceased vegetation, the TWB phenomenon is of special interest because of its rarity, causative factors, occurrence in different species, and possible consequences. TWB occurs when the animals are guided not by the daylight length, but rather by a relative increase in the daylight time (after December 22 in the northern hemisphere). The necessary condition is believed to be sufficient food supply, which supports animal maturation and provides for energy needs during breeding. The height of snow cover and, to a lesser extent, external temperature conditions are also important.

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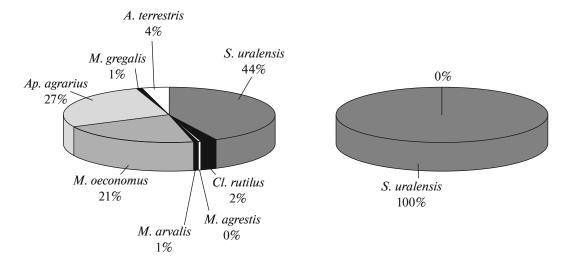
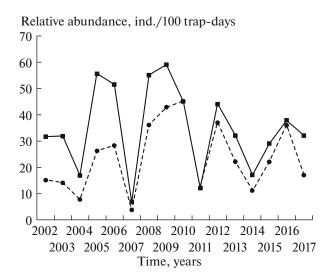


Fig. 1. The cyclomorphic mammal composition of the East Ural Nature Reserve before and after the drought of 2010.

Recently, the situation has changed. The first cases of *S. uralensis* TWB were recorded in the forest—steppe zone of the Southern Urals. This was accompanied by an increase in its proportion within the rodent taxocenes in different landscape—geographic areas of the Urals [7, 8]. In 2004, 2006, 2008, 2012, and 2015, winter catching in the Visim Nature Reserve (dark coniferous taiga of the Middle Urals) showed isolated TWB cases of the red-backed vole (red and red-gray); in 2018, of the *S. uralensis* (Yu.A. Davydova, personal communication). This phenomenon is probably characteristic of some other localities of the Urals, but no proper attention had been paid to it so far.



**Fig. 2.** Average annual abundance of the cyclomorphic mammals in the East Ural Radioactive Trace (EURT) zone (2002–2017). Solid line, rodents; dotted line, *S. uralensis*.

In this study, we aimed at diagnosing and interpreting rodent TWB in the Urals, as well as verifying the hypothesis that extreme environmental conditions cause this phenomenon. As for *S. uralensis*, the drought of 2010 was such an extreme event.

The region of the Eastern Ural Radioactive Reserve, where TWB of S. uralensis has been observed for the first time in 2010, was chosen as an example of this phenomenon in CM. The reserve located in the Trans-Ural forest-steppe is characterized by meadow-steppe spaces, birch and birch-aspen outliers, and, less frequently, pine forests [9]. The data were obtained during a 16-year period of observations of CM populations; the material comprised 500 specimens. The rodents were trapped with crush traps using the method of irreversible removal. The first catches were made in April, when the snow remained on 30— 40% of the plot. The overwintered current-year's young were identified on the basis of a set of features: body weight, coat color, the state of generative system, thymus index (age indicator), and abrasive wear of the chewing surface of teeth (a calendar age indicator) [10].

During the years of observations, *S. uralensis* was a dominant species of the biological community. The proportion of this species in the catches was 40–60% till 2009 (Fig. 1). In the year of drought (2010) [11, 12], CM species composition was reduced to the only species, *S. uralensis* (Fig. 1) [8], which remained monodominant for several years (Fig. 2).

In spring 2010, rodent breeding started a month earlier than the average one for many years. At the end of April, a significant proportion of the overwintering females that have already delivered was observed (the presence of the placental spots are traces of the first pregnancy); other females were at the last terms of gestation. For the first time, we have found a current year's female at the early stage of pregnancy in a sample of 14 individuals. The age diagnosing on the basis

of a set of traits showed that it was born in mid-February. In the May catches, re-pregnant current-year's females were found. Unlike the TWB case of the redbacked voles from the II'men Nature Reserve, the young born in winter 2010 survived successfully and were actively involved in reproduction. The rodent abundance calculated from the results of monthly catches (six series) was accounted for by *S. uralensis* and was 45 individuals/100 t-d; the highest seasonal peak was recorded in September (65 individuals/100 t-d).

Analysis of demography and sex structure of the summer samples, where all animal groups were present, revealed the age cross [8], i.e., the pairs formed by individuals from different generations and functional groups. The overwintering males crossed with both the overwintered females and the current year's females born in February, because adult males are known to have a behavioral dominance over young males. In summer, the proportion of the overwintering females was low because of their early death, but the proportion of the current-year's mature females was high. The current-year's males from the spring cohorts did not breed, which was confirmed by the morphological signs. The higher abundance of the overwintered male population and non-simultaneous death of the overwintered males and females retarded puberty of the current-year's males which led to the age cross and increased genetic heterogeneity of the population [8, 13].

Retrospective analysis of the data obtained during many years showed that the spring catches consisted of overwintering mice until 2010; the first current-year's animals were caught only in May. Other rodent species (Fig. 1) were observed in the middle of summer as a rule. During the next period, up to 2017, currentyear's animals born in winter (February) were present yearly, and part of them was at the early terms of gestation. The total number of these animals was 21% for the period 2010–2017. The interior parameters of the current-year's animals corresponded to those of the overwintered ones. All of the current-year's mice had the thymus; the females had thickened uterus walls or they were pregnant. The overwintered individuals had no thymus. Many overwintering females had embryos (at various stages of the second pregnancy), as well as first pregnancy traces (placental spots in uterus). The likely term of gestation was 13-14 days when the embryo and placenta were well distinguishable through the uterus wall [14]. The current year's animals were born in the middle of February, as it was calculated from the degree of wear of the tooth chewing surface [10], and hence conceiving occurred late in January (the gestation duration in rodents is 21 days). The onset of male puberty depends on the duration of spermatogenesis, which in rodents is about  $31.0 \pm 0.7$ days [15]. Therefore, mouse maturation began in January. Further development of the young born in winter depended usually on the weather and climatic conditions, which were found by ours to be often critical for S. uralensis and to result in death of the first cohort

animals (these were the return of cold in April—May, rapid changes in temperature and night frosts in June).

Thus, the hypothesis discussed was confirmed by the evidence obtained in the forest—steppe zone of the Southern Urals. During the arid 2010, TWB phenomenon in *S. uralensis* population was recorded for the first time. In subsequent years, TWB in mice became common, which is a pronounced climatic pattern. Under extreme environmental conditions (drought), in *S. uralensis*, which is an ecologically plastic species historically preadapted to climate aridization [7], population mechanisms such as age cross and TWB were triggered to increase the population abundance and heterogeneity via transmission of genetic information between different generations [13].

Extreme drought has led to a rapid rearrangement of the rodent community (reduction of its species composition) and induced sub-snow *S. uralensis* reproduction, which enhanced the population abundance in the forest—steppe zone of the Urals. The study of different landscape—geographic zones and various species showed that changes in the strategy of the population functioning occurred during a rather short period of time: something that recently was considered a rare phenomenon becomes quite common.

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# COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests.* The authors declare that they have no conflict of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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