

Variability of Demographic Parameters in a Cyclic Population of the Bank Vole (*Clethrionomys glareolus*)

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Abstract—Analysis of demographic parameters in a local bank vole population has shown that different relationships exist between them. The level of population abundance is directly correlated with the proportion of sexually mature juveniles, the length of the breeding season, and the age of overwintered individuals. The duration of the breeding season shows a delayed dependence on population abundance in the previous year. Variation in the average age of overwintered voles at different phases of the population cycle is characterized by a delayed dependence on the length of the breeding season in the previous year. Intrinsic factors generate the cyclic dynamics of parameters, while extrinsic factors can modify their dynamics.

Keywords: population cycle phases, demographic parameters, bank vole, dynamics of abundance, age structure

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The dynamics of abundance is the key problem in population ecology [1, 2]. It is now generally accepted that the population dynamics of individual species is determined by the influence of intrinsic and extrinsic factors [3–6]. Regular cyclic changes in abundance are typical of small mammal species numerically prevalent in the community, while random, aperiodic changes are typical of species with low abundance [7]. In addition to relatively regular recurrence of different abundance levels (phases of the population cycle), a number of other demographic parameters are typical of the cyclic populations of rodents [8]. They include the inhibition of sexual maturation in juvenile individuals at high population abundance [9–11] and cyclic changes in the length of summer breeding season and the average age of rodents [12, 13, 10, 11]. In addition to direct correlations with current-year population abundance, there are some delayed dependencies. For example, a delayed dependence of the parameters of breeding season on the abundance level in the previous year has been observed in cyclic populations [14].

The purpose of this study was to investigate the dynamics and correlations of different demographic parameters in a local population of bank voles (*Clethrionomys (Myodes) glareolus* Schreber, 1780). We considered the interannual dynamics of abundance and analyzed variation in the parameters of breeding season and the average age and age structure of overwintered bank voles depending on population cycle phase. Both direct and delayed dependencies between the demographic parameters were revealed, which is

important for understanding the mechanisms accounting for population cycles in rodents.

MATERIALS AND METHODS

Observations on the dynamics of a local bank vole population were performed in a marginal area of southern taiga herb–dwarf shrub spruce–fir forest in the Middle Urals (Shigaevo, 57.35° N, 58.71° E), in 1999 to 2017. The bank vole is dominant in the local small mammal community, with its proportion in catches averaging 65%. The animals were caught in the second half of July using live traps set in lines at an interval of 7 m. Pieces of bread with sunflower seed oil were used as bait. The traps were checked three times a day: in the morning, in the afternoon and in the evening. In the first two years, the animals were also trapped in late May, which made it possible to appraise the stability of estimates of population structure obtained in different time intervals. In this case, the method of irreversible removal was used. Three-time trap checking reduces animal competition for traps and provides for higher correspondence (proportionality) between the estimates of abundance and its true values [15]: compared to one-time checking, the number of animals in catches increases by less than 10% at low population abundance, by 15–20% at medium abundance, and by 40–50% or even more at high abundance [15]. Some authors set two traps per signpost with an interval of 7 m and check them one time a day [1].

The marginal forest area inhabited by the local bank vole population has a size of about 8 ha. In its central part (about 4 ha, optimal habitats) there are two piles of windfallen trees located 100 apart, each covering an area of 0.5 ha. Every year, lines of 50–70 traps were set in the center of this area, with some of them passing across the edges of piles. In years of low abundance, trapping with a stationary line in the center of this area was followed by alternate trapping within the piles and closer to the periphery of the area. The data on catches with different lines in the same year were tested for homogeneity, pooled, and recalculated per 100 trap-nights. The total length of lines in the years of low abundance reached 320 traps.

The material collected over a total of 6895 trap-nights consisted of 950 voles, including 722 juveniles and 228 overwintered animals (172 of them collected in July and 56 in May). These specimens are kept in the zoological museum of the Institute of Plant and Animal Ecology (Yekaterinburg, Russia).

Population abundance was evaluated based on the number of animals collected per 100 trap-nights during the first two days. Three levels of abundance were distinguished: low (0–12 ind., depression), medium (13–25 ind., growth), and high (more than 25 ind./100 trap-nights, peak). The age of voles was determined using the root index (the ratio of root length to tooth height) of the second maxillary molar. Based on the data of other authors, we calculated two equations relating the age of voles (y) to the root index (x): (1) $y = 70 + 426.4x$ [16]; (2) $y = 140 + 414.3x$ [17]. The first equation underestimates the age by about 60 days, which can be seen when comparing the absolute terms of the equations. Most probably, the authors used data on the formation of roots in sexually mature juvenile voles, in which they start to appear approximately 2 months earlier [18].

Since the majority of overwintered voles do not reach sexual maturity in the year of birth [19], we used the second equation for calculating animal age and date of birth. The age of voles was recalculated with respect to 15.VII (here and below, Roman numerals refer to months). Based on the date of birth, the voles were divided into four cohorts: (1) 15.IV–31.V, (2) 1.VI–15.VII, (3) 16.VII–31.VIII, and (4) 1.IX–15.X. We present average dates for the study area, and they may be different in other regions. The onset or end date of the breeding season were determined as the average of birth dates within an interval of about 30 days from the extreme date. This interval was selected empirically. The length of the breeding season was determined based on the mean values and 95% confidence interval of its onset and end dates.

With regard to the year of birth, the voles were divided into three groups: (1) voles born in post-peak years, (2) voles born in pre-peak years, and (3) voles born in peak years. The first group included the years of low abundance after the peak and one year with low

abundance (2006) after the year with the same level of abundance; the second group, the years of medium abundance, including 2000, and one year of low abundance (2007) before a peak; and the third group included all the peak years.

The reproductive status of voles was determined from the state of their reproductive system. Pregnant and parous females with placental spots and/or embryos in the uterus and males with a testicular weight of more than 150 mg, well-formed epididymides and active spermatogenesis were classified as sexually mature.

The results were processed statistically using log-linear analysis, analysis of variance, regression analysis, and chi-squared test in STATISTICA for Windows 6.0.

RESULTS AND DISCUSSION

The relative abundance of the bank vole population differed between years (Fig. 1). A year of medium abundance was followed by a year of high abundance. A year of peak abundance was followed by a year of low abundance. There were six full cycles of changes in abundance: four 3-year-long cycles, one 2-year-long cycle and one 4-year-long cycle. The 2-year-long cycle consisted of years with medium (2000) and high (2001) abundance. The 4-year-long cycle consisted of 3 years with low abundance (2005, 2006 and 2007) and a year of peak abundance (2008). The 3-year-long cycles consisted of years with low, medium and high abundance.

Thus, different levels of abundance—low, medium, and high—are repeated in this population with an average period of three years. Deviations from such cyclicity are caused by the influence of extrinsic factors. The absence of a depression year after the peak of abundance in 1999 is probably explained by a high yield of spruce cones in that year. Highly nutritious food available in excess provided for a higher survival rate after the growing season, and animal abundance in summer only decreased to the medium level. Similar phenomena have already been observed: the survival rate of *Clethrionomys* voles in plots where oat and/or sunflower seeds were available proved to be higher in control plots [20–22]. After the depression in 2005, the abundance remained low for two years. This could be due to unfavorable weather conditions in the first two summer months. For example, the weather in June 2006 was hot and dry, while in July it was cold and rainy. In 2007, both June and July were hot and dry. The phases of low abundance lasting for 3 years have been observed by other authors [23, 24].

The variability of local weather conditions can interact with intrapopulation factors and lead to prolongation of certain phases of the abundance cycle [25]. The peak of population density in 2008 was followed by three complete 3-year cycles. In 2017 the abundance of bank voles reached an unprecedented

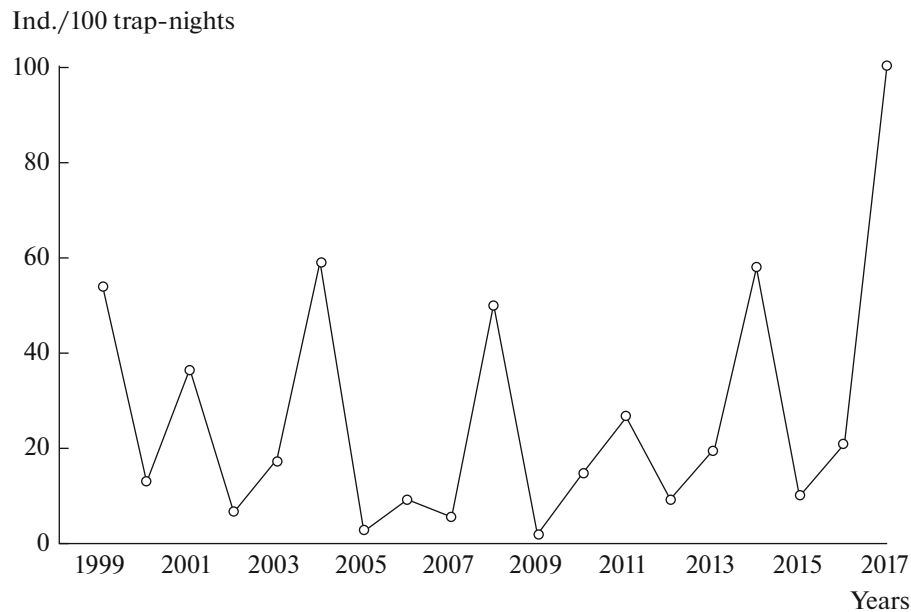


Fig. 1. Long-term dynamics of bank vole population abundance (Shigaevo, the Middle Urals).

value of 100 ind. per 100 trap-nights. This was due to high yield of spruce cones in the previous year and favorable weather conditions. Very high values of relative abundance in the bank vole have been reported by other authors [13, 26].

The stability of estimates of the population structure of overwintered voles was assessed based on the data of the first two observation years. Log-linear analysis revealed to effect of the sampling season or animal sex on the frequency of individuals from different cohorts ($\chi^2 < 1.6$, $df = 1$, $p > 0.20$). Differences in the frequency of animals from early cohorts (1 and 2) between years had a high level of statistical significance ($\chi^2 = 48$, $df = 1$, $p < 0.0001$). In 1999 the proportion of the first two cohorts among overwintered individuals was 12% ($n = 33$) in May and 27% ($n = 15$) in July; in 2000 it reached 91% ($n = 23$) in May, and 100% ($n = 11$) in July. The stability of estimates of the population structure of overwintered voles corresponds with the data of other authors. For example, the absence of selective elimination of bank voles with different birth dates between the end of one season and the beginning of the next season was observed by different authors [27, 28]. The survival rate of overwintered bank voles in the breeding season differs to a greater extent between years than between the cohorts [29, 30].

The proportion of sexually mature juveniles among males and females changes in a similar way depending on the phase of the population cycle: it has minimal values at peak abundance (8.0% in females, $n = 188$ and 0.5% in males, $n = 204$), medium values at low abundance (43.3% in females, $n = 60$ and 33.3% in males, $n = 87$) and maximal values in the growth phase

with medium level of abundance (70.7% in females, $n = 58$ and 55.6% in males, $n = 99$; $\chi^2 > 9.0$, $df = 1$, $p < 0.003$ for pairwise phase comparisons in the subgroups of males and females). The inhibition of sexual maturation in juvenile voles in the years of peak abundance is one of the main demographic characteristics of cyclic rodent populations [10, 11, 31].

The parameters of the breeding season were estimated based on overwintered voles collected in July. The distribution of overwintered voles according to their birth dates for the entire observation period is shown in Fig. 2. It is shaped as a normal distribution curve with close mean (9.VII) and median (10.VII) values. The earliest and latest birth dates are 17.IV and 02.X. The second cohort is most abundant (44%); then follow the third (35%), first (13%) and fourth (8%) cohorts. The distribution of individuals between the cohorts is similar in males and females ($p > 0.40$). The average onset and end dates of the breeding season are 08.V ($n = 16$) and 4.IX ($n = 16$), respectively; its duration averages 119 ± 2 days, or 4 months. In the post-peak years with low abundance, the breeding season starts on 11.V ($n = 6$) and ends on 15.VIII ($n = 3$); its duration is 95 ± 6 days. In the years of peak abundance, the season starts on 11.V ($n = 6$) and ends on 29.VIII ($n = 4$); its duration is 110 ± 5 days. In the pre-peak years, it starts on 28.IV ($n = 4$) and ends on 14.IX ($n = 9$); its duration is 139 ± 5 days. The breeding season in pre-peak years is longer than in other years ($p < 0.001$), mainly because it ends later ($p < 0.02$). The average birth date of voles in these years is 18.VII ($n = 108$), while in all other years this was an earlier date: 22.VI ($n = 28$, post-peak) or 25.VI ($n = 36$, peak) ($p < 0.001$).

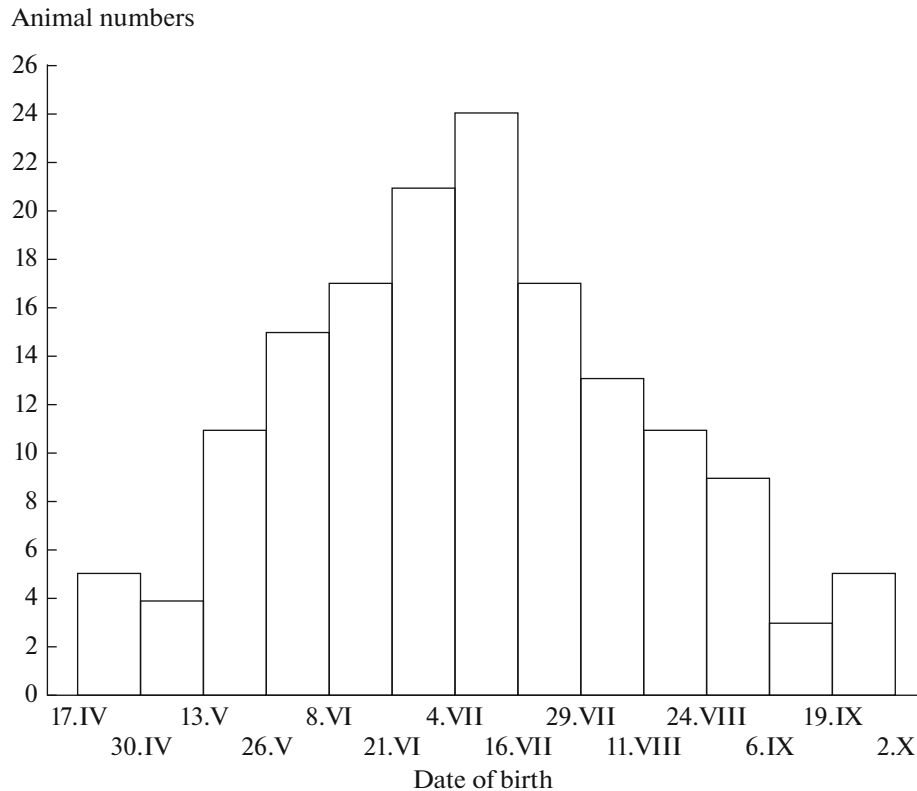


Fig. 2. Distribution of overwintered bank voles according to the date of birth for the entire observation period.

Changes in the duration of the breeding season are also one of the main demographic traits typical of cyclic populations. The breeding season in the phase of peak abundance is sometimes shorter. The growth phase in voles and lemmings is associated with longer breeding season in summer; the duration of this period in case of low abundance is as small as in the years of peak abundance [9, 12]. In our case, this mainly occurs due to its later end.

Regression analysis was used to confirm the dependence of parameters of the breeding season on animal abundance in the previous year. This dependence was not significant for the onset date of the breeding season: $y = 12.V - 0.09x$, where x is the number of individuals per 100 trap-nights ($p > 0.50$), but it proved to be significant for its end date: $y = 16.IX - 0.61x$, $p < 0.02$. For the phase dependence, this equation takes the following form: $y = 29.IX - 15x$, $p < 0.01$, where x is the category of abundance: (1) low, (2) medium, or (3) high. According to this equation, the end of the breeding season in the current year will be 14.IX, 31.VIII, or 16.VIII in case of low, medium, or high abundance in the previous year, respectively. Thus, the higher is the population abundance in the previous year, the earlier is the end date of the breeding season.

Differences in the age of overwintered voles were estimated using ANOVA. We observed a significant effect of the phase of population cycle on this param-

eter ($p < 0.001$) and a significant correlation between the phase of cycle and animal sex ($p < 0.02$). The average age of voles on 15.VII in case of high abundance was estimated at 361 ± 3 days ($n = 108$), i.e., younger than in case of low abundance (382 ± 6 days, $n = 32$) or medium abundance (390 ± 7 days, $n = 32$). The age of females estimated for the years of peak abundance was younger (352 ± 5 days, $n = 46$, $p < 0.01$) than that for other phases of the cycle (growth phase: 386 ± 11 , $n = 9$; depression: 392 ± 8 , $n = 16$). The average age of males was older in case of medium abundance (393 ± 7 days, $n = 23$, $p < 0.05$) than in case of low (372 ± 8 , $n = 16$) or high abundance (370 ± 4 , $n = 62$). Females were found to be younger than males in the years of high abundance ($p < 0.01$), while no sex-related differences were observed in other years ($p > 0.08$).

The values of average female age estimated for the years of high abundance vary from 337 to 360 days and do not overlap with those for other levels of abundance (growth phase: 382–391, depression: 367–434 days). The values of mean years male age in different phases of the population cycle significantly overlap with each other and vary from 347 to 391 days in the peak phase, from 364 to 409 in the growth phase and from 347 to 403 in the phase of depression. The proportion of cohorts 3 and 4 (animals born in the second half of summer) among overwintered voles exceeded 50% in the years with high abundance (56%, $n = 108$, $p < 0.001$),

being significantly lower in the years with low abundance (25%, $n = 32$) and medium abundance (19%, $n = 32$). Females of cohort 4 (born in autumn) were only found in the years of peak abundance (11%); females of cohort 1 (born in spring), only in the years with low (31%) and medium abundance (11%).

Changes in the duration of the breeding season depending on animal abundance and the inhibition of sexual maturation of juveniles in the years with peak abundance are the direct effects observed in the studied population. Another direct dependence is between changes in the average age of overwintered individuals and the phase of population cycle. Young animals will be more abundant even in case of equal initial abundance and similar survival curve. The age structure with the predominance of young animals among overwintered voles leads to peak abundance due to increased survival rate of females and offspring [29, 30]. Thus, younger age of overwintered voles to some extent provides higher abundance of the whole population (direct feedback).

Changes in the average age of overwintered voles are caused by changes in the duration of the breeding season in the previous year. This is a delayed dependence. We observed a delayed dependence of the end date (i.e. duration) of the breeding season on population abundance in the previous year. The mathematical modeling showed that realistic population cycles can be obtained using this dependence alone [32].

CONCLUSIONS

The analysis of demographic traits in a local bank vole population has shown that there are relatively regular 3-year-long fluctuations of its abundance. In addition to regular changes in the level of abundance (phases of the population cycle), other demographic parameters change in a cyclic manner, including the proportion of sexually mature animals, the duration of the breeding season and the age of overwintered animals. Both direct and delayed dependencies between demographic parameters have been observed in the population. Two delayed effects, one after the other, generate the cyclic dynamics of the population, while extrinsic factors (weather conditions and high yield of spruce seeds) can modify these dynamics.

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